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ASSESSMENT OF HABITAT QUALITY FOR RED SNAPPER, *LUTJANUS CAMPECHANUS*, IN THE NORTHWESTERN GULF OF MEXICO: NATURAL VS. ARTIFICIAL REEFS

A Thesis

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
Master of Science

in

The Department of Oceanography and Coastal Sciences

by
Brittany D. Schwartzkopf
B.S., University of California San Diego, 2010
August 2014

To my parents, thank you for always believing in me and supporting me throughout everything. I would not be the person I am today without your guidance

To my grandmother and Mütter, thank you for always spoiling me and telling me to dream big

And to my Popah and grandfather, thank you for being my guardian angels and watching over me

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Finally, I would like to thank my parents, grandparents, and all my aunts, uncles, and cousins for their love, support, and belief in me throughout my time here. Even though I know most of you did not understand what I was actually working on, I appreciate your enthusiasm when asking me about my research.

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ABSTRACT

Habitat quality of natural and artificial reefs for red snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico (Gulf) is important as this area is home to the majority of the Gulf's artificial reef system, in the form of oil and gas platforms, in addition to the largest extent of high vertical relief natural habitat. This study sought to assess habitat quality of natural reefs of varying habitat complexity and an artificial reef complex located on the LA continental shelf. Habitat quality was assessed by comparing red snapper diets and foraging patterns, and nutritional condition using the liver-somatic index (LSI) and caloric densities. The diets at the natural reefs consisted of primarily fish, while the diets at the artificial reefs consisted of primarily fish and zooplankton. Size class was not an important factor for the diets at the natural reefs, but the diet varied between size classes at the artificial reefs. The natural reefs were found to offer a wider diversity of prey items, and reef-dependent species were found only in the diets at the natural reefs. Differences between diets at the natural and artificial reefs reflected differences between the substrates found at each habitat. Red snapper at the natural reefs were found to feed on and above the reef, while feeding at the artificial reefs was predominantly along the surrounding seafloor and water column. Site-specific temporal patterns in both the LSI and caloric density were evident. The LSI of females at the natural reefs was greater than the LSI of females at the artificial reefs. While caloric density statistically differed between habitats and sizes, the differences between values may not be biologically significant. Female red snapper at the natural reefs appear to be in a better nutritional condition than females at the artificial reefs. Results of this study indicate that natural reefs on the LA continental shelf provide high

habitat quality for red snapper. To maximize reproductive output, the better-quality foraging and nutritional condition of red snapper at the natural reefs should be taken into account when evaluating potential areas for the Flower Garden Banks National Marine Sanctuary status.

GENERAL INTRODUCTION

Red snapper (*Lutjanus campechanus*) is an important reef-associated species to both fisheries and fish communities in the Gulf of Mexico (Gulf). Habitat quality is important to reef-associated fishes and is considered optimal if it maximizes energy gained from prey while minimizing the risks of predation (Mittelbach 2002). A habitat of high quality could provide prey resources that allow increases in available energy for foraging, growth, and reproduction. Red snapper in the Gulf have been overfished for at least the last 30 years and remain overfished in the most recent benchmark stock assessment (SEDAR 31 2013); however, it appears that overfishing is no longer occurring in either the eastern or western subunits of the Gulf stock (SEDAR 31 2013). Determining the optimal habitat for red snapper in the Gulf may help managers maximize reproductive output by implementing policies and regulations for the habitats thought to be of high value.

The habitats utilized by red snapper in the Gulf are natural hard-bottom reefs, soft-bottom substrates, and artificial reefs. The natural reefs available on the outer continental shelf in the Gulf are of particular interest due to the unusual topography created by raised structures (reefs) formed by active salt-diapirs buried beneath the slope (Holecombe et al. 2002). Many of the reefs found on the shelf off Louisiana (LA) are associated with active salt-diapirs; however, some reefs are associated with bare bedrock, while others are dominated by encrusting coralgal organisms (Rezak et al. 1985). Differences in relief, depth, surface area, underlying structure, surrounding and overlying sediment, and presence of reef-building corals have been found for the LA shelf reefs (Gardner and Beaudoin 2005).

The natural reefs on the Gulf shelf are considered an ecological network of marine communities because many are both physically and ecologically connected, where the features of each reef offer a “habitat highway” that may allow for reef-associated fishes to move between reefs (Schmal et al. 2008). With increased ecological benefits to fish populations and communities located on the Gulf shelf, some measures to protect the natural reefs were enacted. No Activity Zones (zones of no oil and gas activities) were established at the reefs and several of the reefs have been designated at Habitat Areas of Particular Concern.

Designation as a Coral Essential Fish Habitat or as a National Marine Sanctuary (NMS) provides the only protective measures and regulations. Only three of the shelf-edge reefs in the northwestern Gulf, the East and West Flower Garden Banks and Stetson, have been designated as NMS sites due the presence of well-developed coral reefs, and these as a group have been labeled as the Flower Garden Banks National Marine Sanctuary (FGBNMS; Schmahl et al. 2008). In 2012, a sanctuary boundary expansion subcommittee recommended that eight areas in the Gulf should be considered to be included in the FGBNMS, while an advisory council recommended eleven areas to be considered for inclusion in the FGBNMS (USDOC 2012).

In addition to the natural reefs available in the Gulf, artificial reefs in the form of toppled, standing, and partially removed oil and gas platforms (hereafter platforms) have created the world’s largest artificial reef system, with the majority of these platforms placed in waters off the LA coast (Kasprzak and Perret 1996). Of the total number of platforms originally constructed (~4000), close to 50% remain in place due to rapid decommissioning and around 275 platforms continue to be removed each year (Herb

Leedy, BEESE, personal comm.). Platforms as artificial reefs are believed to have increased biomass in the Gulf when considering all species of non-harvested invertebrates, finfish, and the algae that grow on the structures, and they are also believed to have increased the Gulf carrying capacity for reef fish species, such as red snapper (Scarborough-Bull et al. 2008). Opposition, however, believes that these artificial reefs only attract and congregate reef fish, thereby promoting overexploitation of known fish aggregations (Strelcheck et al. 2005). In addition to platforms, artificial reefs in the eastern Gulf include sunken ships, planes, cars, dry docks, tanks, and other small man-made items such as concrete balls and pyramids (Minton and Heath 1998). Unlike most natural reefs in the Gulf, artificial reefs are not recognized by the Gulf of Mexico Fishery Management Council as essential fish habitat for reef fish (GOMFMC 2000).

From one large cooperative study conducted, the age, growth, reproductive potential, and feeding ecology of red snapper were found to differ between artificial reefs (standing and toppled oil platforms) and natural reefs on the LA continental shelf (Saari 2011, Kulaw 2012, Simonsen 2013). The overall results of Saari (2011), Kulaw (2012), and Simonsen (2013) suggest that natural reefs may provide higher habitat quality than artificial reefs on the LA shelf; however, only the most eastern natural reefs, which are habitats known to be less complex than the reefs farther west, were sampled. Additional studies have also showed that natural reefs in the Gulf may provide high habitat quality for red snapper by directly providing prey resources (Camber 1955, Nelson 1988), whereas artificial reef habitat may be of lesser quality by attracting red snapper due to a behavioral preference instead of increased foraging and nutritional opportunities (Gallaway et al. 1981, McCawley and Cowan 2007, Simonsen 2013). Additional

research on habitat quality of natural and artificial reefs for red snapper in the Gulf can inform management decisions regarding FGBMNS boundary expansion and policies concerning the commercial and recreational red snapper fisheries.

Most recent red snapper studies have been conducted at artificial reefs in nearshore waters off Alabama (AL). The work by Saari (2011) and Kulaw (2012) found the age, growth, and reproductive potential of red snapper to differ between AL and LA regions. The LA outer continental shelf is generally warmer than the nearshore waters off Alabama because it is thought mixed layers on the outer shelf do not penetrate to the bottom (Rezak et al. 1985). The waters off AL also have larger abundances of low-relief natural and artificial reefs, while the waters off LA are composed of more high-relief natural and artificial reefs. Different environmental parameters and habitats between AL and LA may impact red snapper behavior. With previous research finding red snapper life history to differ between habitats and regions in the Gulf, in addition to habitat quality differing between natural and artificial reefs, it appears we may not know as much about regional red snapper populations as believed.

This project expands on previous research conducted and attempts to assess habitat quality of natural reefs with varying habitat complexity, as well as the habitat quality of artificial reefs for red snapper on the LA continental shelf. Prey resources utilized by red snapper, in addition to nutritional condition of red snapper at each reef, were used to assess habitat quality. Chapter 1 determines whether diets and foraging patterns differ between natural reefs of varying complexity as well as between natural and artificial reefs. In addition, Chapter 1 also attempts to evaluate whether specific prey resources are available at the natural reefs that may serve to enhance productivity on the

LA shelf. Diets were assessed with gut-content analysis, and foraging patterns were determined by examining habitat utilization of prey items found in the diet. Chapter 2 establishes whether temporal patterns in the liver-somatic index (LSI) and caloric density, both measures of nutritional condition, are evident at natural and artificial reefs in the Gulf. In addition, Chapter 2 evaluates whether there are differences in the LSI and caloric density between habitats, sizes, and sexes. Data collection for this project was part of a larger cooperative study that also addressed the age, growth, and reproductive potential of red snapper and also examined fish communities present on natural and artificial reefs. The use of both diet and foraging patterns to examine prey resource utilization, and the LSI and caloric density to examine nutritional condition, can provide insight into the habitat quality of artificial and natural reefs and how they may serve to enhance red snapper populations.

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CHAPTER 1: SITE- AND SIZE-SPECIFIC DIETS AND FORAGING OF RED SNAPPER ON LOUISIANA NATURAL AND ARTIFICAL REEFS

Introduction

Red snapper (*Lutjanus campechanus*) is an important species to both fisheries and fish communities in the Gulf of Mexico (Gulf) and is found in abundance on natural and artificial habitats in the northern Gulf. The historic center of abundance for red snapper in the Gulf is thought to be the natural reefs located on the Louisiana (LA) continental shelf edge (Camber 1955). The LA shelf-edge natural reefs are diverse and vary in relief, depth, surface area, underlying structure, surrounding and overlying sediment, and presence of reef-building corals (Gardner and Beaudoin 2005). The northern Gulf, from Pensacola, Florida, to Pass Cavallo, Texas, is approximately 78,328 km^2, yet only around 3.3% of the area consists of natural reef habitat. Of this natural reef habitat, only 1.6% (1,285 km^2) has greater than one meter of relief (Parker et al. 1983), with the greatest amount of this relief occurring off Louisiana (Patterson and Cowan 2003).

In addition to natural reefs in the Gulf, artificial reefs in the form of toppled, standing, and partially removed oil platforms constitute one of the worlds largest artificial reef system, with the majority of these platforms placed in waters off the LA coast (Kasprzak and Perret 1996). It is estimated that these platforms provide an additional 12.1 km^2 of reef fish habitat in the Gulf, yet on a spatial basis their total contribution to high-relief reef habitat is small compared to natural habitats (Gallaway et al. 2009).

Vertical relief is important for red snapper during both juvenile and adult life stages. Red snapper spawning begins in May and extends through September, with peak spawning occurring in May, June, and July (Woods et al. 2003). Buoyant red snapper

eggs subsequently float and hatch, where the post-larvae settle over low-relief areas of sand, mud, or shell ridges (Gallaway et al. 2009). Beginning around age 2, recruitment away from low-relief areas occurs, with red snapper seeking areas of higher vertical relief, such as natural banks, pinnacles, ledges, and artificial reefs like oil and gas platforms (hereafter platforms; Szedlmayer and Lee 2004, Gallaway et al. 2009). Red snapper can grow to lengths greater than 1000 mm total length (TL), weigh more than 20 kg total weight (TW), and have life spans as great as 55 years (Wilson and Nieland 2001). Over the past decade, there has been a decline in size-at-age of red snapper caught in commercial fisheries (Nieland et al. 2007), which has been cited as a response to increased fishing pressures (Jackson et al. 2006).

The study of red snapper diets can be traced back to 1884 when Sterns examined 450 red snapper stomachs, yet found prey items in only one due to stomach eversion (in Bradley and Bryan 1975). Red snapper are opportunistic feeders and their diet has been shown to vary seasonally (Bradley and Bryan 1975, Davis 1975, Gallaway et al. 1981, Nelson 1988, McCawley and Cowan 2007), between habitats (Nelson 1988, Szedlmayer and Lee 2004, Wells et al. 2008, Simonsen et al. in press), ontogenetically (Siegel 1983, McCawley and Cowan 2007, Outz and Szedlmayer 2003), and between day and night (McCawley 2003, Outz and Szedlmayer 2003). Studies of adult red snapper diets have been conducted in both the eastern and western Gulf, focusing on both artificial reefs (Gallaway et al. 1981, Siegel 1983, McCawley 2003, Outz and Szedlmayer 2003, Szedlmayer and Lee 2004) and natural reefs (Camber 1955, Mosely 1965, Bradley and Bryan 1975, Davis 1975, Nelson 1988, Wells et al. 2008), and comparing natural reefs with artificial reefs (Tarnecki and Patterson 2013, Simonsen et al. in press).

The majority of studies that focused on adult red snapper diets at natural reefs are over 20 years old, while more recent studies have focused on adult red snapper diets at artificial reefs. Among the studies of adult red snapper diets in the Gulf, only three (Mosely 1965, Nelson 1988, Simonsen et al. in press; Siegel 1983 looked at juvenile red snapper diets) were located off the coast of LA. The lack of recent studies on diets of adult red snapper in the Gulf off LA is surprising due to the abundance of red snapper found in this area (Patterson et al. 2001). Based upon one study conducted on natural hard-bottom areas off LA, a complete composition of diet was difficult to estimate due to a small sample size (Moseley 1965). A comparison of red snapper diets between artificial reefs (platforms) and three natural reefs in the northwestern Gulf found that the diets at the natural reefs were more varied than the diets at the artificial reefs; however, the diets were more similar between sites than anticipated and overlap in prey items consumed was present (Simonsen et al. in press).

Natural reefs and artificial reefs both play an important role in the life history of red snapper. Artificial reefs, however, continue to be a hot topic for discussions concerning whether these reefs produce new red snapper biomass or if red snapper are attracted to these structures due to behavioral preferences. The production hypothesis states that artificial reefs create new habitat that is available to red snapper, leading to an increase in abundance and production, benefiting fisheries (Strelcheck et al. 2005). Conversely, the attraction hypothesis assumes red snapper are only attracted to artificial reefs by behavioral preferences and redistribute fish from surrounding habitats, which can generate a negative effect on fisheries by promoting overexploitation of known fish aggregations (Strelcheck et al. 2005). Attraction of red snapper to artificial reefs is

thought to be more important in locations where natural reefs are abundant, as is the case for the LA continental shelf (Bohnsack 1989).

One of the variables that Bohnsack's conceptual model uses to differentiate attraction from production is the feeding behavior of red snapper on artificial reefs. Predators are expected to spend more time at a reef with abundant prey resources than at reefs with low prey availability, and they are predicted to leave the reef when the energy gained from those prey resources is reduced (Bohnsack 1989). McCawley and Cowan (2007) found that red snapper caught on artificial reefs off Alabama were feeding on benthic-associated fauna rather than reef-associated organisms, suggesting that they are attracted to artificial reefs because of a behavioral preference instead of increased foraging opportunities. Gallaway et al. (1981) and Simonsen et al. (in press) also concluded that red snapper fed over soft bottom, away from artificial reefs, providing additional support for the claim of McCawley and Cowan (2007).

In contrast, Outz and Szedlmayer (2003) and Szedlmayer and Lee (2004) found that red snapper collected on artificial reef sites fed on a mixed diet of reef and non-reef associated prey items, providing support to the production hypothesis. Cowan et al. (2011) stated that the arguments in support of the production hypothesis are largely faith-based instead of science-based and that few studies have actually demonstrated evidence of biomass production at artificial reefs.

Looking at natural reefs, Camber (1955) and Nelson (1988) both found that red snapper were feeding on reef-associated organisms, whereas Simonsen et al. (in press) and Wells et al. (2008) found that red snapper were feeding on prey items along the seafloor and surrounding water column with little contribution from reef-dependent

organisms. The natural reefs noted in the studies of Camber (1955) and Nelson (1988) were of higher habitat complexity compared to the natural reefs sampled in Simonsen et al. (in press) and Wells et al. (2008).

Recent studies of red snapper diets conducted at more complex natural substrate habitats are lacking. The natural reefs in Simonsen et al. (in press) are the most eastern sites located on the LA shelf, are less complex habitats than the natural reefs farther west, and were in close proximity to the artificial reefs sampled. To account for seasonal, size, and habitat differences in the diet, I sampled different sizes of red snapper throughout the year at both natural reefs with varying habitat complexity and at an artificial reef site. This study design allowed for direct comparisons among red snapper diets at natural reefs of varying complexity, as well as comparison of diets between natural reefs and artificial reefs.

The goal of my study was to expand on previous research and determine whether the diets of red snapper differ among natural reefs of varying habitat complexity, as well as between natural and artificial reefs located on the LA shelf. In addition, I wished to determine whether specific prey resources are available to red snapper at natural reefs that may serve to enhance productivity on the LA shelf. I carried out this study with gut-content analysis to assess short-term diet trends, and foraging patterns were determined by examining the habitat utilization of prey items found in the diets. In this study, I expected to find habitat differences in the diets and foraging of red snapper, with natural and artificial reefs being the most dissimilar. I hypothesized that the natural reefs would be able to provide a wider variety of prey resources compared to the artificial reefs

because the natural reefs are composed of more complex substrate, thereby potentially offering a more diverse community structure.

Methods

Study Area

Red snapper populations at three natural reefs and one artificial reef planning area in the northwestern Gulf were sampled to provide comparisons of diets among natural reefs of varying habitat complexity as well as between natural and artificial reefs (Fig. 1.1). The three natural reefs are located on the LA continental shelf edge and differ in relief, bathymetry, and presence of reef-building corals along an east to west gradient (Gardner and Beaudoin 2005). The three natural reefs sampled, Jakkula, McGrail, and Bright, are characterized by Rezak et al. (1985) as outer-shelf carbonate-capped banks located on complex diapiric structures. The artificial reefs sampled in Block 272 of the East Cameron Artificial Planning Area (hereafter East Cameron) are a complex of both toppled and standing oil platforms located on a bathymetric high comprised of lithified or partially lithified deltaic mud (Cowan et al. 2007). This artificial reef site is located north of the LA continental shelf edge (Fig. 1.1). Differences in bathymetry, relief, surface area, underlying structure, surrounding and overlying sediment, and habitat complexity are apparent among all four reefs (Table 1.1). Habitat complexity was defined as a combination of rugosity of the substrate, substrate diversity, extent of vertical relief, and percentage of hard substrate (Gratwicke and Speight 2005).

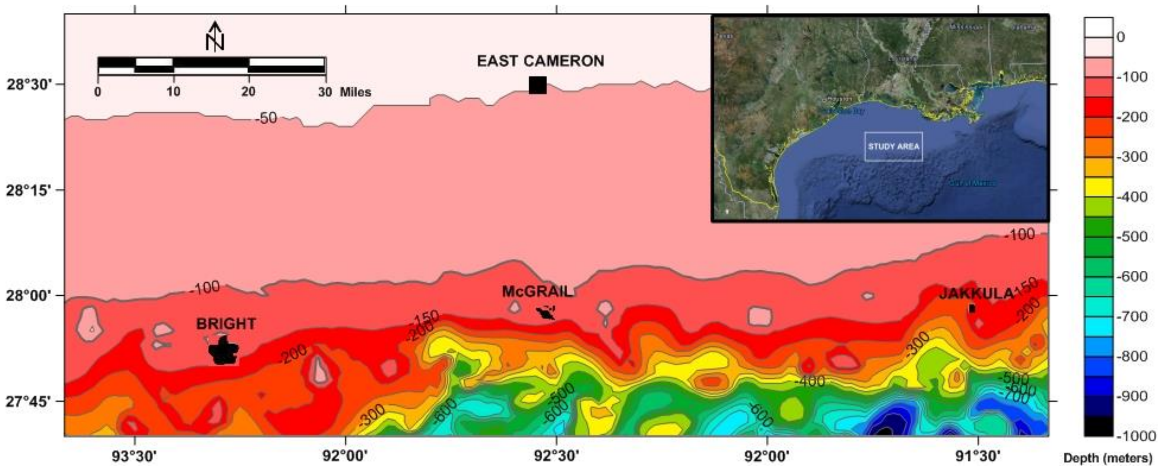

Figure 1.1. Map showing the three natural reefs (Jakkula, McGrail, and Bright) and artificial reefs in the East Cameron Artificial Reef Planning Area (East Cameron) that were selected for sampling of red snapper, *Lutjanus campechanus*, in the northwestern Gulf of Mexico. Depth contour intervals are shown in meters.

Sampling Methods

Red snapper were collected twice per quarter between September 2011 and October 2013. Due to inclement weather and mechanical problems, red snapper were not collected from all sites during six out of the 14 trips. Two 30-hook and two 10-hook vertical-long lines, along with single hook and line rigs, were used to collect red snapper at each site. Thirty hooks, placed approximately 30 cm apart, were used for two of the vertical long lines to capture a diverse suite of species. After the first five trips, it was determined that the two 30-hook vertical long lines were not capturing a more diverse suite of species compared to the 10-hook vertical long lines; therefore, four 10-hook vertical long lines along with single hook and line rigs were instead used for the remainder of the study. Each red snapper collected was given a unique tag number and then placed on ice for a minimum of one hour. All red snapper collected from one study site were processed on the vessel before sampling began at the next study site.

Table 1.1. Comparison of the physical geography of the three natural reefs, Jakkula, McGrail, and Bright, and the artificial reefs in the East Cameron Artificial Reef Planning Area (East Cameron). Values obtained from Dennis and Bright (1988), Gardner and Beaudoin (2005), Cowan et al. (2007), and T.A. Langland personal comm.[1]

	Jakkula	McGrail	Bright	East Cameron
Latitude	27°59'N	27°58'N	27°53'N	28°28'N
Longitude	91°39'W	92°36'W	93°18'W	92°38'W
Surrounding Depth (m)	120-140	110-130	130-150	45-60
Crest Depth (m)	66	45	48-50	43
Vertical Relief (m)	50	65	75	2
Surface Area (km^2)	3.68	7.19	16.67	2
Underlying Structure	Salt Dome	Salt Dome	Salt Dome	Lithified Delta Muds
Habitat Complexity	Low	Medium	Medium	Artificial
Crest Sediment	Medium-Fine Sand	Coarse-Medium Sand	Medium Sand	Lithified or Partially Lithified Delta Mud
Surrounding Seafloor Sediment	Coarse-Fine Silt	Fine Silt	Fine Sand and Silt	Lithified or Partially Lithified Delta Mud

[1] Langland, T.A. 2014. Louisiana State University, Ph.D. Student, Department of Oceanography and Coastal Sciences.

During processing, each red snapper was weighed (TW and eviscerated weight) to the nearest 0.001 kg with a Marel motion compensated scale; standard length (SL), fork length (FL), and TL were measured to the nearest mm, and sex was determined. Additionally, otoliths were collected for age analysis, ovaries were collected from females for reproductive analysis, stomachs were removed for diet composition, livers were weighed to determine the liver-somatic index, and muscle tissue samples were collected for stable isotope and caloric density analyses. A water temperature profile was obtained at each site with a Sea-Bird Electronics 25 Sealogger CTD. The temperature associated with a sample was the bottom temperature during each collection period.

Diet Composition

Stomachs were removed from each red snapper by severing the digestive tract at the esophagus and at the duodenum below the pyloric sphincter. If an individual exhibited stomach eversion due to barotrauma, it was noted and the stomach was not taken, as all of the contents were lost. Each stomach was then placed in an individual jar and immediately frozen to hinder further digestion. In the laboratory, stomachs were thawed, trimmed of excess tissue, weighed to the nearest 0.1 g, and placed in 10% formalin. After a minimum of 48 hours, the stomachs were transferred to a 70% ethanol solution for storage until examination. During examination, stomach contents were removed, identified and sorted to the lowest taxonomic level, dried at 60°C, and weighed to the nearest 0.0001 g. Since red snapper are known to regurgitate, stomachs were categorized as genuinely empty or everted, based upon the classification of Treasurer (1988).

The quantification of stomach contents was accomplished by four methods: 1) percent frequency of occurrence (%FO); 2) percent composition by number (%N); 3) percent composition by dry weight (%W); and 4) percent index of relative importance (%IRI) (Bowen 1996). For analyses, stomach contents were first sorted into nine major prey categories: fishes, crustaceans, crabs, shrimps, squids, gastropods, tunicates, zooplankton (benthic and pelagic), and incidental items (items thought to be eaten as a by-product, such as rocks). Stomach contents were then further subdivided into 58 finer taxonomic levels among all major categories. The diets contained unclassifiable material, defined as material that did not included any bones, hard parts, or recognizable features for further classification into one of the prey categories. Unclassifiable material was excluded from %N, %FO, and %IRI analyses because contribution could not be determined. Each red snapper was placed into one of four size classes based on FL: size class 3 (300-399 mm), size class 4 (400-499 mm), size class 5 (500-599 mm), and size class 6 (>600 mm).

Percent dry weight (%W) was the primary method chosen for analyses of diets because it could be used to assess the nutritional contribution of prey items (Bowen 1996, McCawley 2003). Individual stomachs were treated as replicates, and data were log(x+1) transformed to account for zeros in prey categories and to place more importance on rare prey species. A similarity resemblance matrix was then constructed on the transformed data, using Bray-Curtis similarity coefficients, to assess similarity between weight proportions of prey items for each individual. Site, size class, and a site-by-size class interaction were used as fixed effect factors, and temperature was used as a covariate to control for temperature related effects on the diets. Temperature was used as a covariate

rather than a categorical factor, such as season, because the temperature data obtained at each site revealed no true temperature pattern common to fall, winter, spring, or summer seasons (See Appendix A). Type I Sums of Squares (SS) was used instead of Type III SS to allow factors to be fit after accounting for temperature related effects (Anderson et al. 2008). Size class 3 red snapper were not included in the full analysis because they were collected only at East Cameron. A separate analysis was conducted for red snapper at East Cameron to compare the differences of diets among all size classes. A permutational analysis of variance (PERMANOVA) was then used to test for significant differences in prey weight proportions between sites and size classes for both the nine major prey categories and 58 prey items. If a significant ($p<0.05$) main effect or interaction was found in either PERMANOVA analysis, a subsequent pairwise test was carried out to determine which factors differed from one another. A Similarity Percentages (SIMPER) analysis was then used to examine the contribution that a certain prey category or item made to the average within-group similarity and between-group dissimilarity for all significant main effects or interactions. All statistical analyses were run with the PRIMER+PERMANOVA v.6 statistical package (Clarke and Gorley 2006, Anderson et al. 2008).

Results

A total of 651 red snapper were caught from Jakkula (n=81), McGrail (n=27), Bright (n=215), and East Cameron (n=328) during this study. From the 651 individuals, 362 contained stomach contents, 273 were empty due to regurgitation, and 16 were truly empty. From the 362 with stomach contents, 261 contained identifiable prey items while 101 contained only unclassifiable material or bait. Of the 261 useable stomachs, 23 were

collected from Jakkula, eight were collected from McGrail, 104 were collected from Bright, and 126 were collected from East Cameron (Table 1.2). The stomach contents of red snapper from McGrail were not included in further analyses due to the small sample size. Only two unique prey items were present in the diet at McGrail, *Plesionika* sp. and a coral fragment (likely ingested incidentally), and each item was only found once. After removing those two prey items, only 56 prey items were found in the diets at Jakkula, Bright, and East Cameron.

Table 1.2. The number of red snapper, *Lutjanus campechanus*, stomachs that contained identifiable prey items at Jakkula, McGrail, Bright, and East Cameron during each month sampling occurred.

Month	Jakkula	McGrail	Bright	East Cameron
2011				
September	0	3	9	0
2012				
February	2	0	3	3
March	3	0	11	27
May	4	0	0	0
July	3	5	13	6
October	0	0	6	1
December	0	0	16	5
2013				
February	2	0	0	0
March	0	0	0	0
April	0	0	0	18
May	0	0	13	19
June	3	0	12	21
August	4	0	20	19
October	2	0	1	7

Nine Prey Category Analysis

Unclassifiable material was the most abundant prey category by %W in the diets of red snapper at Jakkula (46.8%), Bright (30.2%), and East Cameron (37.3%). When unclassifiable material was excluded from the analysis, fishes were the most abundant

prey category by %W at Jakkula (57.8%) and Bright (61.7%), followed by tunicates, most likely the pelagic tunicate *Pyrosoma atlanticum* (19.7% and 15.0% respectively; Fig. 1.2). While fish was the most abundant prey category at East Cameron (38.0%), zooplankton was also a large contributor (25.7%; Fig. 1.2). Because %W is the most commonly used index to quantify red snapper diets, %N, %FO, and %IRI results will not be discussed (See Appendix A). The word diet hereafter will represent the proportional contribution by dry weight of the prey categories.

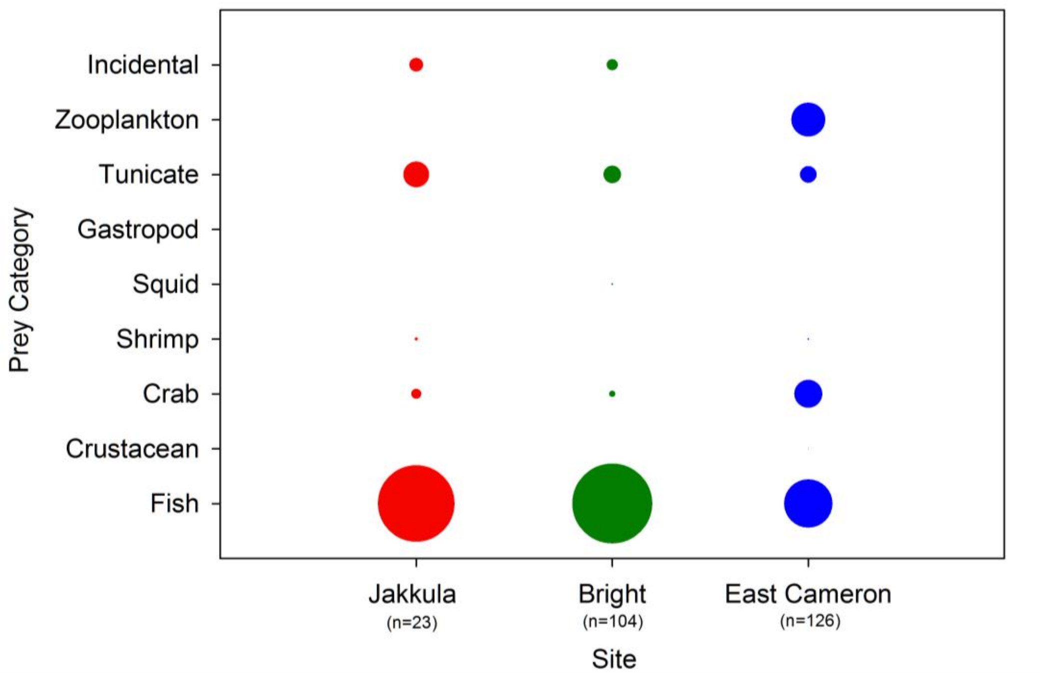

Figure 1.2. Percent dry weight of the nine prey categories found in the diets of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron. The bubbles represent the proportional contribution of each prey category. For raw numbers see Appendix A.

Site, size class, and site-by size-class were all significant contributors to the variation in diets, accounting for temperature (Table 1.3; $p<0.05$). Pairwise tests show that there were no differences in the diets between size classes at Bright and Jakkula,

Table 1.3. Permutational analysis of variance (PERMANOVA) source table for nine prey categories.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Temperature (Te)	1	16379	16379	4.4978	0.0002	9918
Site	2	40348	20174	5.5399	0.0001	9911
Size Class (SC)	2	13716	6857.8	1.8832	0.0175	9883
TexSite	2	15960	7979.8	2.1913	0.0034	9915
TexSC	2	6442.1	3221.1	0.88452	0.5962	9908
SCxSite	4	21813	5453.2	1.4975	0.0282	9876
Res	197	7.17E+05	3641.6			
Total	210	8.32E+05				

but the diet of size class 6 differed from the diets of size class 4 and 5 at East Cameron ($p<0.05$). Pairwise test results also show that within size class 4, the diet at East Cameron differed from the diets at Jakkula and Bright ($p<0.05$). Within size class 4, red snapper at Jakkula consumed the largest proportion of fishes, those at Bright consumed the second largest proportion of fishes as well as the largest proportion of tunicates, and individuals at East Cameron consumed the largest proportion of zooplankton (Fig. 1.3a). SIMPER results indicate that fishes, zooplankton, and crabs were the primary prey categories responsible for the dissimilarities seen in the diets between East Cameron and Bright, as well as between East Cameron and Jakkula within size class 4 (Appendix A).

The diet at East Cameron differed from the diets at Bright and Jakkula within size class 5 ($p<0.05$). Within size class 5, red snapper at Jakkula consumed a large amount of fishes and the largest amount of crabs, those at Bright consumed a large amount of fishes and the largest proportion of tunicates, and individuals at East Cameron consumed the largest proportion of zooplankton (Fig. 1.3b). The diets were found not to differ between sites within size class 6 ($p>0.05$).

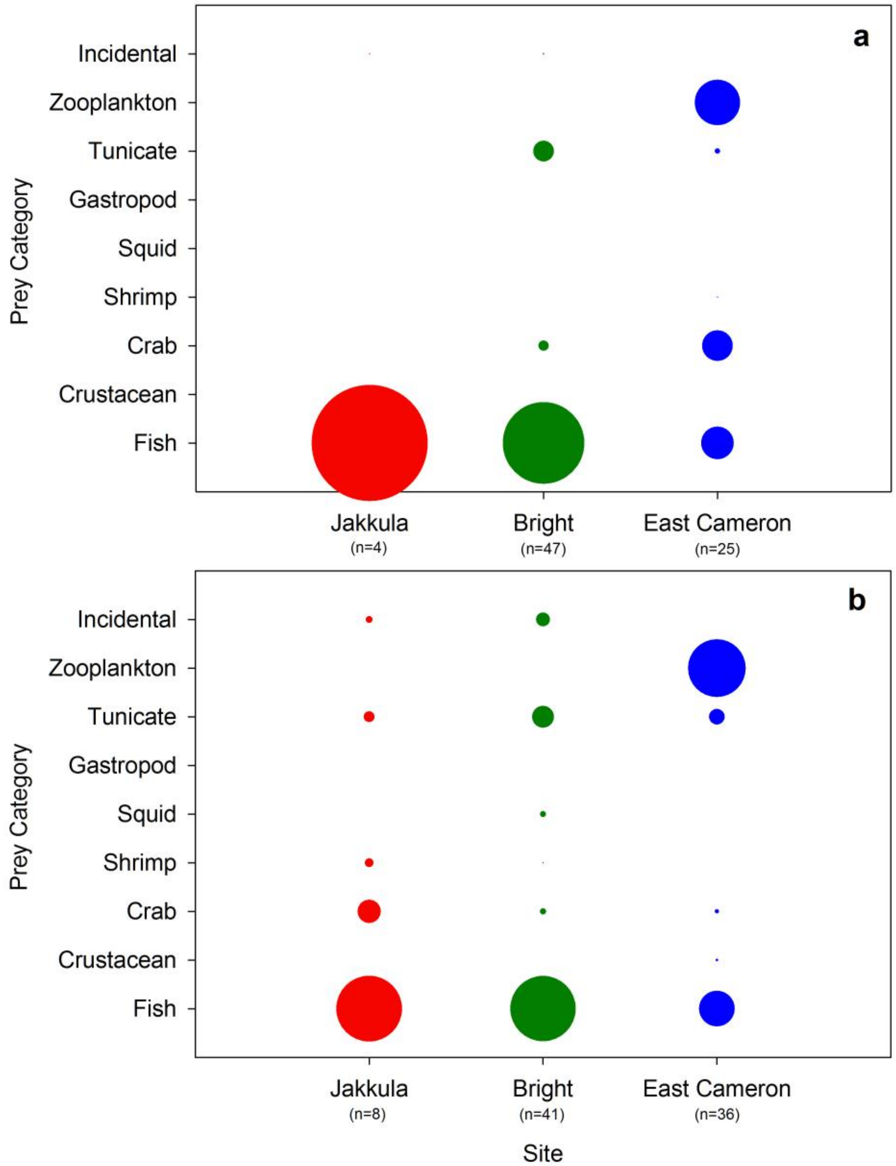

Figure 1.3. Percent dry weight of the nine prey categories found in the diets of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron for; a) size class 4 (400-499 mm) red snapper, and b) size class 5 (500-599 mm) red snapper. The bubbles represent the proportional contribution of each prey category. For raw numbers see Appendix A.

SIMPER results indicate that zooplankton, fishes, and tunicates were the primary prey categories responsible for the dissimilarities in the diets between East Cameron and Bright, as well as between East Cameron and Jakkula within size class 5 (Appendix A).

A separate analysis was carried out for red snapper only at East Cameron in order to include size class 3 in the comparison. PERMANOVA results for East Cameron reveal that, accounting for temperature, the diet varied between size classes, with the diet of size class 3 differing from size class 5, and the diet of size class 6 differing from size class 4 and 5 ($p<0.05$; Fig. 1.4). Size class 6 consumed the largest proportion of fishes, while size class 3, 4, and 5 consumed similar proportion of fishes (Fig. 1.4). Size class 5 consumed the largest proportion of zooplankton, followed by size class 4 and 3, with little zooplankton consumed by size class 6 (Fig. 1.4). SIMPER results indicate that zooplankton, fishes, crabs, and tunicates were the primary prey categories responsible for the dissimilarities seen in the diets between size classes at East Cameron (Appendix A).

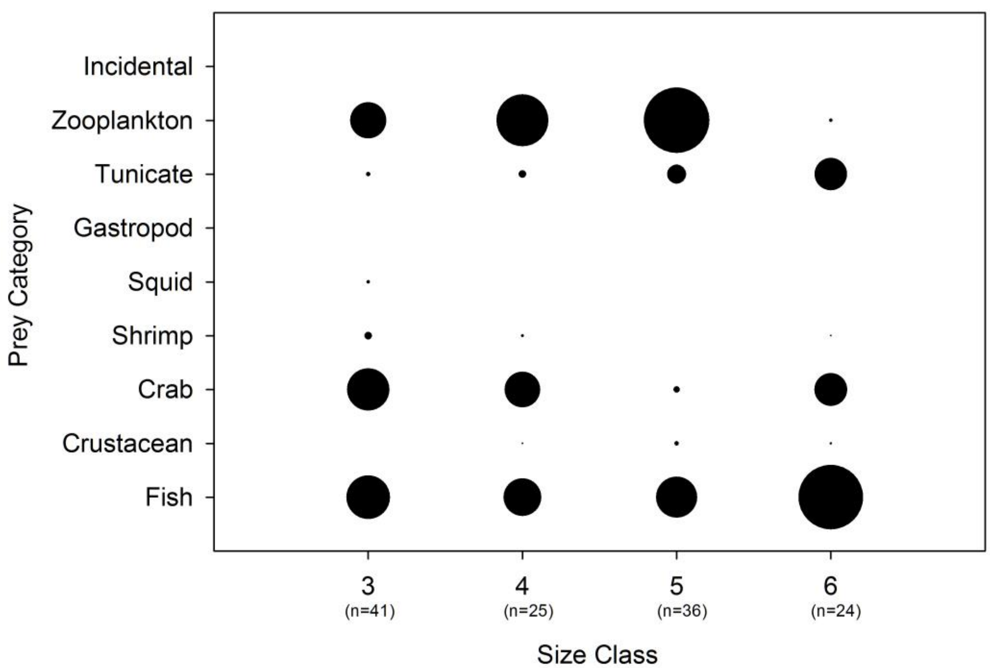

Figure 1.4. Percent by dry weight of nine prey categories found in the diets of size class 3 (300-399 mm), 4 (400-499 mm), 5 (500-599 mm), and 6 (>600 mm) red snapper, *Lutjanus campechanus*, at East Cameron. The bubbles represent the proportional contribution of each prey category. For raw numbers see Appendix A.

Comprehensive Prey Item Analysis

When breaking up the nine major prey categories into 56 finer taxonomic classifications, unclassifiable material was the most abundant prey item in red snapper diets by %W at Jakkula (45.8%), Bright (29.2%), and East Cameron (35.5%; Table 1.4). When unclassifiable material was excluded from analyses, unidentified fishes (51.8%), tunicates (19.5%), and rocks (10.6%, most likely ingested incidentally), and *Calappa galloides* (7.4%) were the most abundant prey items by %W in the diet at Jakkula. Unidentified fishes (43.2%), tunicates (14.7%), *Gymnothorax moringa* (8.3%), algae (6.1%), and *Calappa galloides* (5.1%) were the most abundant prey items by %W in the diet at Bright. Unidentified fishes (29.3%), unidentified zooplankton (22.3%), tunicates (12.7%), and *Achelous spinicarpus* (10.1%) were the most abundant prey items in the diet at East Cameron (Table 1.4). Because %W is the most commonly used index to quantify red snapper diets, %N, %FO, and %IRI results will not be discussed (See Appendix A). The word diet hereafter will represent the proportional contribution by dry weight of the prey categories.

There was little overlap in the diets between Jakkula, Bright, and East Cameron (Table 1.4). The diet at Bright was the most varied and had 19 unique prey items. The diet at East Cameron had the greatest variety of identifiable crabs and had 13 unique prey items, while the diet at Jakkula was the least varied and only had one unique prey item. The only identifiable prey items found in the diets at all three sites were family Bregmacerotidae, *Calappa galloides*, family Squillidae, Class Gastropoda, *Cavolinia* sp., *Heliconoides inflatus*, squids, and tunicates (Table 1.4).

Table 1.4. Percent dry weight (%W) of 56 prey items found in the diets of all size classes of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron. Unclassifiable material was not included in the calculation of %W for each prey type. Asterisk (*) represents prey item unique to the diet at a specific location.

Prey Type	**Jakkula**	**Bright**	**East Cameron**
Unclassifiable material	45.8	29.2	35.5
Fish			
Unidentified fishes	51.84	43.23	29.25
Family Bregmacerotidae	6.23	0.72	0.02
Gymnothorax moringa		8.31*	
Holocentrus adscensionis		0.97*	
Family Lutjanidae		2.67*	
Family Mullidae		0.14*	
Family Ophichthidae		1.87	1.89
Opistognathus aurifrons		0.80*	
Family Pomacentridae		1.35*	
Prionotus sp.		0.30*	
Selene setapinnis		0.12*	
Family Serranidae		0.21	0.32
Subfamily Syngnathinae			0.23*
Synodus sp.		0.90*	
Trichiurus lepturus			4.73*
Crab			
Unidentified crabs	0.44	0.04	1.44
Calappa galloides	7.43	5.10	0.11
Iliacantha sp.			0.82*
Iridopagurus sp.		0.01*	
Superfamily Majoidea			0.23*
Macrocoeloma concavum		0.69*	
Palicus sp.		0.02*	
Parthenope agona			0.74
Phimochirus sp.		0.37*	
Family Portunidae			0.34*
Achelous ordwayi			0.37*
Achelous spinicarpus			10.05*
Callinectes similis			3.63*
Pseudorhombila quadridentata			3.15*
Raninoides louisianensis			0.19*
Shrimp			
Unidentified shrimps	2.39	0.01	0.002
Alpheus sp.			0.17*
Eucalliax sp.	0.35*		
Metapenaeopsis sp.		0.08*	
Odontodactylus sp.		0.28*	
Rimapenaeus sp.		0.35*	
Family Squillidae	0.20	0.002	1.54
Pelagic Zooplankton			
Unidentified zooplankton	0.01	0.08	22.55
Order Amphipoda		0.001	0.85
Phylum Chaetognatha		0.01	0.004
Family Euphausiidae		0.003*	
Cavolinia sp.	0.36	0.43	2.73
Heliconoides inflatus	0.41	0.04	0.06
Crab megalopa		0.01	0.22
Order Mysida		0.001*	
Benthic Zooplankton			
Phylum Annelida		0.003	0.06
Phylum Nematoda		0.03	0.002
Incidental			
Algae		6.11	0.02
Anemone		3.69*	
Rocks	10.62	0.87	
Shark tooth			0.10*
Unidentified crustaceans	0.00	0.61	0.85
Class Gastropoda	0.10	1.85	0.009
Scyllarus chacei			0.15*
Squids	0.09	2.98	0.47
Tunicates	19.53	14.74	12.72

Site, size class, and site-by size-class were all significant contributors to the variation in diets, accounting for temperature (Table 1.5; $p<0.05$). Pairwise tests reveal that there were no differences in the diets between size classes at Bright and Jakkula, but the diet of size class 6 differed from the diets of size class 4 and 5 at East Cameron ($p<0.05$). The diet of size class 4 at Jakkula differed from the diet of size class 4 at East Cameron ($p<0.05$; Table 1.6). Within size class 4, the diet at Jakkula only contained three prey items, the largest proportion consisting of unidentified fishes, followed by rocks (likely ingested incidentally) and unidentified zooplankton.

Within size class 4, the diet at Bright was the most varied and contained large proportions of unidentified fishes and tunicates, with intermediate proportions of family Lutjanidae, family Pomacentridae, and *Calappa galloides*. The diet of size class 4 at East Cameron was also varied but contained large proportions of unidentified zooplankton and unidentified fishes, with intermediate proportions of family Ophichthidae, portunid crabs (*Achelous spinicarpus* and *Callinectes similis*), and *Cavolinia* sp. (Table 1.6). Results from the SIMPER analysis indicate that unidentified fishes and unidentified zooplankton were responsible for 80% of the dissimilarity in the diets between Jakkula and East Cameron for size class 4, with four other prey items making up 10% of the dissimilarity (Table 1.7).

Table 1.5. Permutational analysis of variance (PERMANOVA) source table for 56 prey items.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Temperature (Te)	1	12138	12138	2.9962	0.0011	9911
Site	2	31759	15879	3.9198	0.0001	9893
Size Class (SC)	2	12574	6286.8	1.5519	0.0375	9882
TexSite	2	14812	7406	1.8282	0.0076	9877
TexSC	2	8647.7	4323.9	1.0673	0.3377	9870
SCxSite	4	22677	5669.3	1.3995	0.0254	9825
Res	197	7.98E+05	4051.1			
Total	210	9.01E+05				

Table 1.6. Percent dry weight of 56 prey items found in the diet of size class 4 (400-499 mm) red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Prey Type	Jakkula	Bright	East Cameron	Prey Type	Jakkula	Bright	East Cameron
Fish				**Shrimp**			
Unidentified fishes	98.47	43.26	16.29	Unidentified shrimps		0.04	0.01
Family Bregmacerotidae		2.78		*Alpheus* sp.			
Gymnothorax moringa				*Eucalliax* sp.			
Holocentrus adscensionis		3.75		*Metapenaeopsis* sp.		0.32	
Family Lutjanidae		10.31		*Odontodactylus* sp.			
Family Mullidae				*Rimapenaeus* sp.			
Family Ophichthidae			10.75	Family Squillidae		0.01	1.46
Opistognathus aurifrons		3.07					
Family Pomacentridae		5.22		**Pelagic Zooplankton**			
Prionotus sp.		1.15		Unidentified zooplankton	0.05	0.22	33.37
Selene setapinnis		0.12		Order Amphipoda			0.07
Family Serranidae			1.94	Phylum Chaetognatha			0.01
Subfamily Syngnathinae			0.27	Family Euphausiidae		0.01	
Synodus sp.				*Cavolinia* sp.		0.51	6.46
Trichiurus lepturus			0.42	*Heliconoides inflatus*		0.02	0.04
				Crab megalopa		0.04	
Crab				Order Mysida		0.002	
Unidentified crabs		0.06	0.66				
Calappa galloides		5.16		**Benthic Zooplankton**			
Iliacantha sp.			4.95	Phylum Annelida		0.01	
Iridopagurus sp.		0.04		Phylum Nematoda			
Superfamily Majoidea							
Macrocoeloma concavum		2.21		**Incidental**			
Palicus sp.		0.08		Algae		1.54	
Parthenope agona				Anemone			
Phimochirus sp.		1.41		Rocks	1.47	0.09	
Family Portunidae			2.06	Shark tooth			
Achelous ordwayi							
Achelous spinicarpus			7.26	**Unidentified crustaceans**		0.05	1.95
Callinectes similis			8.42	**Class Gastropoda**			
Pseudorhombila quadridentata				***Scyllarus chacei***			
Raninoides louisianensis				**Squids**		0.78	
				Tunicates		17.78	5.07

Table 1.7. Similarity percentages (SIMPER) results of prey item contribution to between site dissimilarity in the diet of size class 4 (400-499 mm) red snapper, *Lutjanus campechanus*. Diss/SD = Dissimilarity/Standard deviation ratio.

Site	Prey Type	Average Dissimilarity	Diss/SD	% Contribution	% Cumulative Contribution
Jakkula vs. East Cameron		93.06			
	Unidentified fishes	67.76	2.42	72.81	72.81
	Unidentified zooplankton	7.17	0.42	7.7	80.52
	Cavolinia sp.	3.74	0.37	4.02	84.53
	Rocks	2.36	0.52	2.54	87.07
	Callinectes similis	2.22	0.19	2.38	89.45
	Achelous spinicarpus	2.1	0.19	2.25	91.71

The diet of size class 5 at East Cameron differed from the diets of size class 5 at Bright and Jakkula ($p<0.05$; Table 1.8). The diet of size class 5 at Jakkula contained a large proportion of unidentified fishes, *Calappa galloides*, and family Bregmacerotidae, with intermediate proportions of tunicates, unidentified shrimps, and rocks. The diet of size class 5 at Bright was again the most varied and contained large proportions of unidentified fishes and tunicates, with smaller contributions of *Gymnothorax moringa*, an anemone, squids, and *Calappa galloides*. The diet of size class 5 at East Cameron contained large proportions of unidentified zooplankton, unidentified fishes, and tunicates, with smaller contributions of *Cavolinia* sp., and *Achelous spinicarpus* (Table 1.8). Results from the SIMPER analysis indicate that unidentified fishes, tunicates, unidentified zooplankton, and *Cavolinia* sp. were responsible for 70% of the dissimilarity in the diets between Bright and East Cameron for size class 5, with eight other prey items making up 20% of the dissimilarity (Table 1.9). Unidentified fishes, unidentified zooplankton, tunicates, family Bregmacerotidae, and *Calappa galloides* were responsible for 70% of the dissimilarity in the diet between Jakkula and East Cameron for size class 5, with four other prey items making up 20% of the dissimilarity (Table 1.9).

Table 1.8. Percent dry weight of 56 prey items found in the diet of size class 5 (500-599 mm) red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Prey Type	Jakkula	Bright	East Cameron	Prey Type	Jakkula	Bright	East Cameron
Fish				**Shrimp**			
Unidentified fishes	40.10	40.99	28.82	Unidentified shrimps	6.28		
Family Bregmacerotidae	16.41			*Alpheus* sp.			
Gymnothorax moringa		8.87		*Eucalliax* sp.			
Holocentrus adscensionis		3.75		*Metapenaeopsis* sp.			
Family Lutjanidae		10.31		*Odontodactylus* sp.		0.56	
Family Mullidae		0.28		*Rimapenaeus* sp.		0.70	
Family Ophichthidae		3.70		Family Squillidae	0.53		0.26
Opistognathus aurifrons							
Family Pomacentridae				**Pelagic Zooplankton**			
Prionotus sp.				Unidentified zooplankton	0.00	0.04	40.25
Selene setapinnis		0.17		Order Amphipoda		0.002	3.22
Family Serranidae		0.41		Phylum Chaetognatha		0.01	
Subfamily Syngnathinae			0.73	Family Euphausiidae	0.12	0.54	6.11
Synodus sp.		1.79		*Cavolinia* sp.		0.07	0.23
Trichiurus lepturus				*Heliconoides inflatus*		0.004	0.19
				Crab megalopa	0.00	0.04	40.25
Crab				Order Mysida			
Unidentified crabs		0.05					
Calappa galloides	19.56	5.35		**Benthic Zooplankton**			
Iliacantha sp.				Phylum Annelida			0.20
Iridopagurus sp.				Phylum Nematoda		0.05	
Superfamily Majoidea							
Macrocoeloma concavum		0.23		**Incidental**			
Palicus sp.		0.08		Algae		4.76	
Parthenope agona				Anemone		7.32	
Phimochirus sp.				Rocks	6.01		
Family Portunidae				Shark tooth			0.40
Achelous ordwayi							
Achelous spinicarpus			3.66	**Unidentified crustaceans**	0.001	0.0003	1.95
Callinectes similis				**Class Gastropoda**	0.27	0.02	0.02
Pseudorhombila quadridentata				***Scyllarus chacei***			
Raninoides louisianensis				**Squids**	0.23	5.51	
				Tunicates	9.54	18.57	13.36

Table 1.9. Similarity percentages (SIMPER) results of prey item contribution to between site dissimilarity in the diet of size class 5 (500-599 mm) red snapper, *Lutjanus campechanus*. Diss/SD = Dissimilarity/Standard deviation ratio.

Site	Prey Type	Average Dissimilarity	Diss/SD	% Contribution	% Cumulative Contribution
Bright vs. East Cameron		93.12			
	Unidentified fishes	30.76	0.91	33.03	33.03
	Tunicates	20.24	0.72	21.74	54.77
	Unidentified zooplankton	12.13	0.55	13.03	67.81
	Cavolinia sp.	4.32	0.44	4.64	72.44
	Calappa galloides	2.98	0.26	3.2	75.65
	Algae	2.56	0.27	2.74	78.39
	Family Ophichthidae	2.33	0.21	2.5	80.89
	Gymnothorax moringa	2.18	0.16	2.34	83.23
	Squids	2.12	0.18	2.28	85.51
	Anemone	1.69	0.16	1.82	87.33
	Unidentified crustaceans	1.56	0.22	1.67	89
	Rimapenaeus sp.	1.45	0.14	1.56	90.56
Jakkula vs. East Cameron		96.25			
	Unidentified fishes	26.29	0.79	27.31	27.31
	Unidentified zooplankton	12.38	0.55	12.86	40.17
	Tunicates	10.19	0.51	10.59	50.76
	Family Bregmacerotidae	8.99	0.37	9.34	60.1
	Calappa galloides	8.61	0.37	8.95	69.05
	Rocks	7.8	0.35	8.1	77.15
	Eucalliax sp.	4.91	0.29	5.1	82.25
	Cavolinia sp.	4.51	0.41	4.68	86.94
	Unidentified shrimps	4.03	0.37	4.18	91.12

A separate analysis was conducted for red snapper at East Cameron to include size class 3 in the comparison. Results show that the diet at East Cameron varied between size classes, accounting for temperature, with the diet of size class 3 differing from the diet of size class 5, and the diet of size class 6 differing from size class 3, 4, and 5 ($p<0.05$; Table 1.10). Size class 3 consumed large proportions of unidentified fishes, unidentified zooplankton, and *Achelous spinicarpus*. The diet of size class 4 was largely made up of unidentified zooplankton, unidentified fishes, and family Ophichthidae, and also contained a greater diversity of fishes compared to the other size classes. Size class

5 largely consumed unidentified zooplankton and *Cavolinia sp*., while also consuming unidentified fishes and a wide variety of pelagic zooplankton. Size class 6 consumed the largest proportion of unidentified fishes and tunicates, with intermediate proportions of *Trichiurus lepturus*, *Pseudorhombila quadridentata*, and *Achelous spinicarpus*.

The only prey items present in the diet of all four size classes at East Cameron were unidentified fishes, *Achelous spinicarpus*, family Squillidae, unidentified zooplankton, *Cavolinia* sp., and tunicates. SIMPER results indicate that unidentified fishes, unidentified zooplankton, and *Achelous spinicarpus* were the primary prey items responsible for the dissimilarities in the diet between size class 3 and 5, while unidentified fishes, tunicates, and unidentified zooplankton were responsible for the dissimilarities in the diet between size class 3 and 6 at East Cameron (Table 1.11). Unidentified fishes, unidentified zooplankton, and tunicates were the primary items responsible for the dissimilarities in the diet between size class 4 and 6, as well as between size class 5 and 6 at East Cameron (Table 1.11).

Table 1.10. Percent dry weight of 56 prey items found in the diets of size class 3 (300-399 mm), 4 (400-499 mm), 5 (500-599 mm), and 6 (>600 mm) red snapper, *Lutjanus campechanus*, at East Cameron.

Prey Type	**3**	**4**	**5**	**6**	**Prey Type**	**3**	**4**	**5**	**6**
Fishes					**Shrimps**				
Unidentified fishes	31.54	16.29	28.82	34.21	Unidentified shrimps		0.01		
Family Bregmacerotidae	0.10				*Alpheus* sp.	0.68			
Gymnothorax moringa					*Eucalliax* sp.				
Holocentrus adscensionis					*Metapenaeopsis* sp.				
Family Lutjanidae					*Odontodactylus* sp.				
Family Mullidae					*Rimapenaeus* sp.				
Family Ophichthidae	0.44	10.75			Family Squillidae	4.13	1.46	0.26	0.59
Opistognathus aurifrons									

Table 1.10. continued.

Prey Type	3	4	5	6	Prey Type	3	4	5	6
Family Pomacentridae					**Pelagic Zooplankton**				
Prionotus sp.					Unidentified zooplankton	26.33	33.37	40.25	1.38
Selene setapinnis					Order Amphipoda		0.07	3.22	0.12
Family Serranidae		1.94			Phylum Chaetognatha	0.01	0.01		
Subfamily Syngnathinae		0.27	0.73		Family Euphausiidae				
Synodus sp.					*Cavolinia* sp.	0.13	6.46	6.11	0.34
Trichiurus lepturus		0.42		13.85	*Heliconoides inflatus*		0.04	0.23	
					Crab megalopa			0.19	0.51
Crab					Order Mysida				
Unidentified crabs	0.24	0.66		3.79					
Calappa galloides	0.44				**Benthic Zooplankton**				
Iliacantha sp.		4.95			Phylum Annelida	0.05		0.20	
Iridopagurus sp.					Phylum Nematoda	0.01			
Superfamily Majoidea				0.69					
Macrocoeloma concavum					**Incidental**				
Palicus sp.					Algae	0.07			
Parthenope agona				2.20	Anemone				
Phimochirus sp.					Rocks				
Family Portunidae		2.06			Shark tooth			0.40	
Achelous ordwayi	1.49								
Achelous spinicarpus	21.07	7.26	3.66	7.89	**Unidentified crustaceans**	0.48	1.95	0.84	
Callinectes similis	8.94	8.42			**Class Gastropoda**			0.02	0.01
Pseudorhombila quadridentata				9.36	***Scyllarus chacei***			0.59	
Raninoides louisianensis				0.55	**Squids**	1.79			0.04
					Tunicates	2.52	5.07	13.36	23.62

Table 1.11. Similarity percentages (SIMPER) results of prey item contribution to between size class dissimilarity in the diet of red snapper, *Lutjanus campechanus*, at East Cameron. Only those species that made up 80 percent of the cumulative contribution were included. Diss/SD = Dissimilarity/Standard deviation ratio.

Size Class	Prey Type	Average Dissimilarity	Diss/SD	% Contribution	% Cumulative Contribution
3 vs. 5		92.87			
	Unidentified fishes	24.82	0.8	26.73	26.73
	Unidentified zooplankton	23.94	0.81	25.78	52.5
	Achelous spinicarpus	10.65	0.41	11.46	63.97
	Tunicates	8.62	0.4	9.28	73.25
	Cavolinia sp.	6.5	0.49	7	80.24

Table 1.11. continued.

Size Class	Prey Type	Average Dissimilarity	Diss/SD	% Contribution	% Cumulative Contribution
3 vs. 6		93.43			
	Unidentified fishes	27.54	0.88	29.47	29.47
	Tunicates	15.42	0.57	16.51	45.98
	Unidentified zooplankton	11.99	0.52	12.83	58.81
	Achelous spinicarpus	11.31	0.41	12.1	70.91
	Family Squillidae	3.86	0.27	4.13	75.04
	Pseudorhombila quadridentata	3.44	0.29	3.68	78.72
4 vs. 6		95.07			
	Unidentified fishes	23.4	0.74	24.61	24.61
	Tunicates	15.44	0.55	16.24	40.85
	Unidentified zooplankton	13.7	0.56	14.41	55.26
	Cavolinia sp.	8.17	0.42	8.6	63.86
	Achelous spinicarpus	5.99	0.28	6.3	70.16
	Pseudorhombila quadridentata	3.45	0.29	3.63	73.79
	Trichiurus lepturus	3.41	0.25	3.58	77.38
	Unidentified crustaceans	3.2	0.29	3.37	80.74
5 vs. 6		92.4			
	Unidentified fishes	24.96	0.77	27.01	27.01
	Unidentified zooplankton	17.74	0.65	19.2	46.22
	Tunicates	17.29	0.6	18.72	64.93
	Cavolinia sp.	6.55	0.45	7.09	72.02
	Achelous spinicarpus	4.83	0.25	5.23	77.25
	Unidentified crustaceans	4.23	0.32	4.58	81.83

The results for the 56-prey item analysis were similar to the results for the nine-prey category analysis. Both analyses show a significant site-by-size interaction, accounting for temperature, for the diets of red snapper. Only two differences were observed. Within size class 4, the diets differed between East Cameron and Jakkula and between East Cameron and Bright for the nine-prey category analysis, but for the 56-prey item analysis, the diets only differed between East Cameron and Bright. The other difference observed was for the size class analysis carried out for the red snapper at East Cameron. The diet of size class 3 differed from size class 6 for the 56-prey item analysis, but not for the nine-prey category analysis. When the analysis was broken up, size class

3 consumed different species and proportions compared to size class 6, but when prey items were combined into categories, the proportions were similar.

Site-Specific Prey Habitat Associations

Habitat associations were assigned to each prey item in red snapper diets, based upon the published literature, at Jakkula, Bright, and East Cameron (Table 1.12). Habitat associations could not be determined for unidentified fishes, crabs, shrimps, zooplankton, and crustaceans and thus were not assigned a habitat type. After each identifiable prey item was assigned a habitat type, %W was summed to examine the contribution each made to the diets at Jakkula, Bright, and East Cameron. Water-column associated prey contributed the largest %W to the diet at Jakkula (26.6%), hard-substrate associated prey contributed the largest %W to the diet at Bright (26.1%), and soft-substrate associated prey was the largest contributor to the diet at East Cameron (27.3%; Table 1.13). After benthic-associated prey, the smallest contributor to the diet at Jakkula and Bright was soft-substrate associated prey (0.6% and 3.1%, respectively), whereas hard-substrate associated prey contributed the least to the diet at East Cameron (0.3%; Table 1.13).

Table 1.12. Habitat association of prey items found in the diets of red snapper, *Lutjanus campechanus*, at Jakkula (J), Bright (B), and East Cameron (E). H=hard-substrate, S=soft-sediment, WC=water-column, V=various habitats, B=benthic. Superscript is source: 1=Felder and Camp 2009, 2=Felder personal comm.[2], 3=Carpenter 2002a,b.

Prey Type	Habitat Type	Site Found	Prey Type	Habitat Type	Site Found
Fish			**Shrimp**		
Unidentified fishes		B, E, J	Unidentified shrimps		B, E, J
Family Bregmacerotidae	WC[1]	B, E, J	*Alpheus* sp.	V[1]	E

[2] Felder, D.L. 2013. University of Louisiana at Lafayette. Department of Biology.

Table 1.12. continued.

Prey Type	Habitat Type	Site Found	Prey Type	Habitat Type	Site Found
Gymnothorax moringa	H[1]	B	*Eucalliax* sp.	S[2]	J
Holocentrus adscensionis	H[1]	B	*Metapenaeopsis* sp.	V[1]	B
Family Lutjanidae	H[1]	B	*Odontodactylus* sp.	V[1]	B
Family Mullidae	V[1]	B	*Rimapenaeus* sp.	V[1]	B
Family Ophichthidae	S[1]	B, E	Family Squillidae	S[1]	B, E, J
Opistognathus aurifrons	V[1]	B			
Family Pomacentridae	H[1]	B	**Pelagic Zooplankton**		
Prionotus sp.	S[1]	B	Unidentified zooplankton		B, E, J
Selene setapinnis	WC[1]	B	Order Amphipoda	WC[1]	B, E
Family Serranidae	H[1]	B, E	Phylum Chaetognatha	WC[1]	B, E
Subfamily Syngnathinae	V[1]	E	Family Euphausiidae	WC[1]	B
Synodus sp.	S[1]	B	*Cavolinia* sp.	WC[1]	B, E, J
Trichiurus lepturus	S[3]	E	*Heliconoides inflatus*	WC[1]	B, E, J
			Crab megalopa	WC[1]	B, E
Crab			Order Mysida	WC[1]	B
Unidentified crabs		B, E, J			
Calappa galloides	V[1]	B, E, J	**Benthic Zooplankton**		
Iliacantha sp.	S[1]	E	Phylum Annelida	S[1]	B, E
Iridopagurus sp.	H[2]	B	Phylum Nematoda	B[1]	B, E
Superfamily Majoidea	V[1]	E			
Macrocoeloma concavum	H[1]	B	**Incidental**		
Palicus sp.	V[1]	B	Algae	H[1]	B, E
Parthenope agona	S[1]	E	Anemone	H[1]	B
Phimochirus sp.	H[1]	B	Rocks	H	B, J
Family Portunidae	WC[1]	E	Shark tooth	B[1]	E
Achelous ordwayi	S[1]	E			
Achelous spinicarpus	S[1]	E	**Unidentified crustaceans**		B, E, J
Callinectes similis	S[1]	E	**Class Gastropoda**	V[1]	B, E, J
Pseudorhombila quadridentata	S[1]	E	***Scyllarus chacei***	S[1]	E
Raninoides louisianensis	S[1]	E	**Squids**	WC[1]	B, E, J
			Tunicates	WC[1]	B, E, J

Size-Specific Prey Habitat Associations

In this study, red snapper diets differed between size classes at East Cameron. I therefore summed up the %W of prey items for each habitat type for every size class to examine the contribution that a specific habitat type made to diet of each size class at East Cameron (Table 1.14). Soft-sediment associated prey was the largest contributor of %W to the diets of size class 3 (35.7%), size class 4 (4.7%), and size class 6 (32.2%), followed by water-column associated prey (4.6%, 13.6%, and 24.5%, respectively) and various habitat associated prey (1.6%, 11.1%, and 3.0%; Table 1.14). Conversely, for the diet of size class 5 water-column associated prey was the largest contributor of %W (19.9%), followed by soft-sediment associated prey (4.7%; Table 1.14). Soft-sediment associated prey dominated the diets of smaller red snapper at East Cameron, suggesting that they fed closer to the bottom. As the red snapper at East Cameron grew in size, they fed on more water-column associated prey with contributions from soft-sediment species, suggesting that the larger red snapper stayed above the sea floor more but were able to move vertically to feed.

Table 1.13. Summary of percent dry weight contributions of hard-substrate, soft-substrate, water-column, and variety associated prey items found in the diets of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Habitat Type	**Jakkula**	**Bright**	**East Cameron**
Hard substrate	10.62	26.05	0.32
Soft sediment	0.56	3.07	27.30
Water column	26.61	19.05	17.43
Variety	7.53	7.83	0.75
Benthic	0	0.03	0.10

Table 1.14. Summary of percent dry weight contribution of hard-substrate, soft-substrate, water-column, and variety associated prey items found in the diets of size class 3 (300-399 mm), 4 (400-499 mm), 5 (500-599 mm), and 6 (>600 mm) red snapper, *Lutjanus campechanus*, at East Cameron.

Habitat Type	**3**	**4**	**5**	**6**
Hard substrate	0	1.94	0	0
Soft sediment	35.68	22.51	4.71	32.24
Water column	4.63	13.64	19.89	24.52
Variety	1.56	11.10	3.97	3.02
Benthic	0.01	0	0.40	0

Discussion

Findings of the present study appear to be consistent with those reported by Camber (1955), Davis (1975), Nelson (1988), Wells et al. (2008), and Simonsen et al. (in press) who also found that fishes were the predominant prey in diets of red snapper collected on natural habitats. In contrast to the results observed in this study, McCawley and Cowan (2007) and Simonsen et al. (in press) reported prey consumed by red snapper at artificial reefs to be predominantly fish, although the importance of fish did vary with season and size class in McCawley and Cowan (2007). On the other hand, Gallaway et al. (1981) found fish to be important in the diet of red snapper at an artificial reef during the summer, while shrimp were important in spring and fall, and squid were important in winter. From video surveys conducted in this study[3], fish species diversity and richness was found to be lowest at the artificial reefs compared to the natural reefs which may explain the smaller contribution of fish observed in diets there.

[3] All video survey information found in this study obtained from T.A. Langland.[1]

The largest quantities of zooplankton at the artificial reefs were observed in March 2012, April 2013, and May 2013. Bottom water temperatures in these time periods were the lowest observed at the artificial reefs over the course of the study (21°C, 21.48°C, and 22.24°C respectively). It may be that red snapper are bioenergetically constrained during these cold months, feeding on zooplankton as they drift by, thus expending less energy while foraging (Kitchell et al. 1977). In the coldest month at the artificial reefs, February 2012 (20.47°C), only three red snapper stomachs were collected. Zooplankton were not prevalent in diets of red snapper on low-relief artificial reefs off Alabama in winter, but were instead found in higher numbers during spring and fall (McCawley and Cowan 2007); however, it is unclear if the months sampled by McCawley and Cowan (2007) in winter were the coldest months during their study period.

One difficulty with most studies on red snapper diets is the high amount of regurgitation and large number of everted stomachs due to barotrauma stress. Red snapper often suffer barotrauma as they are brought to the surface from deep water due to a sudden decrease in ambient pressure. One consequence of barotrauma is catastrophic decompression that can cause regurgitation of stomach contents or eversion of the stomach (Schmidt-Nielson 1997). Bowman (1986) found some species of fish to be more prone to regurgitation as sampling depth increased. The deepest sampling depth in this study occurred at Jakkula (~90 m) and caused the high eversion rate (72%) and the small number of usable stomachs observed (n=23), which led to the lowest prey diversity in the diet. Conversely, the shallower sampling depths at Bright (~60 m) and East Cameron

(~50 m) allowed more retention of stomach contents (52% and 62% eversion rate respectively) leading to higher diversity of prey items in diets at these sites.

Todd Langland (personal comm.[1]) classified, as per the classification categories of Schmahl et al. (2008), the majority of one of the natural reefs, Jakkula, as a deep coral habitat, composed of rock outcrops, drowned reefs, pavement, and rubble. He classified the other natural reef, Bright, as a coralline algal reef, composed of algal nodules, pavement, patch reef, low-relief outcrop, and molluscan reef. Cowan et al. (2007) reported the substrate at the artificial reef complex in the East Cameron Artificial Reef Planning Area to be composed of lithified or partially-lithified delta mud, and the artificial reefs were placed on top of a natural bathymetric high on the seafloor.

Differences between diets at the natural reefs and artificial reefs appear to reflect differences between characteristics of each habitat. The deep coral and coralline algal habitat characteristics at the natural reefs were reflected in large contributions of hard-substrate associated prey and small contributions of soft-sediment associated prey in both diets. The predominance of mud at the artificial reefs was reflected in large contributions of soft-sediment associated prey and almost zero contribution from hard-substrate associated prey in the diets. In a study of caloric content of red snapper prey, McCawley (2003) found that hard-substrate associated prey items had the highest average caloric density of all the prey types, followed by water-column and soft-sediment associated prey types being the next highest. There were 16 common prey items between McCawley's (2003) study and mine and if this trend holds true, diets at the natural reefs in the present study were more calorically rich than diets at the artificial reef.

It should be noted that rocks were found in the stomachs of red snapper at Jakkula. These were likely ingested incidentally, but seem to indicate that red snapper at this site were feeding upon prey found on rocky substrates and thus this "prey item" was classified as hard-substrate associated prey. Also, the soft-sediment associated fishes, crabs, and shrimps found in diets at the natural reefs are associated more with sandy substrates as opposed to muddy substrates, whereas the majority of the soft-sediment associated fishes, crabs, and shrimps found in diets at the artificial reefs are associated with muddy substrates as opposed to sandy substrates (Felder, personal comm[2].).

Taking into account habitat classifications of the natural and artificial reefs and habitat associations of prey items present in the diets, I conclude that red snapper at both natural reefs are feeding on prey found on and above the reef, while red snapper at the artificial reefs are feeding on prey found on the surrounding seafloor and water column. Large overlaps were seen in fish prey items found in the diet at Bright and species of fish seen on the reef in video surveys at Bright (Langland[1] personal comm.) further supporting this line of reasoning. The majority of fish species observed in video surveys at Jakkula were also observed in video surveys at Bright. Overlaps between prey items in the diet at Jakkula and those seen on video surveys could have been possible if a larger sample size of stomachs had been obtained.

Camber (1955) and Nelson (1988) also concluded that red snapper at natural reefs were feeding on prey items found on and above the reef. In contrast, Davis (1975), Wells et al. (2008), and Simonsen et al. (in press) concluded that red snapper at natural reefs were feeding on prey from the surrounding sea floor and water column rather than reef-associated prey. The natural reef (Seven and One-Half Fathom Reef) sampled by Davis

(1975) is located in shallow water off the Texas coast and is small in comparison to natural reefs off the LA shelf. Wells et al. (2008) sampled low-relief natural reefs located in the eastern Gulf, whereas the natural reefs in the present study are high-relief natural reefs located in the western Gulf. Simonsen et al. (in press) pooled three natural reefs on the eastern LA shelf (Jakkula, Alderdice, and Bouma), and the surface substrate at Alderdice and Bouma are known to be less complex than Jakkula (Gardner and Beaudoin 2005).

McCawley and Cowan (2007), Gallaway et al. (1981), and Simonsen et al. (in press) also concluded that red snapper collected on artificial reefs fed on prey from the surrounding seafloor and water column. In contrast, Outz and Szedlmayer (2003) found that red snapper consumed prey from various habitats and that all prey habitat types were important in diets at a low-relief artificial reef off Alabama. Outz and Szedlmayer (2003) identified habitat types of each prey taxon based on literature, personal observations, and personal communications, but they do not provide a list of each prey taxon found in the diets and what habitat type it was assigned to.

Unlike studies at natural reefs in the eastern Gulf, specific reef-dependent species were found in diets at the natural reefs in the western Gulf in this study. The only other study to find reef-dependent species (i.e. *Holocentrus* sp., pomacanthids, etc.) in the diet of red snapper has been Nelson (1988), who sampled the East and West Flower Garden Banks, which are also located on the western Gulf outer continental shelf. The natural reefs on the Gulf outer continental shelf are considered an ecological network of marine communities because many are both physically and ecologically connected, where the

features of each reef offer a “habitat highway” that may allow for reef-associated fishes to move between reefs (Schmal et al. 2008).

To date, the present work represents the most extensive concurrent study on the diet of red snapper at natural reefs of varying habitat complexities, as well as concurrently at an artificial reef complex; however, limitations did arise. The largest limitation was the lack of a balanced design. All sites could not be sampled during every trip, and if all sites were sampled, collection of red snapper was not guaranteed for each site. This limitation was a direct result of inclement weather conditions, boat maintenance, and scheduling difficulties, as the sites that were selected for sampling were located roughly 100 miles offshore, with approximately 40 to 60 miles between each site. Cold fronts during the winter months limited sampling time and the number of sites visited, and mechanical issues required the boat to go back to dock in the middle of three sampling trips, with no time to reschedule.

For future studies of the natural reefs on the LA shelf, more video surveys should be conducted and the strength of currents in different areas on the bank should be profiled. Video surveys have the ability to capture red snapper feeding, which may help with identification of stomach contents and provide more insight into the feeding habitats on these unique reefs. Diet barcoding techniques are now being utilized to identify digested fish prey items in red snapper diets (Brewton and Szedlmayer 2013). This technique may be useful in future studies to further elucidate whether there is overlap in fish species consumed between various natural reefs or between natural and artificial reefs. Profiling the strength of currents may help discern when red snapper consume more water-column associated prey.

My results support the findings of Gallaway et al. (1981), McCawley and Cowan (2007), and Simonsen et al. (in press) that red snapper are not gaining nutrition derived from artificial reefs and that red snapper may be attracted to these structures due to a behavioral preference. Conversely, red snapper at the natural reefs appear to be gaining nutrition derived directly from the reef, which could be bioenergetically favorable. With red snapper at the natural reefs consuming more calorically rich hard substrate and water-column associated prey, it is possible that prey resources found on and above the natural reefs can serve to enhance productivity and sustain populations found there. I thus conclude that natural reefs offer a higher habitat quality in the form of prey resources than artificial reefs.

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CHAPTER 2: TEMPORAL PATTERNS IN LIVER-SOMATIC INDEX AND CALORIC DENSITY OF RED SNAPPER ON LOUISIANA NATURAL AND ARTIFICIAL REEFS

Introduction

Nutritional condition of red snapper, *Lutjanus campechanus*, in the Gulf of Mexico (hereafter Gulf) can affect growth and reproduction and can give insight about the relative quality of habitats on which they reside. Nutritional condition as defined here is the state of an animal's energy reserves (Kaufaman et al. 2007). Red snapper is an important species to fisheries and fish communities in the Gulf and have been overfished for at least the last 30 years and remain overfished in the most recent benchmark stock assessment (SEDAR 31 2013). Fish condition is considered a valuable tool that can be used in stock assessments, yet fish condition is not taken into account in most assessments (Lloret et al. 2014).

The liver is an important organ in fishes and plays a prominent role in both anabolism and catabolism. Functions of the liver include storage of lipids and carbohydrates, digestion, immune defense, and energy for reproduction (Brusule and Anadon 1996). As such, impairment of the liver can have detrimental effects upon the health of a fish. There are many variables that can affect fish livers *in situ* including, but not limited to, temperature, salinity, pH, oxygen concentration, food quantity and quality, pollutants, biotoxins, parasites, and infections (Brusule and Anadon 1996). The relationships among temperature, food quantity and quality, and reproductive state of the fish are the principal factors for the changes observed in fish livers. The physical position of the liver in a fish makes it one of the first organs to receive ingested nutrients. The liver absorbs nutrients from the plasma after feeding and releases stored nutrients

during states such as starvation and/or stress (Hinton and Segner 2008). Fish can utilize stored energy in the liver for gonad growth during reproduction. Decreases in liver weight may be observed both before spawning when energy is used for gonad growth, and during spawning when energy is being utilized to release eggs. Condition of the liver can also reflect short-term energy intake and reproductive and temperature related metabolic demands (Adams and Mclean 1985). Thus, fish condition can be inferred by evaluation of liver condition because of the liver's sensitivity to changes in food consumption, reproduction, and temperature.

One index used to determine condition of the liver is the liver-somatic index (LSI; also referred to as the hepatic-somatic index). One fundamental assumption of the use of organosomatic indices, such as the LSI, is that there must be a persistent relationship between fish size and the ratio of organ weight (Goede and Barton 1990). The LSI varies between and within species and depends upon differences in season, sex, age, feeding, reproduction, and stress (Brusule and Anadon 1996).

Energy reserves have been shown to be stored in the liver of mature fish in preparation for high-energy demands of spawning (Bulow et al. 1978). The stored energy reserves in the liver are used for gonadal maturation in some species, resulting in a decline of the LSI (Adams and Mclean 1985). Gonad maturation plays an important role in weight changes of the liver in fish and in general, the LSI is higher in females than in males, which may be a consequence of a greater energetic investment for females during spawning (Larson 1973, Brusule and Anadon 1996). The LSI is correlated with the quantity and quality of food and is highly sensitive to the nutritional status of fish, which can be used as an indicator of condition (Brusule and Anadon 1996). Liver weight

increases with feeding rate and storage of fat (Bulow et al. 1978), with mean LSI values correlated to the amount of fat deposition, which is species specific (Brusule and Anadon 1996).

Caloric density of fish muscle has been used either as an indicator of fish condition, or in studies of fish energetics. Caloric density of fish tissue provides information about the energy density of organic materials or energy that is utilized for metabolism (Busacker et al. 1990). Calorimetry, used to determine caloric density, measures the heat given off by chemical reactions and other various processes, where the heat generated is related to the total available energy in a sample (Busacker et al. 1990). Calorimetry is important for bioenergetics studies because it expresses growth in terms of energy equivalents and allows energy intake to be partitioned into anabolic and catabolic processes (Busacker et al. 1990). Calorimetry also provides insight into the condition of fish because energy is stored in tissues as complex mixtures of carbohydrates, lipids, and proteins, where the ratio can vary according to the general physiological condition of fish. Caloric analysis often accounts for temporal changes in stored constituents and can provide insight into the physiological condition of fish (Adams and Breck 1990).

Food consumption represents the only source of energy input where all energy acquired must be used in metabolic processes, lost as wastes, or synthesized into new tissues (Adams and Breck 1990). Foraging strategies, spawning patterns, and environmental conditions impact how consumed energy is partitioned into functional processes of growth, metabolism, and reproduction (Adams and Breck 1990). As a result of differences in life histories, energy density of individual fish and populations have been shown to vary seasonally (Kelso 1973, Adams and Mclean 1985, Bryan et al. 1996),

ontogenetically (Deegan 1986, Bryan et al. 1996, Wuenschel et al. 2006), geographically (Schultz and Conover 1997), and between sexes (Bulow et al. 1978, Adams et al. 1982, Smith et al. 1990, Nunes et al. 2011).

Primary factors governing caloric density and energy allocation are prey availability and quality of food, because a fish must balance the need for food and time spent foraging against the risk of predation. A greater amount of energy can be utilized for metabolism, reproduction, and growth if the time and energy spent foraging is minimized (Wootton 1990). When food is abundant, energy storage can occur, but when fish experience low food intake, stored energy reserves in the body tissues must be utilized, decreasing caloric density and growth rate of the individual (Busacker et al. 1990, Dygert 1990). High caloric density values are reflective of a better nutritional state and, as a result, a greater growth potential. Spawning and environmental conditions, such as temperature, will affect caloric density seasonally. When spawning occurs, female fishes have the potential to lose up to 85% of their somatic energy reserves (Adams and Breck 1990). Overall, caloric density and allocation of energy are determined by complex interactions between foraging strategies, quality and quantity of food consumed, reproductive state, and environmental conditions.

Knowledge of temporal patterns in the LSI and caloric density of red snapper from the Gulf are lacking. Miller et al. (2005) examined the LSI for juvenile and sub-adult red snapper, but the fish were tank-reared and the purpose of the study was to determine the effects of different percentages of dietary lipid and protein. Only one previous study has evaluated caloric density of red snapper caught on oil platforms and natural reefs (Simonsen 2013); however, only the overall mean of caloric density at each

site was examined, so possible differences between seasons, sexes, and sizes are unknown. To account for seasonal, size, sex, and habitat differences in the LSI and caloric density, I sampled different sizes and sexes of red snapper throughout the year at natural and artificial reefs.

The goal of my study was to establish whether temporal patterns are evident in LSI and caloric density of red snapper at natural and artificial reefs in the Gulf. In addition, I wished to determine whether the LSI and caloric density differed between habitats, sizes, and sexes. In this study, I expected to observe habitat differences in both the LSI and caloric density because each study site can have unique environmental parameters and differences in available prey resources. I also expected to observe sex and size differences, with sex differences being greater for the LSI due to reproductive disparities, and size differences being greater for caloric density because of energy partitioning strategies.

Methods

Study Area

Red snapper populations at three natural reefs and one artificial reef planning area in the northwestern Gulf were sampled to provide comparisons of the LSI and caloric density among natural reefs of varying habitat complexity as well as between natural and artificial reefs (Fig. 2.1). The three natural reefs are located on the Louisiana (LA) continental shelf edge, and differ in relief, bathymetry, and presence of reef-building corals along an east to west gradient (Gardner and Beaudoin 2005). The three natural reefs sampled, Jakkula, McGrail, and Bright, are characterized by

Rezak et al. (1985) as outer-shelf carbonate-capped banks located on complex diapiric structures. The artificial reefs sampled in Block 272 of the East Cameron Artificial Planning Area (hereafter East Cameron) are a complex of both toppled and standing oil platforms located on a bathymetric high comprised of lithified or partially lithified deltaic mud (Cowan et al. 2007). This artificial reef site is located north of the LA continental shelf edge (Fig. 2.1). Differences in bathymetry, relief, surface area, underlying structure, surrounding and overlying sediment, and habitat complexity are apparent among all four reefs (Table 2.1). Habitat complexity was defined as a combination of rugosity of the substrate, substrate diversity, extent of vertical relief, and percentage of hard substrate (Gratwicke and Speight 2005).

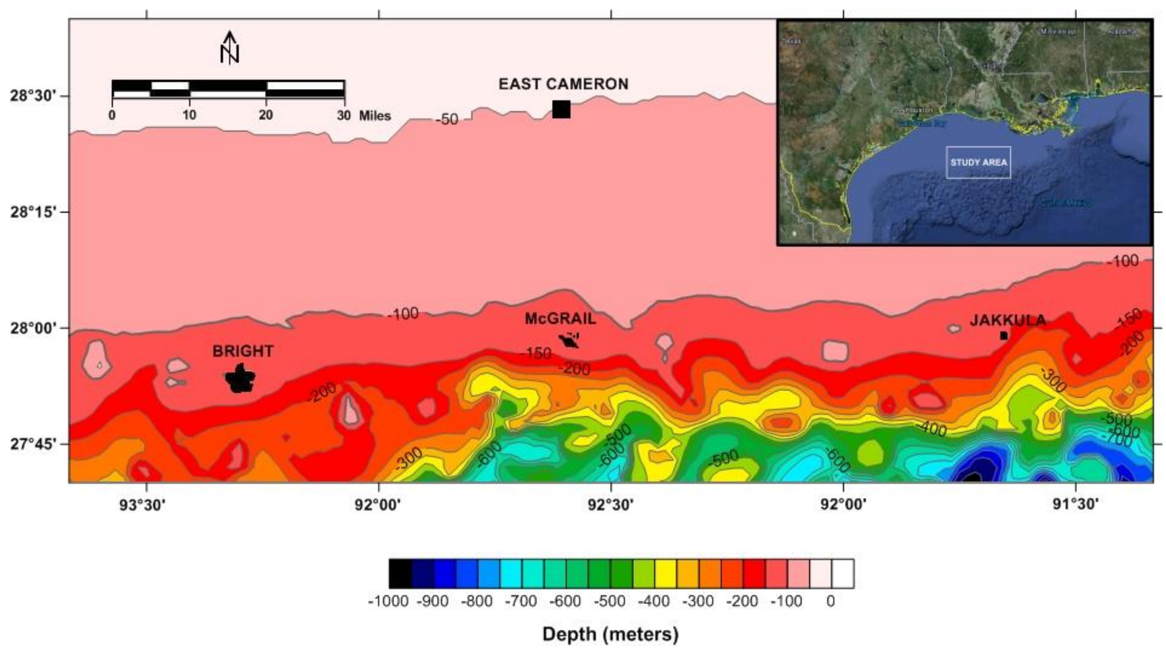

Figure 2.1. Map showing the three natural reefs (Jakkula, McGrail, and Bright) and artificial reefs in the East Cameron Artificial Reef Planning Area (East Cameron) that were selected for sampling of red snapper, Lutjanus campechanus, in the northwestern Gulf of Mexico. Depth contour intervals are shown in meters.

Table 2.1. Comparison of the physical geography of the three natural reefs Jakkula, McGrail, and Bright, and artificial reefs in the East Cameron Artificial Reef Planning Area (East Cameron). Values obtained from Dennis and Bright (1988), Gardner and Beaudoin (2005), Cowan et al. (2007), and T.A. Langland personal comm.[4]

	Jakkula	**McGrail**	**Bright**	**East Cameron**
Latitude	27°59'N	27°58'N	27°53'N	28°28'N
Longitude	91°39'W	92°36'W	93°18'W	92°38'W
Surrounding Depth (m)	120-140	110-130	130-150	45-60
Crest Depth (m)	66	45	48-50	43
Vertical Relief (m)	50	65	75	2
Surface Area (km^2)	3.68	7.19	16.67	2
Underlying Structure	Salt Dome	Salt Dome	Salt Dome	Lithified Delta Muds
Habitat Complexity	Low	Medium	Medium	Artificial
Crest Sediment	Medium-Fine Sand	Coarse-Medium Sand	Medium Sand	Lithified or Partially Lithified Delta Sediment
Surrounding Seafloor Sediment	Coarse-Fine Silt	Fine Silt	Fine Sand and Silt	Lithified or Partially Lithified Delta Sediment

[4] Langland, T.A. 2014. Louisiana State University, Ph.D. Student, Department of Oceanography and Coastal Sciences.

Sampling Methods

Red snapper were collected twice per quarter between September 2011 and October 2013. Due to inclement weather and mechanical problems, red snapper were not collected from all sites during six out of the 14 trips. Two 30-hook and two 10-hook vertical-long lines, along with single hook and line rigs, were used to collect red snapper at each site. Thirty hooks, placed approximately 30 cm apart, were used for two of the vertical long lines to cover a larger vertical portion of the water column and to capture a diverse suite of species. After the first five trips, it was determined that the two 30-hook vertical long lines were not capturing a more diverse suite of species compared to the 10-hook vertical long lines; therefore, four 10-hook vertical long lines along with single hook and line rigs were instead used for the remainder of the study. Each red snapper collected was given a unique tag number and then placed on ice for a minimum of one hour. All red snapper collected from one study site were processed on the vessel before sampling began at the next site.

During processing, each red snapper was weighed for total weight (TW) and eviscerated body weight (EW) to the nearest 0.001 kg with a Marel motion compensated scale; standard length (SL), fork length (FL), and total length (TL) were measured to the nearest mm, and sex was determined. Additionally, otoliths were collected for age analysis, ovaries were collected from females for reproductive analysis, stomachs were removed for diet composition, livers were weighed to determine the liver-somatic index, and muscle tissue samples were collected for stable isotope and caloric density analyses. A water temperature profile was obtained at each site with a Sea-Bird Electronics 25

Sealogger CTD. The temperature associated with a sample was the bottom temperature during each collection period.

Each red snapper was placed into one of four size classes based on FL: size class 3 (300-399 mm), size class 4 (400-499 mm), size class 5 (500-599 mm), and size class 6 (>600 mm). Size class 3 red snapper were not included in any further analyses because they were collected only at East Cameron. Red snapper from McGrail were also not included in the analysis due to a small sample size (n=27).

Liver-Somatic Index

Nutritional condition of red snapper was assessed with the liver-somatic index (LSI) calculated as:

$$\text{LSI} = \frac{\text{Liver weight (g)}}{\text{Eviscerated body weight (g)}} \times 100$$

Whole livers were removed from each red snapper, placed in individual labeled bags, frozen, and transported to the laboratory. In the laboratory, livers were thawed, trimmed of adhering non-liver tissue, blotted dry, and weighed to the nearest 0.01 g. In calculations of LSI, EW was used rather than TW to eliminate bias from stomach fullness and reproductive state.

The mean LSI for each month was plotted to determine whether a temporal pattern in LSI was evident. A smooth, possibly cubic trend was apparent (Appendix B), thus orthogonal polynomial coefficients were generated with the orpol function in SAS PROC IML to degree 3 (x=36) for equally spaced months sampled over 2011, 2012, and 2013. Interpreting a month effect was not of primary interest, so the orthogonal

polynomial coefficients were used as a smoother to control for temporal changes in the LSI. To meet the assumption of normality, the LSI was log transformed with a Shapiro-Wilk test statistic of 0.99 and a p-value for normal residuals of 0.0022. A Shapiro-Wilk test statistic of 1.0 is perceived as perfect normality, so the disparity seen between the test statistic and p-value is likely attributable to a few large, but biologically significant, LSI values. A semi-parametric model was used to assess whether the LSI differed between sites, sexes, and size classes, controlling for temperature and temporal effects, in the form

$$\ell og(LSI) = \beta_0 + \delta Tem + \beta_1 T_1 + \beta_2 T_2 + \beta_3 T_3 + Site + Sex + SC + Site*Sex + Site*SC + SC*Sex + \varepsilon$$

where Tem = temperature data (°C); continuous covariate
T_1 = Linear orthogonal polynomial covariate
T_2 = Quadratic orthogonal polynomial covariate
T_3 = Cubic orthogonal polynomial covariate
Site = Jakkula, Bright, East Cameron; class variable
Sex = Female, Male; class variable
SC = Size class 4, 5, 6; class variable

The model is semi-parametric because it effectively has both a nonparametric part and a parametric part. The model is nonparametric for time because a smooth trend is modeled with polynomial basis functions and it is parametric because the effect parameters are being estimated by the method of restricted maximum likelihood. A Bonferroni correction factor was made for each interaction term, calculated as α/k where $\alpha = 0.05$ and k = number of pairwise comparisons for each term. For the site-by-sex and size class-by-sex interaction comparisons, statistical significance was set at $\alpha = (0.05/15) = 0.0033$, and for the site-by-size class interaction comparisons, statistical significance was set at $\alpha = (0.05/36) = 0.0014$. All statistical tests were run using SAS v.9.3 (SAS Institute Inc. 2011).

Caloric Density

Caloric density of red snapper muscle tissue was determined and used as a second measure (in addition to the LSI) of the nutritional condition of red snapper. Caloric density (calories/gram) was estimated directly by adiabatic bomb calorimetry. Tissue samples were taken from the left flank epaxial muscle of individuals, placed in individual labeled bags, frozen, and then taken back to the laboratory. In the laboratory, tissue samples were placed on aluminum foil and dried in an oven at 60°C for a minimum of 48 hours. Once completely dried, tissue samples were hand ground in a ceramic mortar and pestle and placed in individual labeled glass scintillation vials until analyzed. One gram of ground muscle tissue was then pressed into a pellet, with the addition of 300 μL of deionized water to ensure cohesion, using a Parr pellet press. Each pellet was subsequently dried for 36 hours to allow for water to evaporate.

Caloric density was measured from the dried pellets using a Parr 6200 adiabatic oxygen bomb calorimeter according to the Parr instruction manual (Parr Instrument Co. 2010). Maintenance and part replacement were done on the two oxygen bomb cylinders either every 500 combustions or every six months to ensure that wear and corrosion did not bias results. Four benzoic acid pellets, one for each oxygen bomb and water bucket set, were run at the beginning of every sampling day to insure proper calibration. Two replicates of each red snapper tissue were then run to test for sample homogeneity. If the difference between the two replicated samples was more than 100 cal/g, a third pellet was run to obtain sample homogeneity. The final caloric density value (cal/g) used per sample was calculated as the average of the two replicated samples.

The mean caloric density for each month was plotted to determine whether a temporal pattern in caloric density was evident. A smooth, possibly cubic trend was apparent (Appendix B), thus the same orthogonal polynomial coefficients generated for the LSI were used as a smoother to control for temporal changes. A semi-parametric model was used to assess whether caloric density differed between sites, sexes, and size classes, controlling for temperature and temporal effects, in the form

$$CD = \beta_0 + \delta Tem + \beta_1 T_1 + \beta_2 T_2 + \beta_3 T_3 + Site + Sex + SC + Site*Sex + Site*SC + SC*Sex + \varepsilon$$

where CD = Caloric density (calories/g)
Tem = temperature data (°C); continuous covariate
T_1 = Linear orthogonal polynomial covariate
T_2 = Quadratic orthogonal polynomial covariate
T_3 = Cubic orthogonal polynomial covariate
Site = Jakkula, Bright, East Cameron; class variable
Sex = Female, Male; class variable
SC = Size class 4, 5, 6; class variable

The model produced a Shapiro-Wilk test statistic of 0.97, near the optimal value of 1.0. Yet, the p-value for normal residuals displays statistical significance (<0.0001). This statistical rejection of normality is attributable to a few large, but biologically significant, caloric density values. For clarity, Studentized residual plots were examined and no extreme violations of normality were present and they reflected a distribution that is symmetric and continuous without heavy tails. Minor violations of the normality assumption, such as those present here, lead to robust testing and do not severely affect the corresponding F-distribution associated with the F-test statistics under this models setting (Freund et al. 2010). For a more complete discussion, see the established text by Milliken and Johnson (2009) on the analysis of messy data. After a Bonferroni correction was made, statistical significance was set at $\alpha = 0.0033$ for the site-by-sex and

size class-by-sex interaction term comparisons and α = 0.0014 for the site-by-size class interaction term comparisons. All statistical tests were run using SAS v.9.3 (SAS Institute Inc. 2011).

Results

A total of 651 red snapper were caught from Jakkula (n=81), McGrail (n=27), Bright (n=215), and East Cameron (n=328) during this study. From the 651 red snapper caught, 536 red snapper from Jakkula (n=78), Bright (n=207), and East Cameron (n=251) were used in the analysis of LSI and caloric density (Table 2.2). The discrepancy observed between the number of red snapper caught and the number of samples used in the analyses is due to damage from predators while individuals were being retrieved from the sites.

Table 2.2. Number of liver and muscle tissue samples used in the analysis of the liver-somatic index and caloric density of red snapper. *Lutjanus campechanus*, from Jakkula, Bright, and East Cameron for each month sampling occurred.

Month	**Jakkula**	**Bright**	**East Cameron**
2011			
September	0	18	0
2012			
February	7	3	13
March	12	12	49
May	18	1	0
July	11	31	36
October	2	21	21
December	0	28	45
2013			
February	2	0	0
March	1	0	0
April	0	0	30
May	3	20	10
June	4	36	23
August	13	35	19
October	5	2	5

Liver-Somatic Index

Temporal patterns in LSI were evident for red snapper at Jakkula, Bright, and East Cameron. Monthly means combined over years were varied and peaked in May and declined thereafter until December (Fig. 2.2a). Comparing the monthly means by year, the LSI was similar only during March and May of both 2012 and 2013 (Fig. 2.2b). The average value of LSI, combined over all months, as well as the maximum LSI value observed, was greatest at Jakkula, followed by Bright, and East Cameron (Table 2.3). The temporal pattern in LSI differed between Jakkula, Bright, and East Cameron (Fig. 2.3).

A temporal pattern in LSI was evident at Jakkula, where the LSI decreased from February to March, increased in May, and declined thereafter until August with a peak observed in October (Fig. 2.4a). There was a general, but weak inverse relationship between the LSI and water temperature at Jakkula (Fig. 2.4a). Monthly means of the LSI by year at Jakkula were greater in February and May in 2012 than in 2013, and was greater in October 2013 than in October 2012 (Fig. 2.4b). The high variability in LSI observed in July, August, and October at Jakkula was due to a few large females with an LSI of 1.33 in July, 1.78 and 1.09 in August, and 1.28 and 1.56 in October. Similar temporal patterns were observed for females and males at Jakkula, but monthly means were greater for females than for males (Fig. 2.4c). Similar temporal patterns also were observed for size class 4, size class 5, and size class 6 at Jakkula with little difference between monthly means, except in October (Fig. 2.4d); however, only one size class 5 red snapper was collected in October.

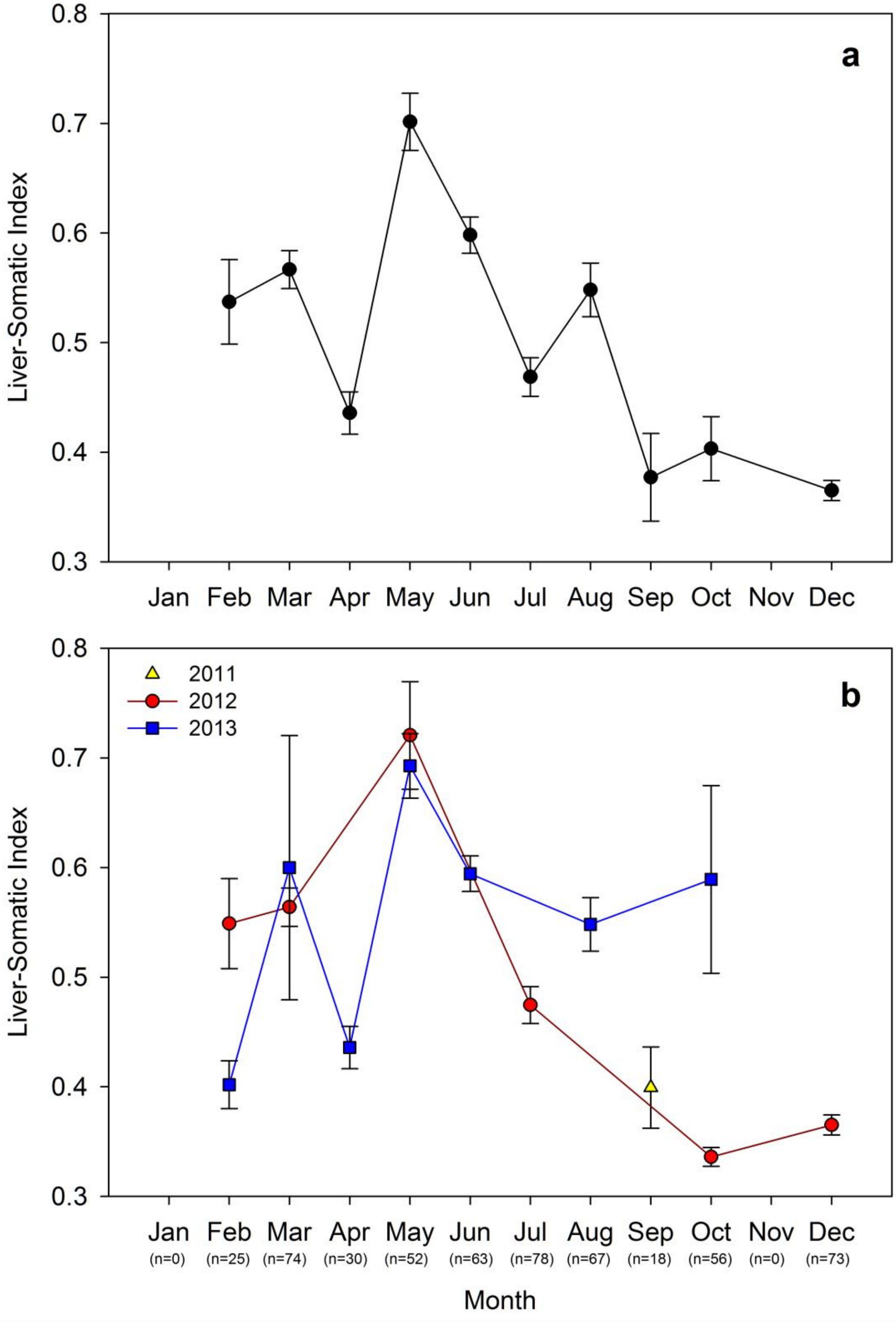

Figure 2.2. a) The monthly means combined over years for the liver-somatic index (LSI) of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron (n=536); b) Monthly means for the LSI for 2011 (n=18; yellow triangle), 2012 (n=310; red circles), and 2013 (n=208; blue squares). Vertical lines represent ± standard error of the monthly means.

Table 2.3. Mean, standard error, minimum, and maximum values for the liver-somatic index of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Site	Mean	Std. Error	Min	Max
Jakkula	0.6574	0.0312	0.3501	1.7808
Bright	0.4960	0.0123	0.2253	1.1273
East Cameron	0.4698	0.0086	0.2644	0.9213

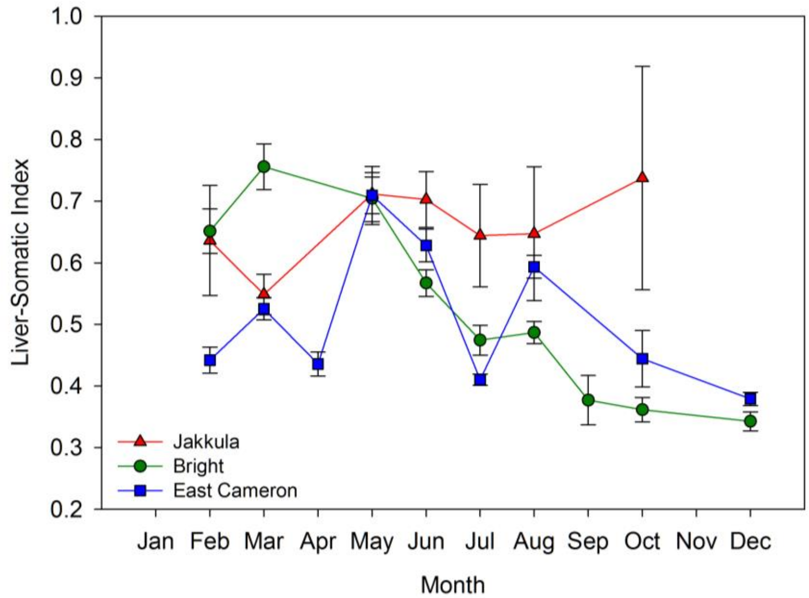

Figure 2.3. The monthly means combined over years for the liver-somatic index of red snapper, *Lutjanus campechanus*, at Jakkula (n=78; red triangles and line), Bright (n=207; green circles and line), and East Cameron (n=251; blue squares and line). Vertical lines represent ± standard error of the monthly means.

A temporal pattern in LSI was evident at Bright, where the LSI increased from February to March and continued to decline to the lowest point in December (Fig. 2.5a). A strong inverse relationship between water temperature and the LSI was evident at Bright, where the LSI decreased as temperature increased, except in September (Fig. 2.5a). Monthly means of the LSI by year at Bright were greater in all months in 2013 (Fig. 2.5b); however only one red snapper was collected in May 2012. Similar temporal patterns were observed for females and males at Bright, but the monthly means of LSI

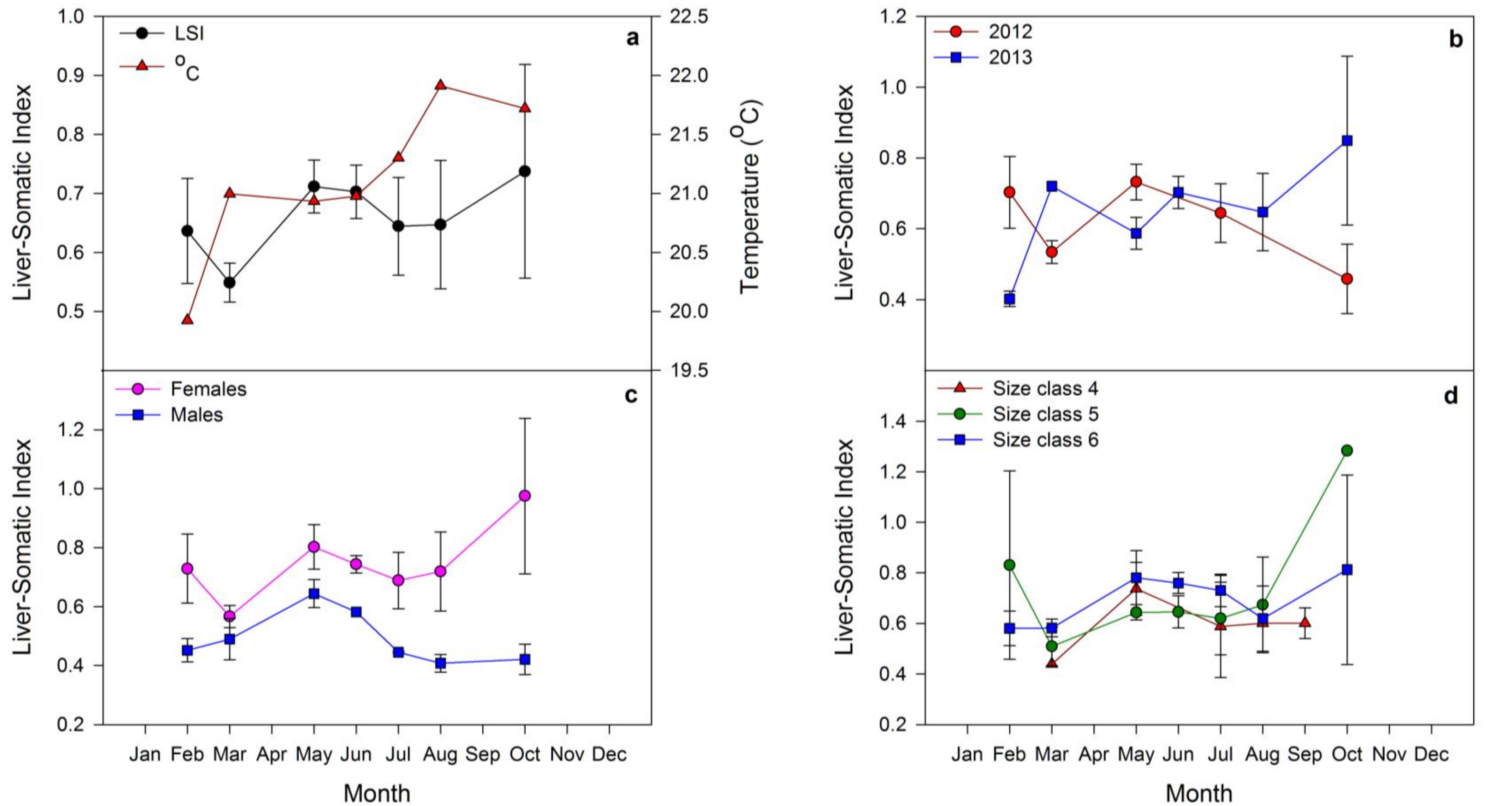

Figure 2.4. a) Monthly means combined over years for the liver-somatic index (LSI; black circles and line)) of red snapper, *Lutjanus campechanus*, at Jakkula (n=78) plotted against bottom water temperature (°C; red triangles and line); b) Monthly means for the LSI at Jakkula in 2012 (n=50; red circles) and 2013 (n=28; blue squares); c) Monthly means combined over years for the LSI of females (n=51; pink circles) and males (n=27; blue squares) at Jakkula; d) Monthly means combined over years for the LSI of size class 4 (400-499 mm; n=12; red triangles), size class 5 (500-599 mm; n=31; green circles), and size class 6 (>600 mm; n=35; blue squares) at Jakkula. Vertical lines represent ± standard error of the monthly means.

were greater for females, except in September (Fig. 2.5c). Similar temporal patterns also were observed for size class 4, size class 5, and size class 6 at Bright with little difference between monthly means, except in October (Fig. 2.5d); however, only one red snapper of size class 6 was collected in October.

A highly variable temporal pattern in LSI was evident at East Cameron, where the LSI peaked in May and was low in December (Fig. 2.6a). There is a general inverse relationship between the LSI and water temperature at East Cameron, but this relationship is not consistent and appears to be evident only from June to December (Fig. 2.6a). Monthly means of the LSI by year at East Cameron were greater in 2013 than in 2012 (Fig. 2.6b). Similar temporal patterns were observed for females and males at East Cameron, with little difference between monthly means, except in June (Fig. 2.6c). The LSI for size class 4, size class 5, and size class 6 at East Cameron were comparable, with the exceptions of the monthly means in March, April, and October being greater for size class 4 (Fig. 2.6d).

Site, sex, site-by-sex, and site-by-size class were all significant contributors to variation of the LSI, after controlling for both temperature and time (Table 2.4; $p<0.05$). The LSI of females differed from males at Jakkula and Bright ($p<0.0033$), while no difference in the LSI was observed between males and females at East Cameron ($p>0.0033$; Fig. 2.7). The LSI of females at East Cameron differed from females at Jakkula and Bright ($p<0.0033$), while no difference in the LSI was observed between sites for males ($p>0.0033$; Fig. 2.7).

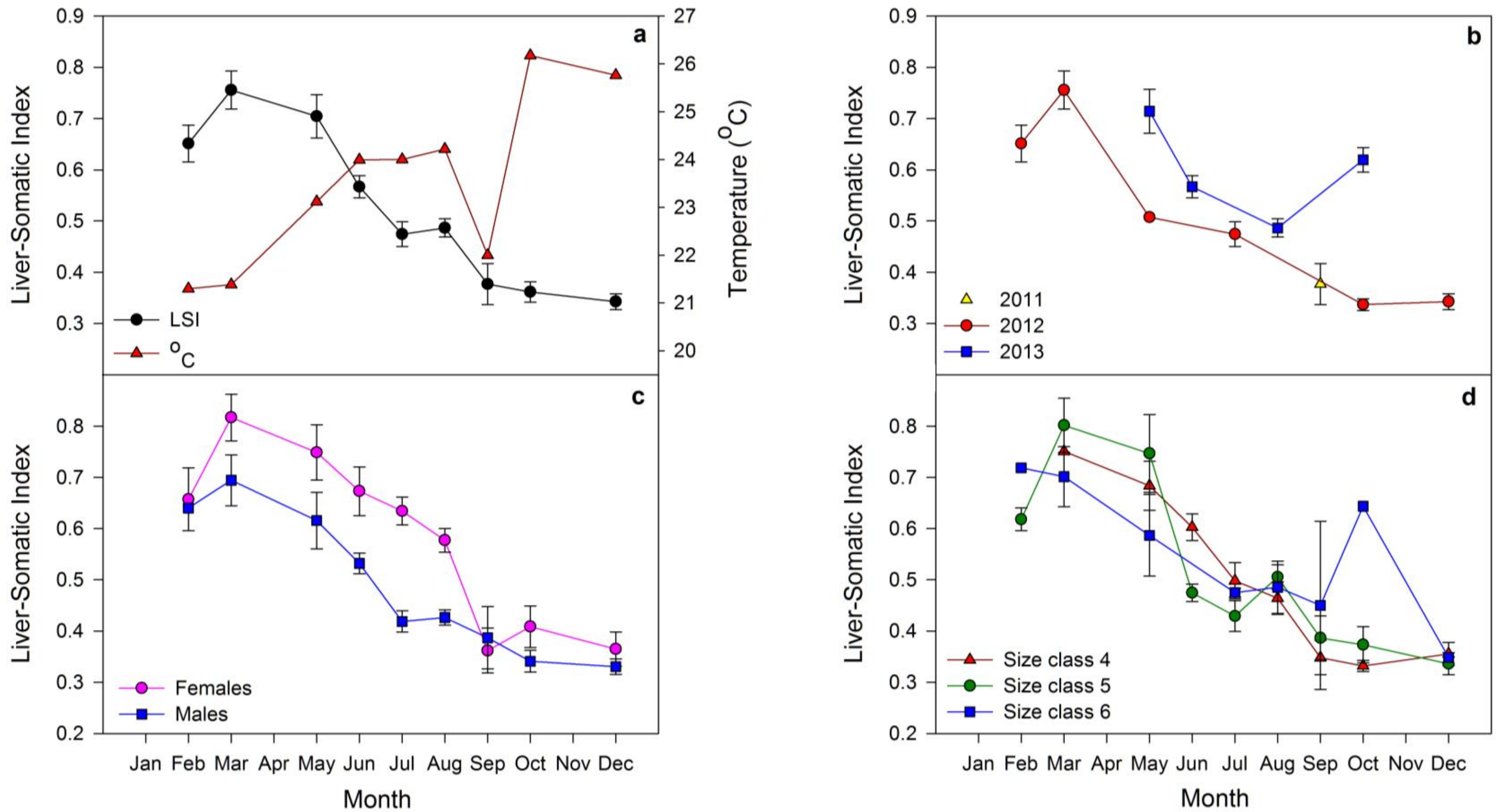

Figure 2.5. a) Monthly means combined over years for the liver-somatic index (LSI; black circles and line) of red snapper, *Lutjanus campechanus*, at Bright (n=207) plotted against bottom water temperature (°C; red triangles and line); b) Monthly means for the LSI at Bright in 2011 (n=18; yellow triangle), 2012 (n=96; red circles) and 2013 (n=93; blue squares); c) Monthly means combined over years for the LSI of females (n=77; pink circles) and males (n=130; blue squares) at Bright; d) Monthly means combined over years for the LSI of size class 4 (400-499 mm; n=102; red triangles), size class 5 (500-599 mm; n=85; green circles), and size class 6 (>600 mm; n=20; blue squares) at Bright. Vertical lines represent ± standard error of the monthly means.

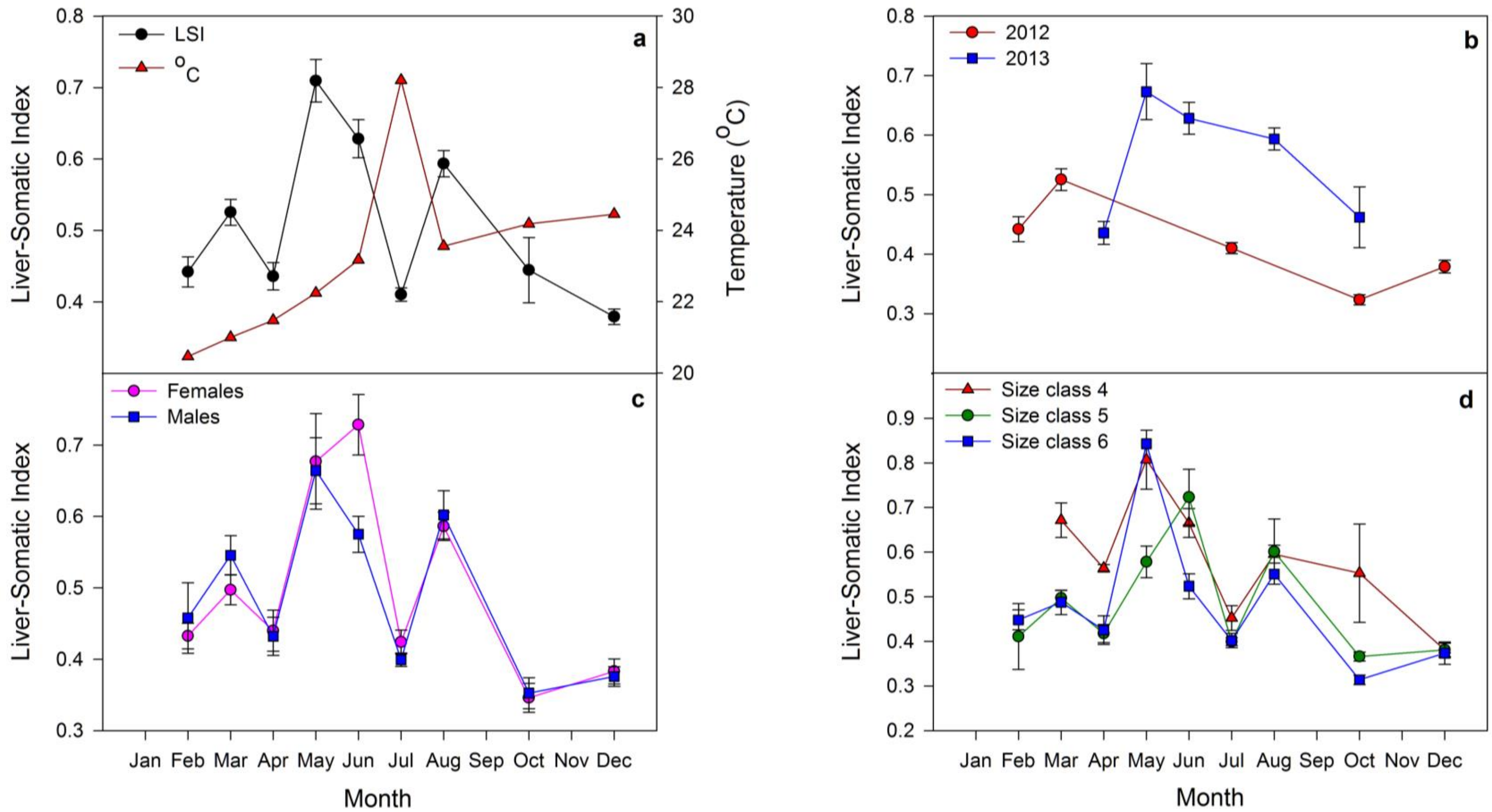

Figure 2.6. a) Monthly means combined over years for the liver-somatic index (LSI; black circles and line) of red snapper, *Lutjanus campechanus*, at East Cameron (n=251) plotted against temperature (°C; red triangles and line); b) Monthly means for the LSI at East Cameron in 2012 (n=164; red circles) and 2013 (n=87; blue squares); c) Monthly means combined over years for the LSI of females (n=114; pink circles) and males (n=137; blue squares) at East Cameron; d) Monthly means combined over years for the LSI of size class 4 (400-499 mm; n=56; red triangles), size class 5 (500-599 mm; n=100; green circles), and size class 6 (>600 mm; n=95; blue squares) at East Cameron. Vertical lines represent ± standard error of the monthly means.

Table 2.4. Semi-parametric model Type III test of fixed effects for the liver-somatic index of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Temperature	1	518	86.58	<.0001
T1	1	518	47.17	<.0001
T2	1	518	24.76	<.0001
T3	1	518	32.68	<.0001
Site	2	518	7.7	0.0005
Sex	1	518	44.23	<.0001
Size Class (SC)	2	518	2.02	0.1342
Site*Sex	2	518	13.25	<.0001
Site*SC	4	518	7.18	<.0001
SC*Sex	2	518	1.25	0.287

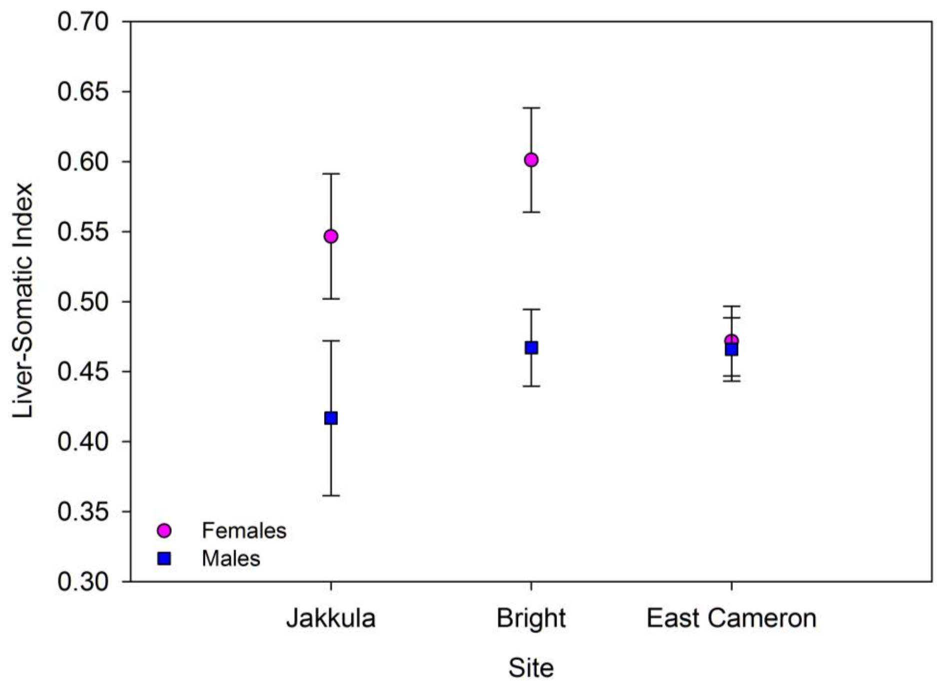

Figure 2.7. Site-by-sex interaction graph of LSMeans estimates for the liver-somatic index of red snapper, *Lutjanus campechanus*. Vertical lines represent ± standard error of LSMeans estimate.

There were no significant differences in the LSI observed between size classes at Jakkula and Bright ($p>0.0014$), but the LSI of size class 4 differed from size class 5 and 6 at East Cameron ($p<0.0014$; Fig. 2.8). The LSI of size class 5 at Bright differed from size class 5 at East Cameron, and the LSI size class 6 at Bright differed from size class 6 at East Cameron ($p<0.0014$; Fig. 2.8). Size class-by-sex interaction was still investigated, even though it was not significant, as I was looking for differences between sexes within each size class. The LSI of females differed from males within size class 4, 5, and 6 ($p<0.0033$; Fig. 2.9). The non-significance of the size class-by-sex interaction term was likely driven by the absences of differences in the LSI between size classes of the same sex.

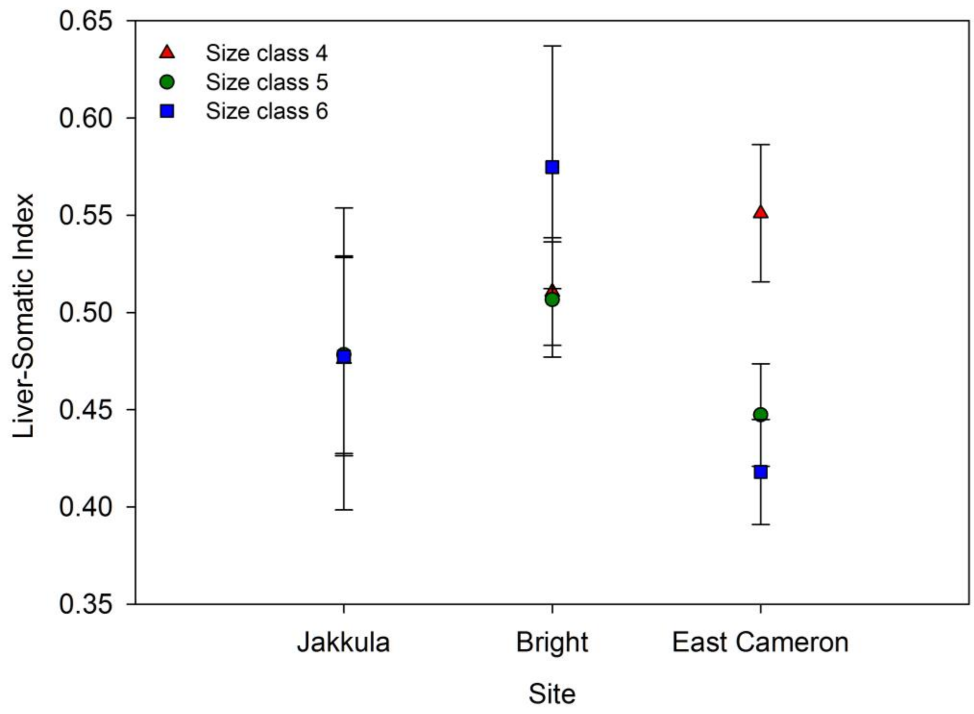

Figure 2.8. Site-by-size class interaction graph of LSMeans estimates for the liver-somatic index of red snapper, *Lutjanus campechanus*. Vertical lines represent ± standard error of LSMeans estimate.

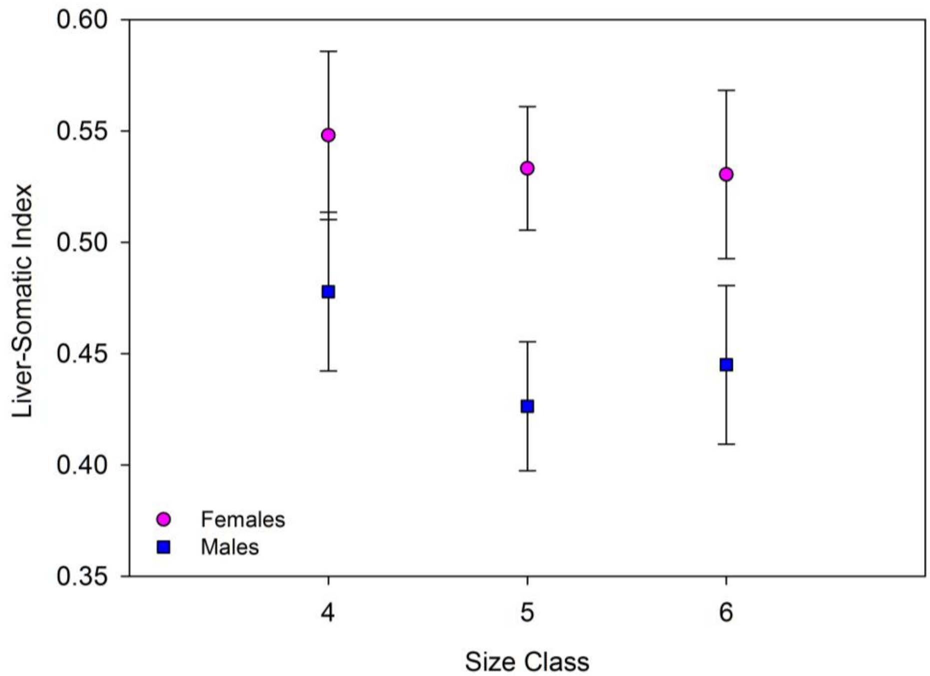

Figure 2.9. Sex-by-size class interaction graph of LSMeans estimates for the liver-somatic index of red snapper, *Lutjanus campechanus*. Vertical lines represent ± standard error of LSMeans estimate.

Caloric Density

Temporal patterns in caloric density muscle tissue were evident for red snapper at Jakkula, Bright, and East Cameron. Monthly means for caloric density peaked in February, had a low in September followed by an increase in October, with a small decline in December (Fig. 2.10a). Monthly means of caloric density by year were greater in February, March, and May in 2012 than in 2013 (Fig. 2.10b). The temporal patterns are contradictory in 2012 and 2013, where caloric density generally increased throughout 2012 and generally decreased throughout 2013 (Fig. 2.10b). The average value of caloric density, combined over all months, as well as the maximum caloric density observed, was greatest at Jakkula, followed by East Cameron and Bright (Table 2.5).

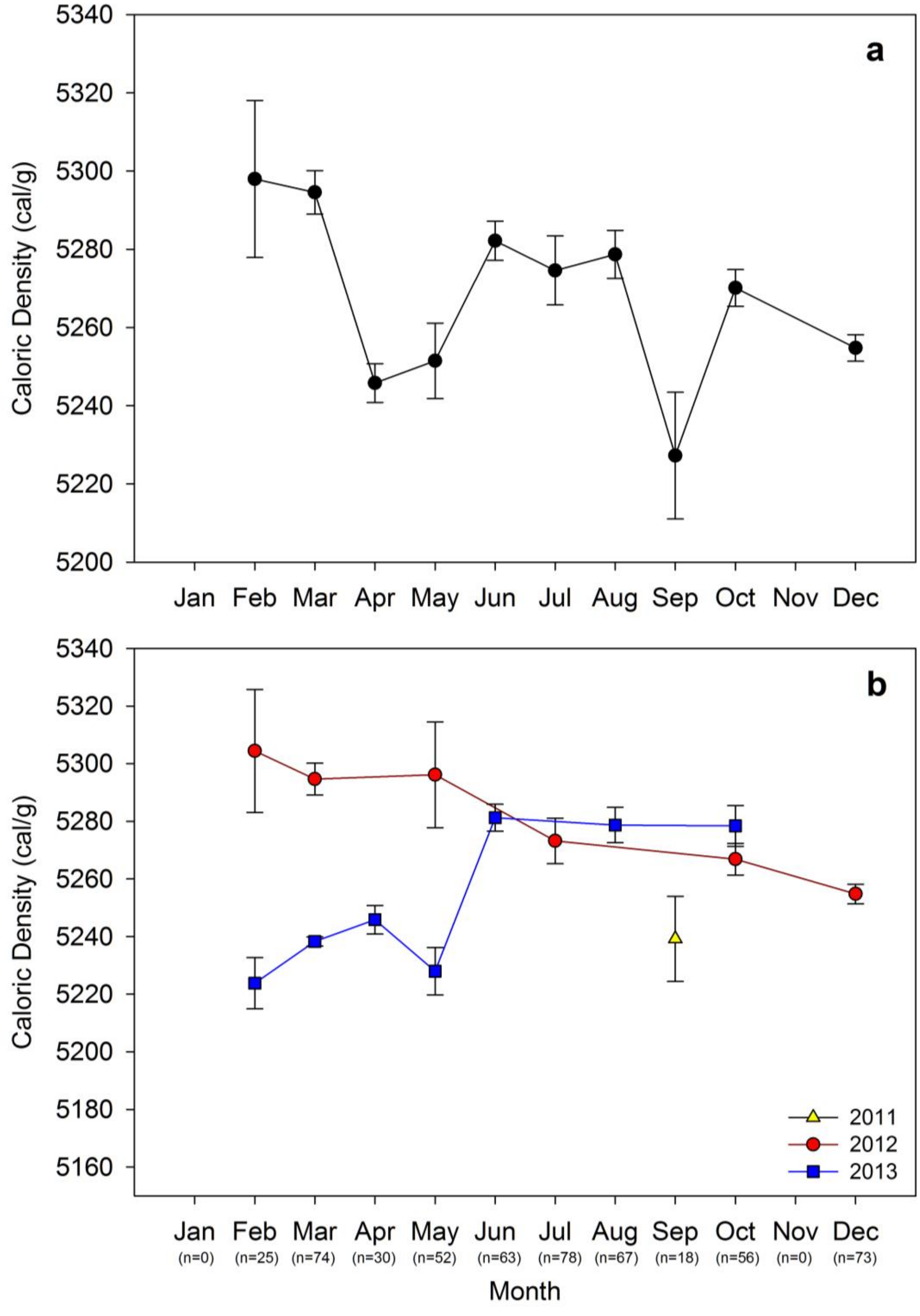

Figure 2.10. a) The monthly means combined over years for caloric density (calories/g) of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron (n=536); b) The monthly means for caloric density (cal/g) of red snapper for 2011 (n=18; yellow triangle), 2012 (n=310; red circles), and 2013 (n=208; blue squares). Vertical lines represent ± standard error of the monthly means.

Table 2.5. The mean, standard error, minimum, and maximum values of caloric density (calories/g) for red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Site	Mean	Std. Error	Min	Max
Jakkula	5317.92	11.614	5201.45	5890.53
Bright	5256.91	2.9217	5112.43	5377.06
East Cameron	5268.83	2.5349	5117.83	5430.36

Different temporal patterns in caloric density were observed between Jakkula, Bright, and East Cameron (Fig. 2.11). At Jakkula, caloric density peaked in February, declined in May, increased until July, and then dropped to the lowest value in October (Fig. 2.12a). The large standard errors in caloric density observed in February, June, and July at Jakkula are due to a few large values of 5590.2 cal/g, 5504.2 cal/g, and 5473.2 cal/g in February, 5422.8 cal/g in June, and 5890.5 cal/g in July. There was an inverse relationship between caloric density and water temperature for February, March, August, and October at Jakkula (Fig. 2.12a). Monthly means of caloric density at Jakkula were greater in 2012 than in 2013, except in the month of October (Fig. 2.12b). The temporal patterns for females and males at Jakkula differed during May, June, and July (Fig. 2.12c). Similar temporal patterns were observed among size classes at Jakkula, but monthly means for size class 6 were greater, except in October (Fig. 2.12d).

The caloric density at Bright was variable between months. Caloric density at Bright increased from February to the peak in March, dropped in May, increased again in June, decreased to a low in September, and gradually increased until December (Fig. 2.13a). There was no apparent relationship between caloric density and water temperature at Bright (Fig. 2.13a). Caloric density at Bright was larger in May 2012 than in 2013 (Fig. 2.13b); however, only one red snapper was collected at Bright in May 2012.

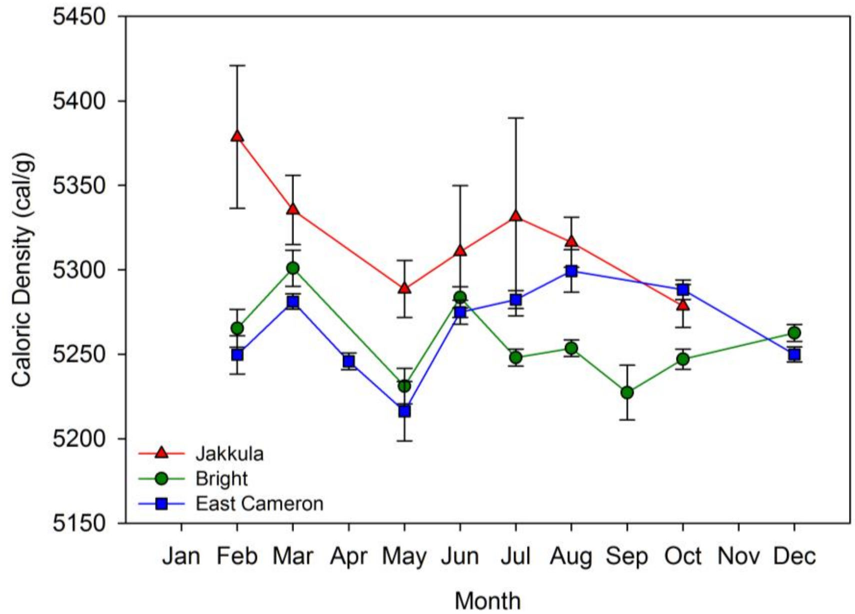

Figure 2.11. Combined monthly means of all years for caloric density (cal/g) of red snapper, *Lutjanus campechanus*, at Jakkula (n=78; red triangles), Bright (n=207; green circles), and East Cameron (n=251; blue squares). Vertical lines represent ± standard error of the monthly means.

Similar temporal patterns and monthly means were observed for females and males at Bright (Fig. 2.13c). Size class 4 and 5 at Bright exhibited similar temporal patterns, but a different pattern was observed for size class 6 (Fig. 2.13d).

Caloric density varied between months at East Cameron. Caloric density at East Cameron increased in March, declined to a low in May, peaked in August, and then decreased in December (Fig. 2.14a). There was no consistent relationship between caloric density and water temperature at East Cameron (Fig. 2.14a). Monthly means of caloric density were similar between 2012 and 2013 at East Cameron (Fig. 2.14b). Similar temporal patterns and monthly means were observed for females and males at East Cameron (Fig. 2.14c). Similar temporal patterns were also observed between size classes at East Cameron, with the exception of a lower monthly mean in May for size class 6; however, only one red snapper of size class 6 was collected in May (Fig. 2.14d).

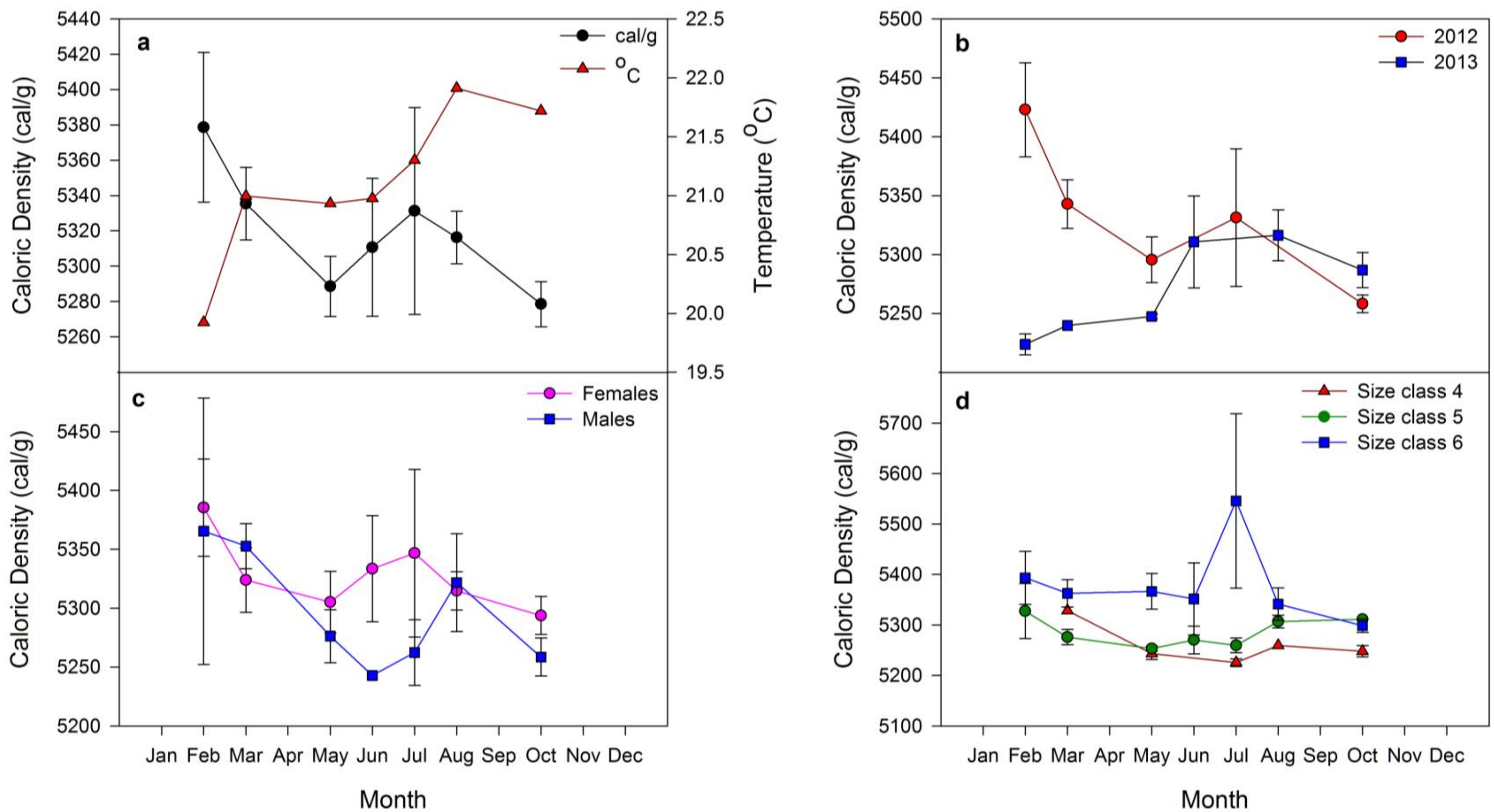

Figure 2.12. a) Monthly means combined over years for caloric density (calories/g; black circles and line) of red snapper, *Lutjanus campechanus*, at Jakkula (n=78) and bottom water temperature (°C; red triangles and line); b) Monthly means for caloric density (cal/g) at Jakkula in 2012 (n=50; red circles) and 2013 (n=28; blue squares); c) Monthly means combined over years for caloric density (cal/g) of females (n=51; pink circles) and males (n=27; blue squares) at Jakkula; d) Monthly means combined over years for caloric density (cal/g) of size class 4 (400-499 mm; n=12; red triangles), size class 5 (500-599 mm; n=31; green circles), and size class 6 (>600 mm; n=35; blue squares) at Jakkula. Vertical lines represent ± standard error of the monthly means.

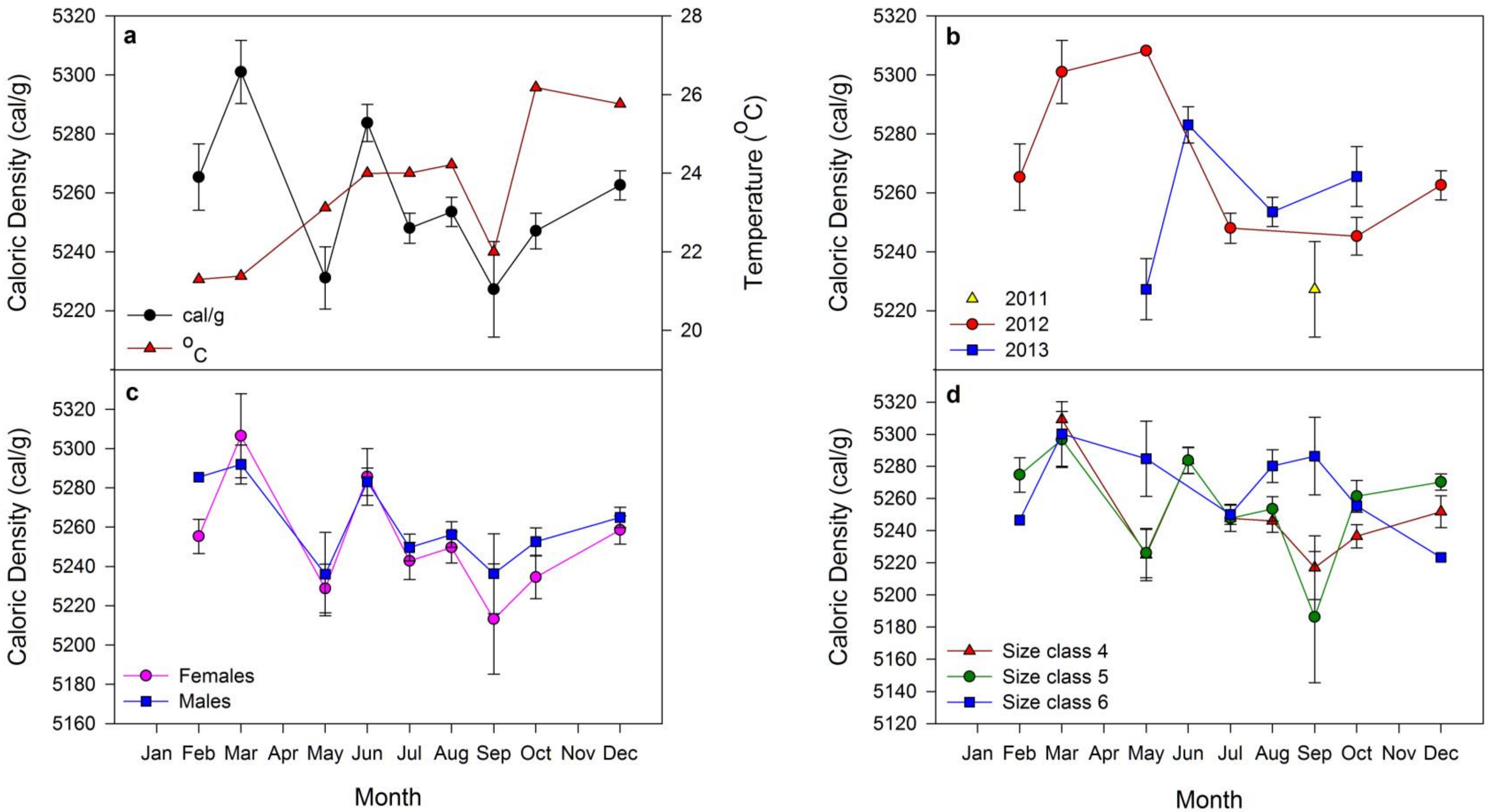

Figure 2.13. a) Monthly means combined over years for caloric density (calories/g; black circles and line) of red snapper, *Lutjanus campechanus*, at Bright (n=207) plotted against bottom water temperature (°C; red triangles and line); b) Monthly means for caloric density (cal/g) at Bright in 2011 (n=18; yellow triangle), 2012 (n=96; red circles), and 2013 (n=93; blue squares); c) Monthly means combined over years for caloric density (cal/g) of females (n=77; pink circles) and males (n=130; blue squares) at Bright; d) Monthly means combined over years for caloric density (cal/g) of size class 4 (400-499 mm; n=102; red triangles), size class 5 (500-599 mm; n=85; green circles), and size class 6 (>600 mm; n=20; blue squares) at Bright. Vertical lines represent ± standard error of the monthly means.

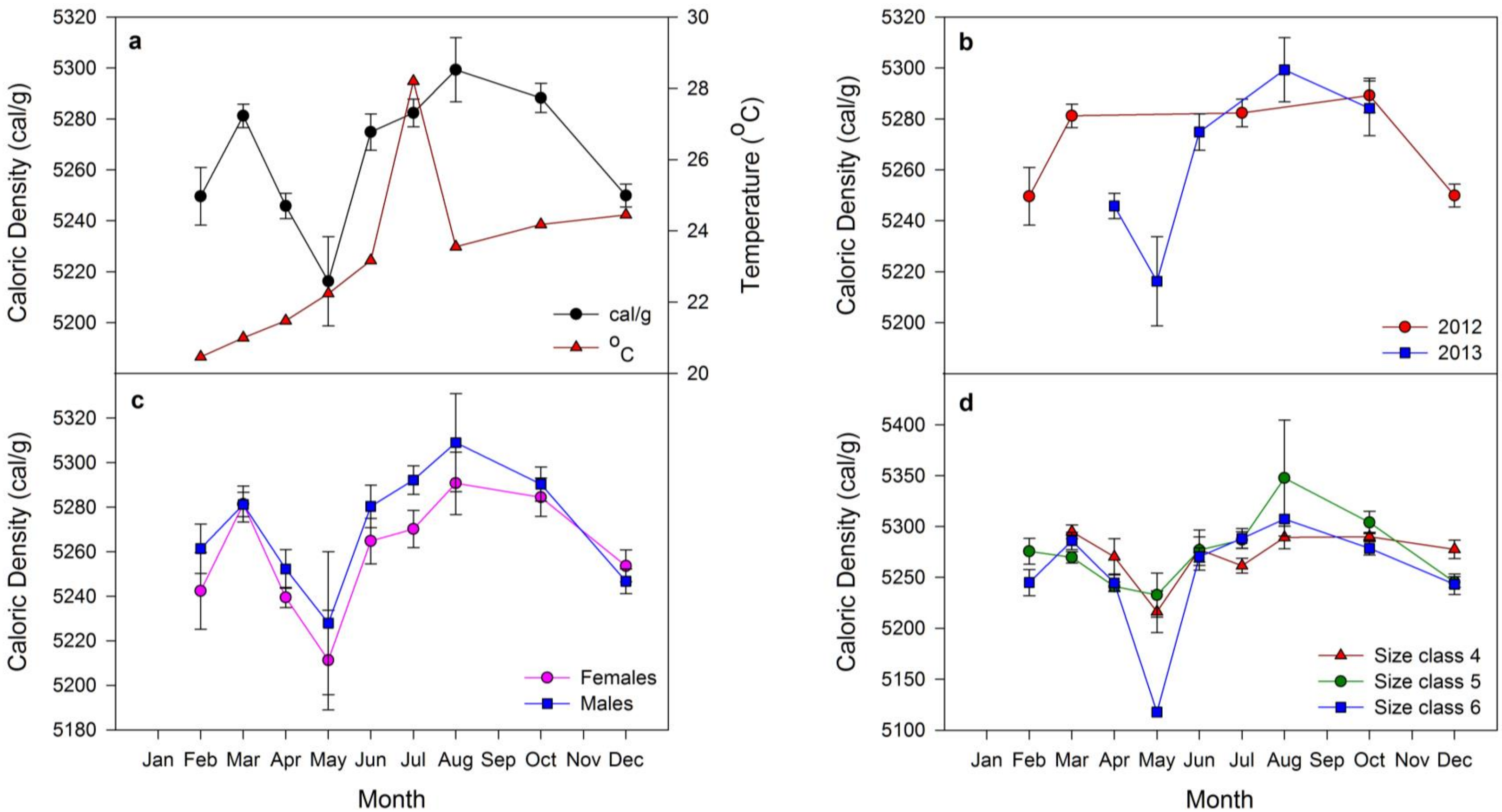

Figure 2.14. a) Monthly means combined over years for caloric density (calories/g; black circles and line) of red snapper, *Lutjanus campechanus*, at East Cameron (n=251) plotted against bottom water temperature (°C; red triangles and line); b) Monthly means for caloric density (cal/g) at East Cameron in 2012 (n=164; red circles), and 2013 (n=87; blue squares); c) Monthly means combined over years for caloric density (cal/g) of females (n=114; pink circles) and males (n=137; blue squares) at East Cameron; d) Monthly means combined over years for caloric density (cal/g) of size class 4 (400-499 mm; n=56; red triangles), size class 5 (500-599 mm; n=100; green circles), and size class 6 (>600 mm; n=95; blue squares) at East Cameron. Vertical lines represent ± standard error of the monthly means.

Site, size class, and site-by-size class were all significant contributors to variation in caloric density, after controlling for temperature and time (Table 2.6; $p<0.05$). Caloric density of size class 6 differed from size class 4 and 5 at Jakkula ($p<0.0014$), while no significant differences were observed between size classes at Bright and East Cameron ($p>0.0014$; Fig. 2.15). Caloric density of size class 6 at Jakkula differed from size class 6 at Bright and East Cameron ($p<0.0014$; Fig. 2.15). Site-by-sex and size class-by-sex interactions were still investigated, even though the terms were not significant. There were no significant differences in caloric density between females and males at any site ($p>0.0033$); however, caloric density of females at Jakkula differed from females at Bright and East Cameron ($p<0.0033$; Fig. 2.16). There were no significant differences in caloric density between females and males within any size class ($p>0.0033$), but size class 6 females and males differed from size class 4 and 5 females and males ($p<0.0033$; Fig. 2.17).

Table 2.6. Semi-parametric model Type III test of fixed effects for the caloric density of red snapper, *Lutjanus campechanus*, at Jakkula, Bright, and East Cameron.

Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Temperature	1	518	1.85	0.1746
T1	1	518	10.81	0.0011
T2	1	518	9.77	0.0019
T3	1	518	20.83	<.0001
Site	2	518	6.54	0.0016
Size Class (SC)	2	518	20.85	<.0001
Sex	1	518	0	0.9846
Site*Sex	2	518	2.74	0.0653
Site*SC	4	518	17.61	<.0001
SC*Sex	2	518	0.25	0.7827

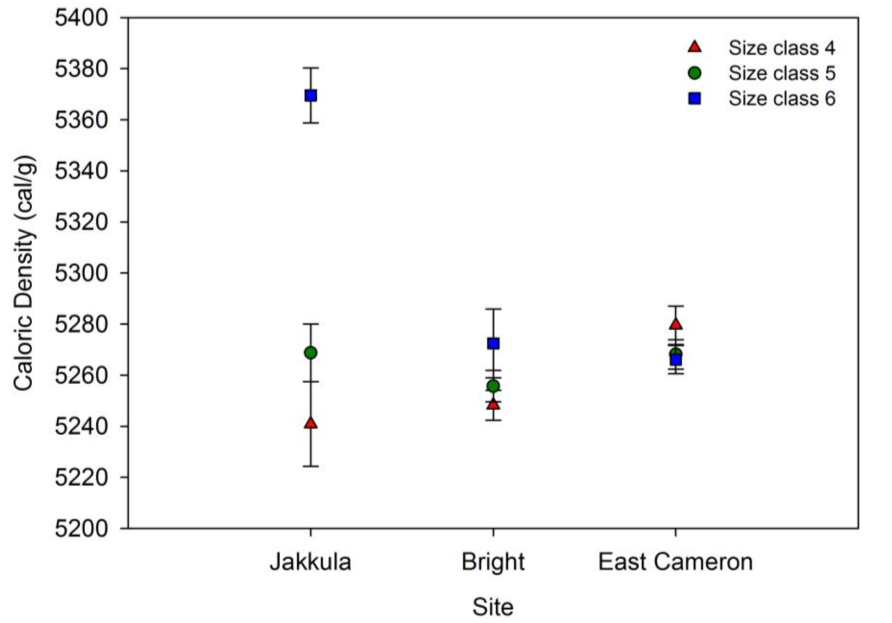

Figure 2.15. Site-by-size class interaction graph of LSMeans estimates for caloric density (calories/g) of red snapper, *Lutjanus campechanus*. Vertical lines represent ± standard error of LSMeans estimate.

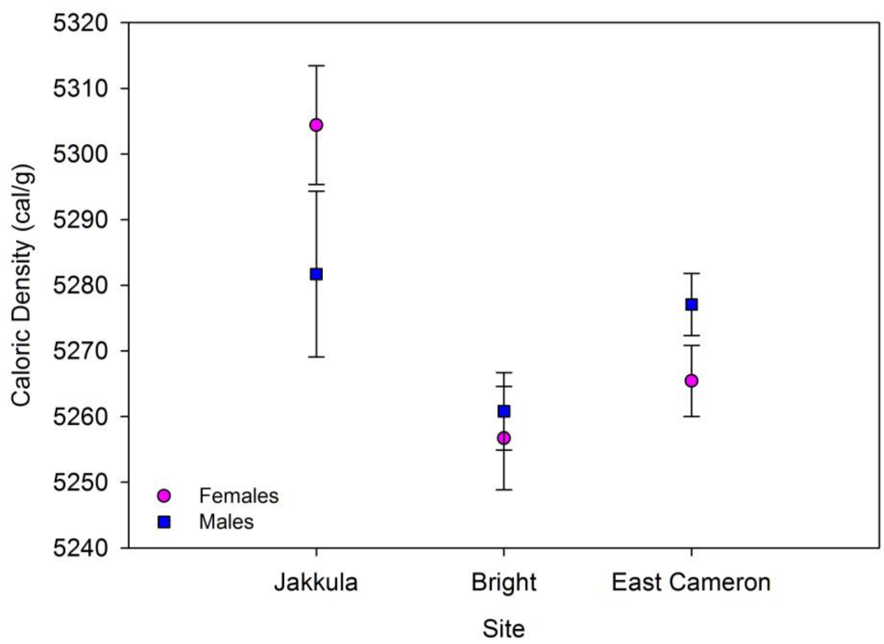

Figure 2.16. Site-by-sex interaction graph of LSMeans estimates for caloric density (calories/g) of red snapper, *Lutjanus campechanus*. Vertical lines represent ± standard error of LSMeans estimate.

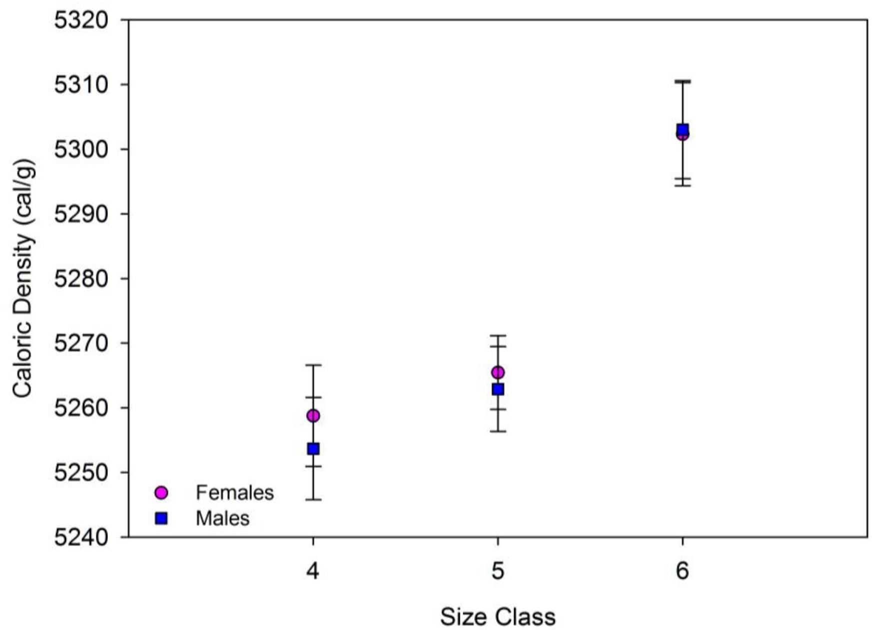

Figure 2.17. Size class-by-sex interaction graph of LSMeans estimates for caloric density (calories/g) of red snapper, *Lutjanus campechanus*. Vertical lines represent ± standard error of LSMeans estimate.

Relationship between the Liver-Somatic Index and Caloric Density

One consistent trend was apparent in the relationship between the LSI and caloric density of red snapper at Jakkula, Bright, and East Cameron. Caloric density at all of these sites was low in May and increased in June, while the LSI was high in May and decreased in June (Fig. 2.18). At Jakkula, the temporal patterns in LSI and caloric density also departed when caloric density declined from July to October, while the LSI increased from July to October (Fig. 2.18). At Bright, the temporal pattern in LSI and caloric density also departed when caloric density increased from September to December, while the LSI declined from September to December (Fig. 2.18).

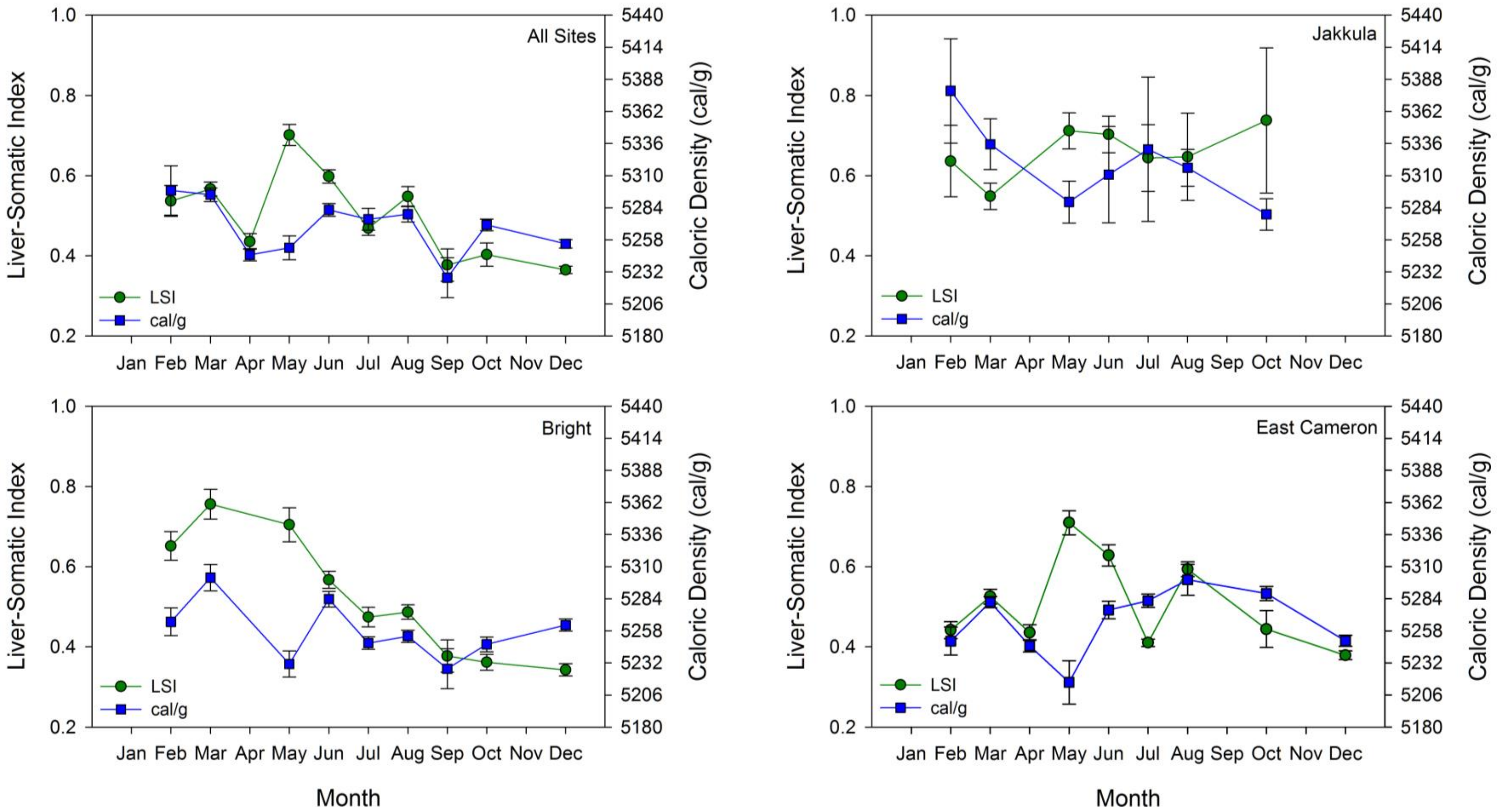

Figure 2.18. The combined monthly means for the liver-somatic index (LSI; green circles and line) and caloric density (calories/g; blue squares and line) of red snapper, *Lutjanus campechanus*, at all sites combined (n=536), Jakkula (n=78), Bright (n=207), and East Cameron (n=251). Vertical lines represent ± standard error of the monthly means.

Discussion

Liver-Somatic Index

Temporal patterns in LSI were evident for red snapper inhabiting natural and artificial reefs in the Gulf, with the LSI peaking in May and declining thereafter until December. I know of no published research evaluating temporal patterns for the LSI of wild caught red snapper; however, studies have observed temporal patterns for the LSI of mature, predatory fish. Craig et al. (2000) found that the LSI of red drum (*Sciaenops ocellatus*) peaked one month before the peak of spawning, suggesting that some of the energy to support reproductive development was acquired from the liver. Bulow et al. (1978) found the LSI of bluegills (*Lepomis macrochirus*) from two Tennessee lakes to be highest during spring when feeding was elevated and gonad maturation had begun, and the LSI subsequently declined during spawning when energy was being expended and feeding declined. Bulow et al. (1978) concluded that stored reserves in the liver were extracted and expended during high-energy demands of spawning activities when food intake declines.

The LSI has been shown to vary between females and males in largemouth bass (*Micropterus salmoides*; Adams et al. 1982), bluegills (Bulow et al. 1978), Atlantic sardine (*Sardina pilchardus*; Nunes et al. 2011), and Pacific cod (*Gadus macrocephalus*; Smith et al. 1990). This difference in the LSI between males and females is not surprising because female fishes use the liver in support of an additional function than males: the liver of female fishes is the site of synthesis for vitellogenin, the egg-yolk precursor (Brusule and Anadon 1996). The liver is thought to provide short-term supplies of intense energy for activities like reproduction (Adams et al. 1982). The LSI

of females is generally greater than males, which may result from a larger energetic investment for females during spawning (Brusule and Anadon 1996). While the LSI of females was greater than males at the natural reefs, the LSI did not differ between males and females at the artificial reefs, which may imply similar energetic investments between males and females at artificial reefs.

Red snapper spawning begins in May and continues through September, with peak spawning months of May, June, and July (Woods et al. 2003). One index used to assess the spawning potential of fishes is the gonadosomatic index (GSI). The GSI of red snapper in this study peaked in June and declined thereafter until December (GSI data obtained from Hilary Glenn[5]). Red snapper appeared to build up energy reserves in the liver prior to spawning and depleted those reserves during and after spawning.

The GSI of females at the artificial reefs was found to be lower than the GSI of females at the natural reefs (Glenn unpublished). Lower GSI values at the artificial reefs may have been produced by the lower LSI values compared to the natural reefs. Females at the natural reefs appear to invest more energy in reproduction than females at the artificial reefs, which is reflected in the LSI values. Fish in poor condition have been observed to produce smaller offspring with a decreased probability of survival (Morgan and Lilly 2006). Morgan and Lilly (2006) found a significant relationship between liver condition and the probability that an adult female Flemish cap cod (*Gadus morhua*) would spawn. If these relationships hold true for red snapper, females at artificial reefs may spawn less frequently and/or produce smaller offspring with a decreased probability of survival compared to females at natural reefs.

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[5] Glenn, H.D. 2014. Louisiana State University, Master Student, Department of Oceanography and Coastal Sciences.

The LSI is also correlated with both the quantity and quality of food and is highly sensitive to nutritional condition (Brusule and Anadon 1996). Diets of red snapper at the natural reefs were found to be more calorically rich than diets at the artificial reefs (Schwartzkopf, this study), which could have provided more energy to be stored in the liver. Diets of red snapper at the artificial reefs were also found to vary between size classes (Fig. 1.4), where smaller red snapper fed upon bottom dwelling prey, while larger red snapper fed at on the sea floor and up into the water column (Table 1.14). Differences in the diet between size classes at the artificial reefs may have led to differences observed in the LSI between size classes. Expending less energy by feeding upon bottom dwelling prey could also have allowed smaller red snapper to have a greater LSI than larger red snapper at the artificial reefs.

Water temperature has also been shown to affect the LSI, with the LSI decreasing as temperature increases (Heidinger and Crawford 1977). Sampling depth was greatest at Jakkula, and the temperature at sampling depth ranged from 19.1°C to 23.4°C over all sampling periods (Appendix A). The stability of the temperature over the sampling months at Jakkula likely created the weak relationship between temperature and the LSI of all three sites and allowed other factors, such as energetic demands of spawning, to affect the overall LSI. The stronger relationship between temperature and the LSI at Bright and East Cameron may be due the slightly warmer temperatures and greater ranges than at Jakkula. Red snapper spawning, however, also coincides with warmer temperatures and is likely the main factor affecting the overall temporal patterns in LSI, with temperature also contributing to the patterns.

Caloric Density

Temporal patterns in caloric density were evident for red snapper inhabiting natural and artificial reefs in the Gulf. When spawning occurs, female fishes have the potential to lose up to 85% of their somatic energy (Adams and Breck 1990). This loss of somatic energy during spawning was not apparent in this study, as the GSI of female red snapper peaked in June (Appendix B). Yet, caloric density increased from May to June and remained constant through August. There was no evidence that red snapper feeding declined during spawning months in this study (Appendix A), thus muscle energy stores may not have been utilized. Glenn (unpublished data) observed a developmental progression in oocyte maturation and an increase in the GSI beginning in March. Temporal patterns in caloric density are highly affected by spawning seasons because of the large amount of energy utilized in gonad development. The decline in caloric density from March to May could be attributed to energy content in the muscle being utilized for gonad growth.

Flath and Diana (1985) found caloric density in alewives (*Alosa pseudoharengus*) to be highest during peak feeding and lowest during the spawning season, with sizeable losses of body energy in fish that fasted during the spawning season. Foltz and Norden (1977) found a seasonal pattern in caloric density of smelt (*Osmerus mordax*), with high values in fall and low values during spawning, and concluded that smelt underwent a period of energy storage prior to winter and spawning. Caloric density in this study was not low during spawning as was observed by Flath and Diana (1985) and Foltz and Norden (1977). This difference may have resulted from different foraging strategies and

spawning patterns for red snapper compared to smelt and alewives, as well as different environmental conditions of study areas.

Metabolic energy demands can decrease with decreasing temperature because foraging activities may be reduced (Bureau et al. 2002). The water temperature at Jakkula, which only varied by 4.3°C throughout the course of the study, was lower than the water temperature at the other natural reef, Bright, and the artificial reefs, East Cameron, during each sampling trip. Red snapper at Jakkula were found to have a large contribution of fishes in their diet (Fig. 1.2). The larger caloric density values observed at Jakkula might have resulted from a greater amount of energy storage due to the consumption of large amounts of fishes and lower temperatures.

A greater caloric density is indicative of better nutritional condition, and animals in better condition are thought to have a higher probability of survival and reproductive success (Kaufaman et al. 2007). The GSI of females at Jakkula was higher than the GSI of females at both Bright and East Cameron in May and June, suggesting better reproductive potential (Glenn unpublished data). Based on distribution data of age 8+ red snapper and age 0 to 1 red snapper, spawning is thought to occur over most of the western Gulf shelf at depths between 50 and 100 m, where larvae are subsequently transported toward the shore (Gallaway et al. 2009). While spawning does occur across the shelf, the majority of spawning is believed to occur on less complex habitats in waters of ~50 m in depth (Gallaway et al. 2009). Red snapper may prefer to spawn on less complex habitats, like that found at Jakkula, due to reduced abundance of egg consuming predators. Females in better nutritional condition may have been found at Jakkula compared to Bright and East Cameron because it may be a preferred spawning habitat.

Conclusion

This study indicates that red snapper at LA natural and artificial reefs experience temporal fluctuations in energy reserves. It appears that stored energy within the muscles is utilized to build up gonads, while stored energy from the liver is then utilized during and after spawning at both the natural reefs and artificial reef. Apparent differences in the LSI between sexes and differences in caloric density between size classes were as great as hypothesized. The relationships among partitioning of energy and external processes and activities, such as temperature, reproduction, and feeding are very complex. It should be noted that this study is an oversimplification of complex processes that occur in red snapper.

There has been no study done to evaluate how red snapper store or utilize energy biomechanically; therefore, this study can only provide a general representation of nutritional condition and energetic patterns of red snapper at LA natural and artificial reefs. It has been noted that caution should be used to evaluate condition of fishes based upon results of calorimetric analyses due to the complexity of tissue composition (Busacker et al. 1990). The LSI and caloric density appear to be good indicators of nutritional condition of red snapper, but the proximate composition of liver and muscle tissue were not determined in this study, and future studies on nutritional condition of red snapper should evaluate these relationships. While caloric density statistically differed between habitats and sizes, differences may not be biologically significant as the change between caloric density values was small.

My interpretation of the data is that female red snapper at natural reefs appear to be in better nutritional condition than female red snapper at artificial reefs. Recognizing

that nutritional condition of red snapper differs between habitats could enhance future red snapper stock assessments. Looking at red snapper energy reserves right before spawning, in addition to reproductive potential, may give an indication of potential for the upcoming spawning season. The LSI was a simple and time effective index to determine and appeared sensitive to spawning patterns. As such it may be a more useful index to evaluate nutritional condition of red snapper than caloric density. There is no simple explanation for the temporal patterns in LSI and caloric density observed in this study because many factors and processes occur simultaneously and affect each pattern, thus care should be taken in interpreting these conclusions.

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GENERAL SUMMARY AND CONCLUSIONS

The objective of my research was to assess the habitat quality of natural and artificial reefs located on the Louisiana (LA) continental shelf for red snapper (*Lutjanus campechanus*). Habitat quality was assessed by examining the diets, foraging patterns, and nutritional condition of red snapper at natural and artificial reefs. The nutritional condition of red snapper in the Gulf of Mexico (hereafter Gulf) can affect growth and reproduction, and can give insight about the relative quality of habitats on which they reside. A fish must balance the need for food and the time spend foraging with the risk of predation, and a greater amount of energy can be utilized for metabolism, reproduction, and growth if the time and energy spent foraging is minimized. My goal was to gain insight into how natural and artificial reefs might serve to enhance red snapper populations by examining the interactions between diets, foraging patterns, and nutritional condition, as well as temperature and reproduction.

Chapter 1 examined the diets and foraging patterns at two natural reefs (Jakkula and Bright) and one artificial reef planning area (East Cameron) located on the LA continental shelf. Diets were assessed with gut-content analysis, and foraging patterns were determined by examining the habitat utilization of prey items found in the diets. The diet at the natural reefs consisted of primarily fish, while the diet at the artificial reefs consisted of primarily fish and zooplankton. The diet at Bright was the most varied with respect to all prey items, and the diet at East Cameron was the most varied with respect to crustacean prey items. Size class was not an important factor for the diet at the natural reefs, but the diet varied between size classes at the artificial reefs. The natural reefs were found to offer a wider diversity of prey items than the artificial reefs, and specific

reef-dependent species were found in the diet at the natural reefs but not in the diet at the artificial reefs.

The differences between diets at the natural artificial reefs reflect differences between the characteristics of each habitat. The deep coral and coralline algal habitat characteristics at the natural reefs were reflected in large contributions of hard-substrate associated prey and small contributions of soft-sediment associated prey in both diets. Conversely, the predominance of mud at the artificial reefs was reflected in large contributions of soft-sediment associated prey and almost zero contribution from hard-substrate associated prey in the diet. The diet at the natural reefs in this study was more calorically rich than the diet at the artificial reefs due to the large contribution from hard-substrate and water-column associated prey items.

Red snapper at the natural reefs were found to feed on and above the reef, while red snapper at the artificial reef were found to feed on the surrounding seafloor and water column. It also appeared that at the artificial reefs, smaller red snapper fed closer to the bottom, while larger red snapper fed across a wider vertical gradient. I concluded that there was very little overlap in the diets between the natural reefs and the artificial reefs, and that the natural reefs offered a higher habitat quality in the form of prey resources.

My interpretation of the data provides support for the attraction hypothesis of artificial reefs, as the diet at the artificial reefs was not derived from reef-associated prey items. Attraction of red snapper to artificial reefs is thought to be more important in locations with abundant natural reefs, as is the case for the LA continental shelf. Red snapper at the artificial reefs on the LA continental shelf may not be gaining increased foraging benefits and instead congregate at these structures based on behavioral

preferences, thereby promoting overexploitation of the population. My results provide evidence to further support the attraction hypothesis, but they do not refute the possibility for production of red snapper at artificial reefs.

Chapter 2 determined the nutritional condition at two natural reefs (Jakkula and Bright) and one artificial reef planning area (East Cameron), located on the LA continental shelf, by examining temporal patterns in LSI and caloric density. Temporal patterns in LSI and caloric density were evident at both the natural and artificial reefs. In general, the LSI peaked in May while caloric density peaked in February, but temporal patterns both in LSI and caloric density were site specific. It appeared that stored energy within the muscles was utilized to build up gonads, while stored energy from the liver was then utilized during and after spawning at both the natural and artificial reefs. The LSI of females was greater compared to males at the natural reefs, while the LSI did not differ between females and males at the artificial reefs. The LSI of females at the natural reefs was also greater than the LSI of females at the artificial reef. This may be indicative of a greater energetic investment in reproduction and a better spawning potential for females at the natural reefs.

The most notable finding was that overall, large females at Jakkula were found to have the most energy stored within both the liver and muscle, which may have resulted from a greater amount of energy storage due to the available prey resources and lower temperatures. These large energy stores may allow females at Jakkula to invest more energy in reproduction, leading to an enhanced spawning potential. Females in better nutritional condition could have been found at Jakkula, a less complex habitat, compared to Bright and East Cameron because it may be a preferred spawning habitat.

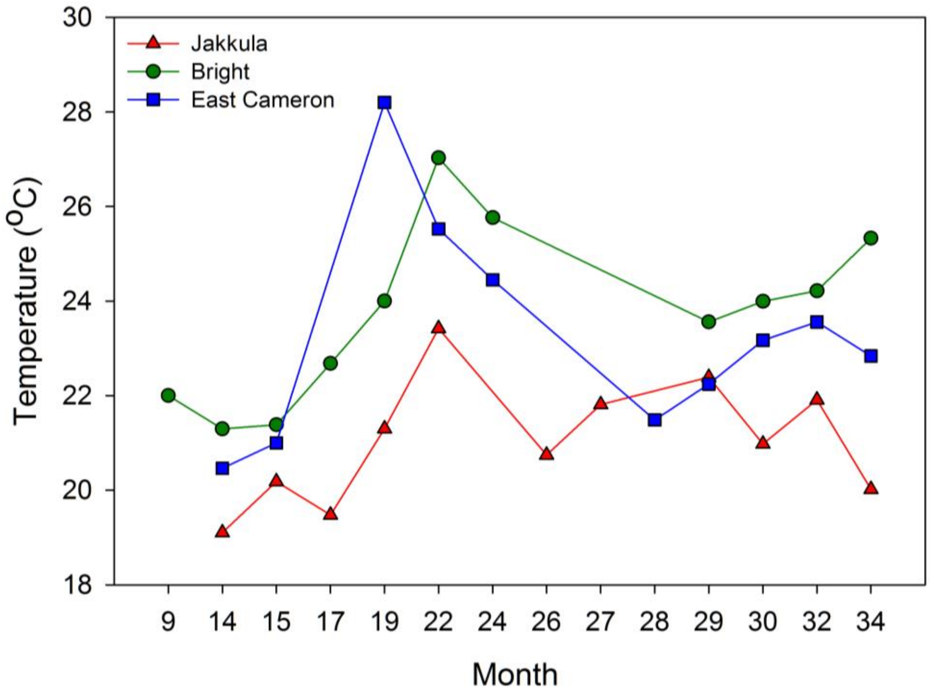
The LSI and caloric density appear to be a good indicator of nutritional condition of red snapper, but the proximate composition of liver and muscle tissues were not determined in this study. While caloric density statistically differed between habitats and sizes, the differences between values may not be biologically significant and determining the proximate composition of muscle tissues could provide more insight. I concluded that female red snapper at natural reefs appear to be in better nutritional condition than females at the artificial reefs, and recognizing that the nutritional condition of differs between habitats could enhance future stock assessments.

Less energy may be expended at the natural reefs by foraging on prey found on and above the reef, while more energy may be expended at the artificial reefs by moving off the reef to forage on prey found on the surrounding seafloor and water column. More time should be spent at reefs with abundant prey resources than at reefs with low prey availability, and leaving the reef occurs when the energy gained from those prey resources is reduced. It is likely that red snapper at the natural reefs spend more time on the reef due to the abundance of prey resources, while red snapper at the artificial reefs leave to forage because of reduced prey availability on the reef.

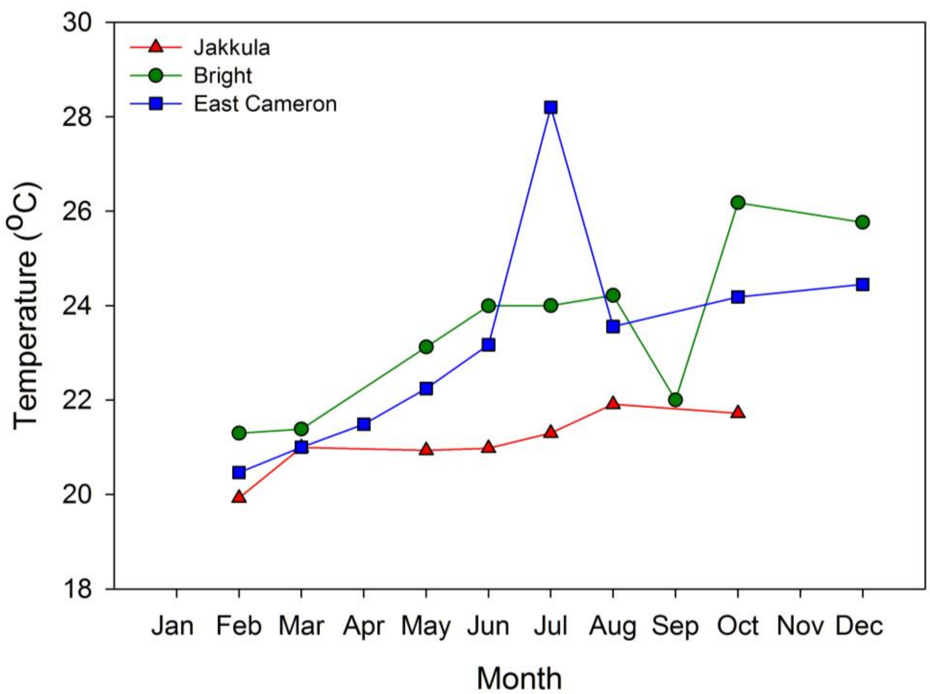
The natural reefs on the LA continental shelf sampled in this study are a part of an extensive network of reefs located on the northwestern Gulf continental shelf. The features of each reef provide ecological benefits by allowing movement of species between reefs. With increased ecological benefits to fish populations and communities, some measures to protect the natural reefs were enacted. No Activity Zones (zones of no oil and gas activities) were established at the reefs and several of the reefs have been designated at Habitat Areas of Particular Concern (HAPC). Jakkula and Bright, the two

natural reefs sampled in this study, are designated as HAPCs. Designation as a National Marine Sanctuary provides the only protective measures and regulations. In 2012, a sanctuary boundary expansion subcommittee and advisory committee evaluated 19 areas (Bright and Jakkula were among those) for inclusion under the management and protection of the Flower Gardens Banks National Marine Sanctuary (FGBNMS). Out of those 19 areas, the subcommittee recommended eight for inclusion, while the advisory committee recommended 11. Bright was placed on both the subcommittee and advisory council recommendation list for inclusion as a part of the FGBNMS, while Jakkula was absent from either list. Both Bright and Jakkula were found to provide high habitat quality for red snapper, and the results found in this study support the notion that Bright should be included in the FGBNMS and also indicate that Jakkula should be considered for FGBNMS status.

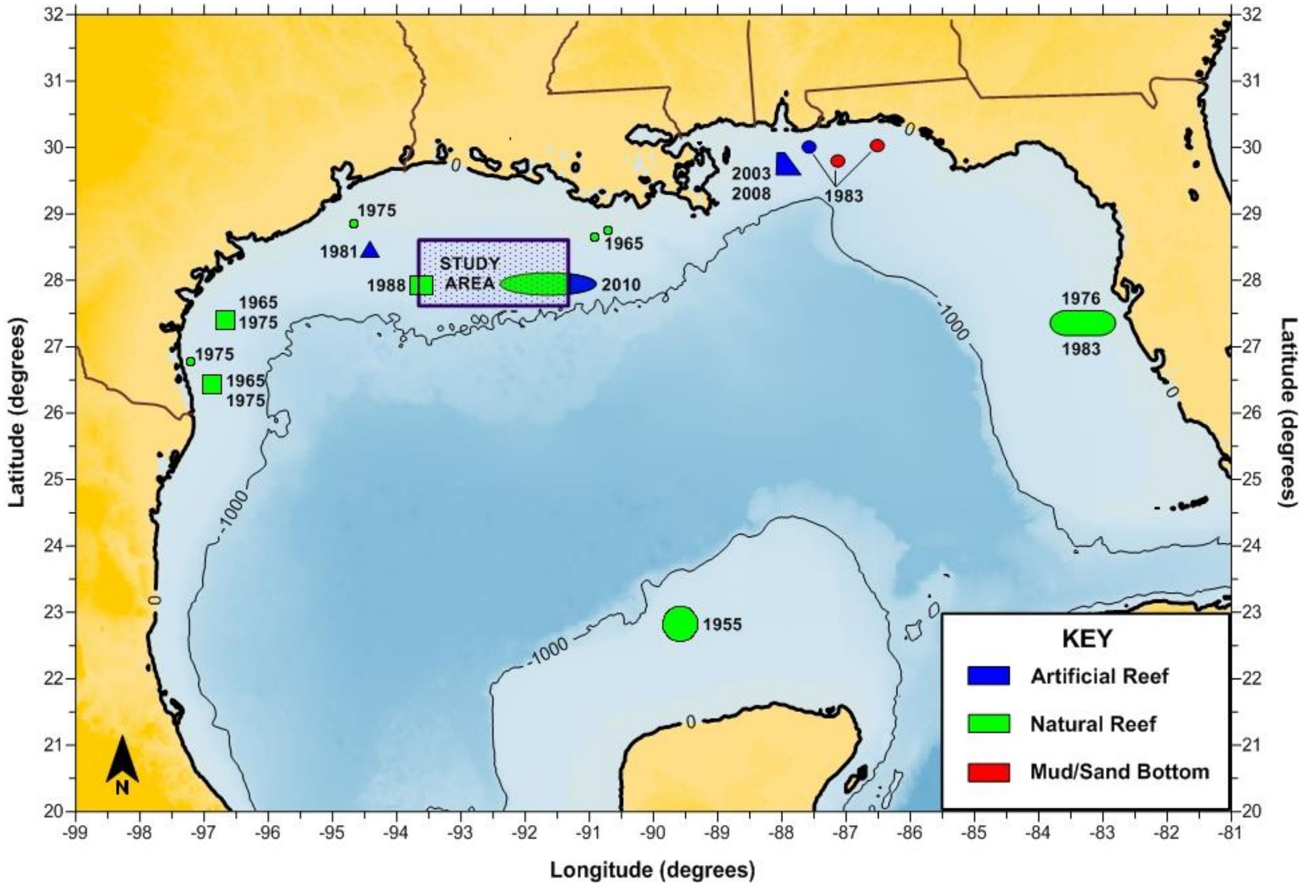
APPENDIX A: CHAPTER 1 SUPPLEMENTARY DATA



The bottom water temperature (°C) during each month sampled at Jakkula, Bright, and East Cameron. Months are numbered sequentially from 9 to 34 (9 = September 2011; 34 = October 2013).



The average monthly bottom water temperature (°C) sampled at Jakkula, Bright, and East Cameron.



Map showing adult red snapper diet studies previously conducted within the Gulf of Mexico, along with year published. The sizes of the individual shapes are approximate and correspond to the total sampling area covered by each study, with the colors referring to the type of substrate. The purple stippled rectangular box labeled "Study Area" corresponds to the total area sampled during this study.

Classification table of all prey items found in the diet of red snapper at Jakkula, McGrail, Bright, and East Cameron.

Prey Type	Prey Type	Prey Type	Prey Type
Unclassifiable material	Unidentified crustaceans		
Fish	**Crab**	**Shrimp**	**Pelagic Zooplankton**
Unidentified fishes	Unidentified crabs	Unidentified shrimps	Unidentified zooplankton
Family Bregmacerotidae	Family Calappidae	Family Alpheidae	Order Amphipoda
Family Carangidae	*Calappa galloides*	*Alpheus* sp.	Phylum Chaetognatha
Selene setapinnis	Family Leucosiidae	Family Callianassidae	Family Euphausiidae
Family Holocentridae	*Iliacantha* sp.	*Eucalliax* sp.	Order Thecosomata
Holocentrus adscensionis	Superfamily Majoidea	Family Pandalidae	*Cavolinia* sp.
Family Lutjanidae	Family Majidae	*Plesionika* sp.	*Heliconoides inflatus*
Family Mullidae	*Macrocoeloma concavum*	Family Penaeidae	Crab meglaopa
Family Muraenidae	Family Paguridae	*Rimapenaeus* sp.	Order Mysida
Gymnothorax moringa	*Iridopagurus* sp.	*Metapenaeopsis* sp.	
Family Ophichthidae	*Phimochirus* sp.	Family Odontodactylidae	**Benthic Zooplankton**
Family Opistognathidae	Family Palicidae	*Odontodactylus* sp.	Phylum Annelida
Opistognathus aurifrons	*Palicus* sp.	Family Squillidae	Phylum Nematoda
Family Pomacentridae	Family Parthenopidae		
Family Serranidae	*Parthenope agona*	**Lobster**	**Mollusc**
Subfamily Syngnathinae	Family Portunidae	Family Scyllaridae	Class Gastropoda
Family Synodontidae	*Achelous ordwayi*	*Scyllarus chacei*	
Synodus sp.	*Achelous spinicarpus*		**Incidental**
Family Trichiuridae	*Callinectes similis*	**Cephalopod**	Algae
Trichiurus lepturus	Family Pseudorhombilidae	Squids	Anemone
Family Triglidae	*Pseudorhombila quadridentata*		Black Coral
Prionotus sp.	Family Raninidae	**Tunicate**	Rocks
	Raninoides louisianensis	Family Pyrosomatidae	Shark tooth
		Pyrosoma atlanticum	

Percent by dry weight of ten prey categories for all size classes of red snapper at Jakkula Bright, and East Cameron.

Prey Category	Jakkula	Bright	East Cameron
Unclassifiable material	46.81	30.16	37.26
Fish	57.83	61.73	36.61
Crustacean	0.00	0.62	1.00
Crab	7.92	6.34	21.41
Shrimp	2.90	0.74	1.72
Squid	0.09	3.03	0.47
Gastropod	0.10	1.88	0.01
Tunicate	19.68	14.99	12.81
Zooplankton	0.77	0.59	25.94
Incidental	10.70	10.07	0.02

Percent by number of nine prey categories for all size classes of red snapper at Jakkula Bright, and East Cameron. Unclassifiable material was not included because contribution to percent by number cannot be determined.

Prey Category	Jakkula	Bright	East Cameron
Fish	34.17	34.06	12.55
Crustacean	2.07	3.57	4.03
Crab	4.14	7.14	6.94
Shrimp	8.95	2.74	9.09
Squid	2.07	3.15	0.78
Gastropod	5.36	1.66	0.43
Tunicate	12.43	13.31	3.26
Zooplankton	22.52	30.80	62.71
Incidental	8.29	3.57	0.22

Percent frequency of occurrence of nine prey categories for all size classes of red snapper at Jakkula Bright, and East Cameron. Unclassifiable material was not included because contribution to percent frequency of occurrence cannot be determined.

Prey Category	Jakkula	Bright	East Cameron
Fish	60.87	65.38	39.20
Crustacean	4.35	7.69	9.60
Crab	8.70	15.38	20.00
Shrimp	13.04	5.77	13.60
Squid	4.35	6.73	2.40
Gastropod	8.70	3.85	1.60
Tunicate	26.09	30.77	12.00
Zooplankton	30.43	27.88	52.00
Incidental	13.04	7.69	0.80

Percent index of relative importance of nine prey categories for all size classes of red snapper at Jakkula Bright, and East Cameron. Unclassifiable material was not included because contribution to percent index of relative importance cannot be determined.

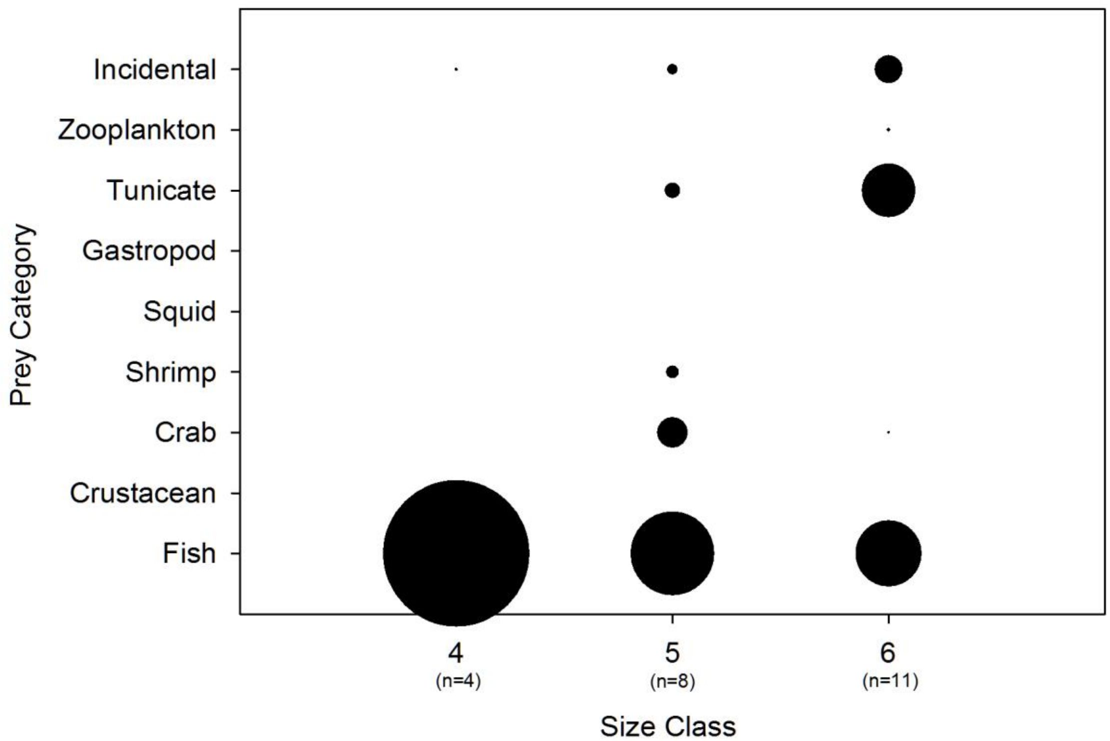
Prey Category	**Jakkula**	**Bright**	**East Cameron**
Fish	72.54	74.30	25.71
Crustacean	0.12	0.38	0.64
Crab	1.36	2.46	7.56
Shrimp	2.00	0.24	1.96
Squid	0.12	0.49	0.04
Gastropod	0.62	0.16	0.01
Tunicate	10.85	10.33	2.57
Zooplankton	9.18	10.39	61.50
Incidental	3.21	1.25	0.00

Percent by weight, percent by number, percent frequency of occurrence, and percent index of relative importance of ten prey categories for all size classes of red snapper at McGrail (n=8).

Prey Category	**%W**	**%N**	**%FO**	**%IRI**
Unclassifiable material	40.44			
Fish	82.08	57.48	75.00	91.14
Crustacean	0	0	0	0
Crab	7.21	13.78	25.00	4.57
Shrimp	3.35	6.89	12.50	1.12
Squid	0	0	0	0
Gastropod	0	0	0	0
Tunicate	0	0	0	0
Zooplankton	0.02	10.92	12.50	1.19
Incidental	7.34	10.92	12.50	1.99

Percent by dry weight of nine prey categories found in the diet of size class 4, 5, and 6 red snapper at Jakkula.

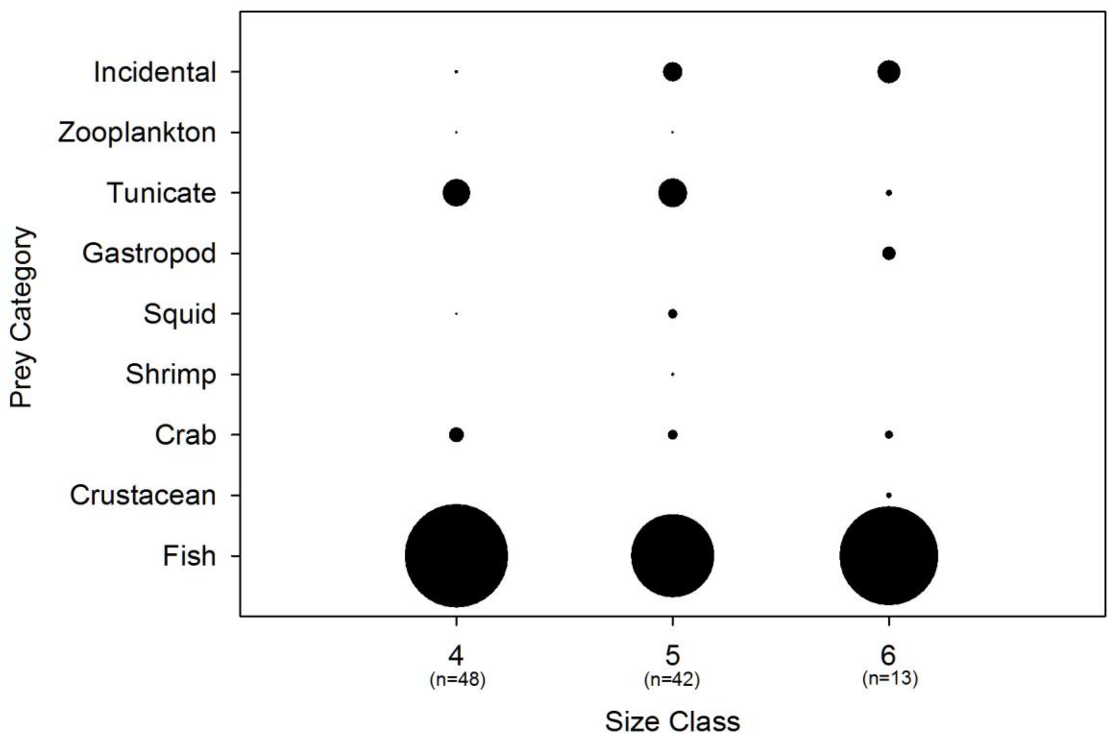
Prey Category	3	4	5	6
Fish	32.41	27.96	30.53	48.60
Crustacean	0	0.47	2.59	0.85
Crab	31.51	26.31	3.93	24.16
Shrimp	4.86	1.44	0.27	0.59
Squid	1.81	0	0	0.04
Gastropod	0	0	0.02	0.01
Tunicate	2.55	4.95	13.61	23.89
Zooplankton	26.79	38.87	49.05	1.85
Incidental	0.07	0	0	0



Percent by dry weight of nine prey categories found in the diet of size class 4, 5, and 6 red snapper at Jakkula. The bubbles represent the proportion of contribution of each prey category.

Percent by dry weight of nine prey categories found in the diet of size class 4, 5, and 6 red snapper at Bright.

Prey Category	**4**	**5**	**6**
Fish	69.30	55.72	66.37
Crustacean	0.05	0.0003	2.62
Crab	9.09	5.70	4.64
Shrimp	0.37	1.28	0
Squid	0.79	5.57	0
Gastropod	0	0.02	8.08
Tunicate	17.98	18.78	3.32
Zooplankton	0.78	0.72	0.12
Incidental	1.65	12.22	14.85



Percent by dry weight of nine prey categories found in the diet of size class 4, 5, and 6 red snapper at Bright. The bubbles represent the proportion of contribution of each prey category.

Percent by dry weight of nine prey categories found in the diet of size class 3, 4, 5, and 6 red snapper at East Cameron.

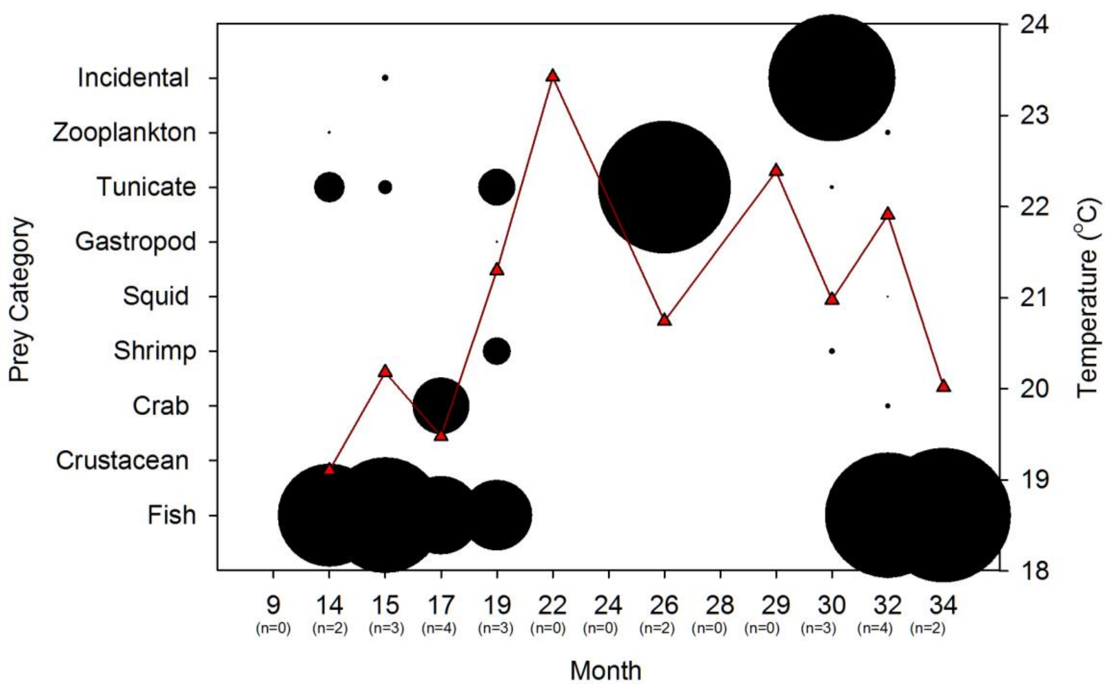
Prey Category	3	4	5	6
Fish	32.41	27.96	30.53	48.60
Crustacean	0	0.47	2.59	0.85
Crab	31.51	26.31	3.93	24.16
Shrimp	4.86	1.44	0.27	0.59
Squid	1.81	0	0	0.04
Gastropod	0	0	0.02	0.01
Tunicate	2.55	4.95	13.61	23.89
Zooplankton	26.79	38.87	49.05	1.85
Incidental	0.07	0	0	0

Similarity percentages (SIMPER) results of prey category contribution to between site dissimilarity in the diet of red snapper for size class 4 and 5. Diss/SD = Dissimilarity/Stand deviation ratio.

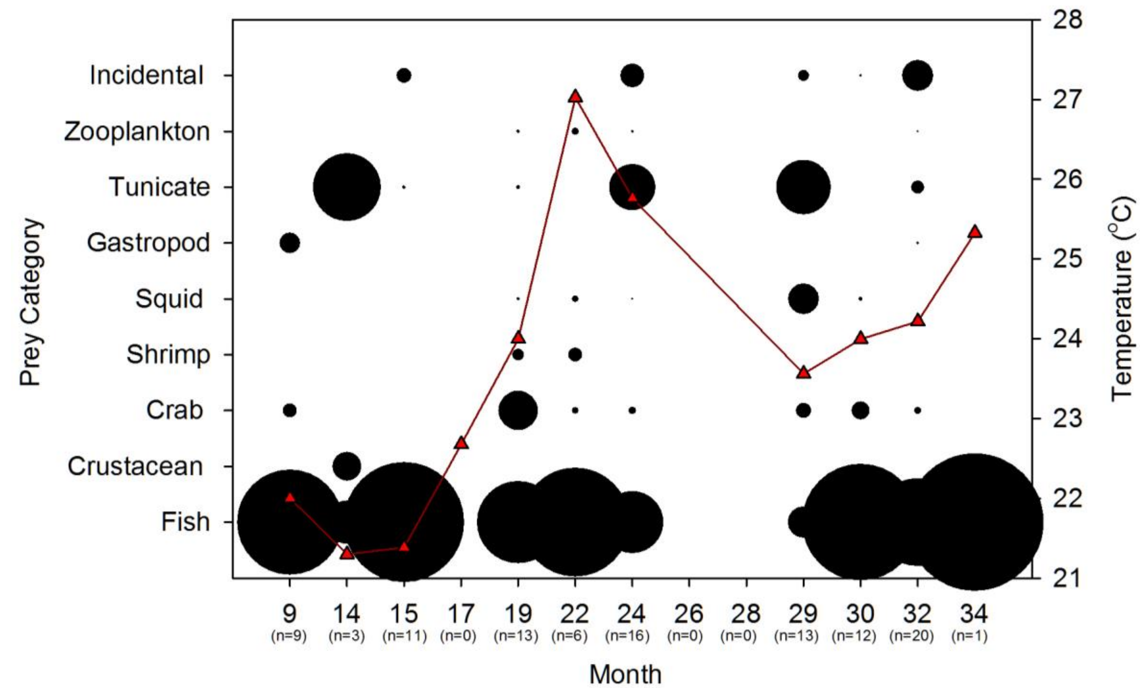
Site	Prey Type	Average Dissimilarity	Diss/SD	% Contribution	% Cumulative Contribution
Size Class 4					
Bright vs. East Cameron		90.19			
	Fishes	41.6	1.19	46.12	46.12
	Zooplankton	17.64	0.68	19.56	65.68
	Crabs	12.75	0.49	14.14	79.82
	Tunicates	12.32	0.5	13.66	93.48
Jakkula vs. East Cameron		90.5			
	Fishes	67.17	2.37	74.22	74.22
	Zooplankton	10.9	0.59	12.05	86.27
	Crabs	7.17	0.38	7.92	94.19
Size Class 5					
Bright vs. East Cameron		90.83			
	Fishes	37.81	1.07	41.62	41.62
	Tunicates	20.33	0.72	22.38	64.01
	Zooplankton	16.99	0.7	18.7	82.71
	Crabs	5.13	0.36	5.64	88.35
	Incidental	4.25	0.3	4.68	93.04
Jakkula vs. East Cameron		94.77			
	Fishes	34.8	0.93	36.72	36.72
	Zooplankton	17.89	0.69	18.88	55.6
	Tunicate	10.31	0.51	10.88	66.48
	Crabs	10	0.42	10.55	77.03
	Shrimps	9.3	0.48	9.81	86.85
	Incidental	7.82	0.35	8.26	95.1

Similarity percentages (SIMPER) results of prey category contribution to between size class dissimilarity in the diet of red snapper caught on East Cameron. Diss/SD = Dissimilarity/Standard deviation ratio.

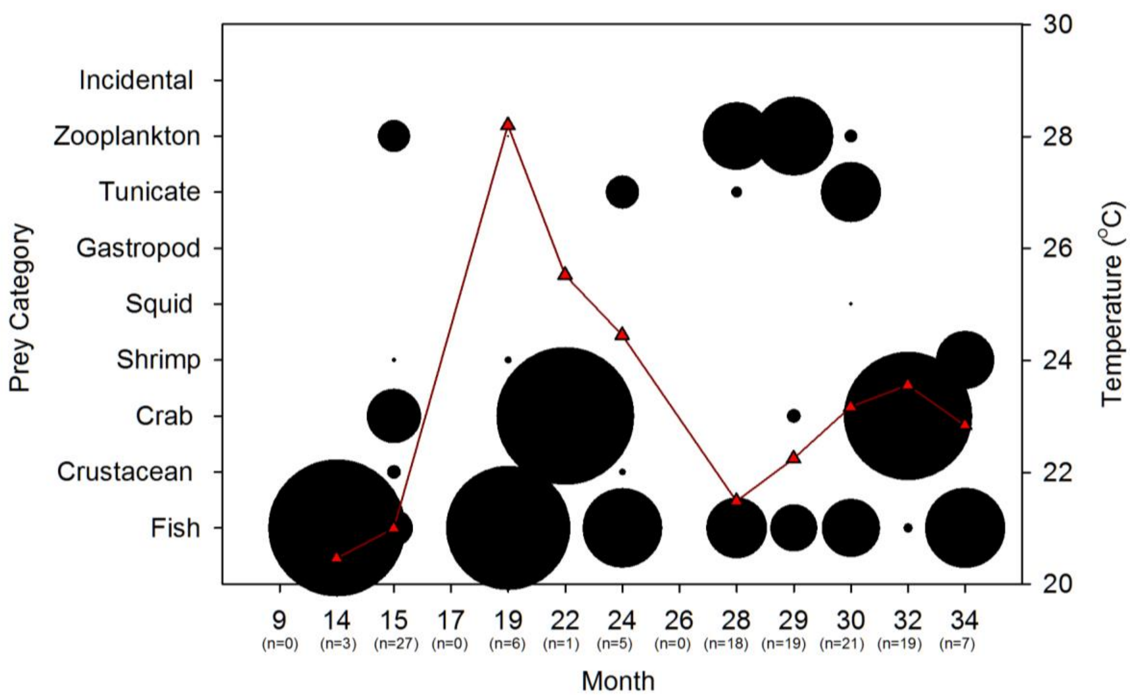
Size Class	Prey Type	Average Dissimilarity	Diss/SD	% Contribution	% Cumulative Contribution
3 vs 5		89.74			
	Zooplankton	29.81	0.99	33.22	33.22
	Fishes	26.21	0.85	29.2	62.42
	Crabs	14.35	0.5	15.99	78.41
	Tunicates	8.69	0.4	9.68	88.09
	Shrimps	5.61	0.33	6.25	94.34
4 vs 6		90.28			
	Fishes	27.85	0.86	30.85	30.85
	Crabs	20.99	0.63	23.25	54.1
	Zooplankton	19.86	0.71	22	76.1
	Tunicates	15.44	0.55	17.1	93.2
5 vs 6		89.44			
	Fishes	28.24	0.86	31.57	31.57
	Zooplankton	23.57	0.8	26.35	57.92
	Tunicates	17.38	0.6	19.43	77.36
	Crabs	15.02	0.52	16.8	94.15



Percent by dry weight of nine prey categories found in the diet of red snapper during each sampling moth at Jakkula plotted against temperature (°C; red triangles and line). The bubbles represent the proportion of contribution of each prey category. Months are numbered sequentially from 9 to 34 (9 = September 2011; 34 = October 2013).



Percent by dry weight of nine prey categories found in the diet of red snapper during each sampling moth at Bright plotted against temperature (°C; red triangles and line). The bubbles represent the proportion of contribution of each prey category. Months are numbered sequentially from 9 to 34 (9 = September 2011**; 34** = October 2013).



Percent by dry weight of nine prey categories found in the diet of red snapper during each sampling moth at East Cameron plotted against temperature (°C; red triangles and line). The bubbles represent the proportion of contribution of each prey category. Months are numbered sequentially from 9 to 34 (9 = September 2011; 34 = October 2013).

Percent by number of 56 prey items for all size classes of red snapper at Jakkula, Bright, and East Cameron. Unclassifiable material was not included because contribution to percent by number cannot be determined.

Prey Type	Jakkula	Bright	East Cameron	Prey Type	Jakkula	Bright	East Cameron
Fish				**Shrimp**			
Unidentified fishes	29.76	23.93	9.22	Unidentified shrimps	1.96	0.96	0.19
Family Bregmacerotidae	3.92	1.86	0.30	*Alpheus* sp.			0.38
Gymnothorax moringa		0.75		*Eucalliax* sp.	1.96		
Holocentrus adscensionis		0.37		*Metapenaeopsis* sp.		0.37	
Family Lutjanidae		1.12		*Odontodactylus* sp.		0.37	
Family Mullidae		0.59		*Rimapenaeus* sp.		0.37	
Family Ophichthidae		0.96	0.50	Family Squillidae	5.89	0.37	7.45
Opistognathus aurifrons		0.37					
Family Pomacentridae		0.37		**Pelagic Zooplankton**			
Prionotus sp.		0.37		Unidentified zooplankton	3.92	9.61	43.45
Selene setapinnis		0.75		Order Amphipoda		0.75	3.58
Family Serranidae		0.37	0.19	Phylum Chaetognatha		0.59	0.38
Subfamily Syngnathinae			0.38	Family Euphausiidae		0.37	
Synodus sp.		0.37		*Cavolinia* sp.	11.29	19.61	16.30
Trichiurus lepturus			0.73	*Heliconoides inflatus*	8.75	2.67	1.50
				Crab megalopa		0.96	1.68
Crab				Order Mysida		0.37	
Unidentified crabs	1.96	1.12	0.69				
Calappa galloides	1.96	1.86	0.19	**Benthic Zooplankton**			
Iliacantha sp.			0.19	Phylum Annelida		0.96	0.64
Iridopagurus sp.		0.37		Phylum Nematoda		1.05	0.30
Superfamily Majoidea			0.19				
Macrocoeloma concavum		0.75		**Incidental**			
Palicus sp.		0.37		Algae		2.24	0.19
Parthenope agona			0.19	Anemone		0.37	
Phimochirus sp.		1.12		Rocks	7.85	0.75	
Family Portunidae			0.19	Shark tooth			0.19
Achelous ordwayi			0.19				
Achelous spinicarpus			2.14	**Unidentified crustaceans**	1.96	3.20	3.37
Callinectes similis			0.38	**Class Gastropoda**	5.07	1.49	0.38
Pseudorhombila quadridentata			0.38	***Scyllarus chacei***			0.19
Raninoides louisianensis			0.19	**Squids**	1.96	2.83	0.69
				Tunicates	11.77	11.93	2.88

Percent frequency of occurrence of 56 prey items for all size classes of red snapper at Jakkula, Bright, and East Cameron. Unclassifiable material was not included because contribution to percent frequency of occurrence cannot be determined.

Prey Type	Jakkula	Bright	East Cameron	Prey Type	Jakkula	Bright	East Cameron
Fish				**Shrimp**			
Unidentified fishes	60.87	54.81	34.13	Unidentified shrimps	4.35	1.92	0.79
Family Bregmacerotidae	4.35	2.88	0.79	*Alpheus* sp.			1.59
Gymnothorax moringa		1.92		*Eucalliax* sp.	4.35		
Holocentrus adscensionis		0.96		*Metapenaeopsis* sp.		0.96	
Family Lutjanidae		2.88		*Odontodactylus* sp.		0.96	
Family Mullidae		0.96		*Rimapenaeus* sp.		0.96	
Family Ophichthidae		1.92	1.59	Family Squillidae	8.70	0.96	11.11
Opistognathus aurifrons		0.96					
Family Pomacentridae		0.96		**Pelagic Zooplankton**			
Prionotus sp.		0.96		Unidentified zooplankton	8.70	13.46	34.92
Selene setapinnis		1.92		Order Amphipoda		1.92	4.76
Family Serranidae		0.96	0.79	Phylum Chaetognatha		0.96	1.59
Subfamily Syngnathinae			1.59	Family Euphausiidae		0.96	
Synodus sp.		0.96		*Cavolinia* sp.	17.39	23.08	26.98
Trichiurus lepturus			1.59	*Heliconoides inflatus*	8.70	3.85	3.17
				Crab megalopa		1.92	4.76
Crab				Order Mysida		0.96	
Unidentified crabs	4.35	2.88	2.38				
Calappa galloides	4.35	4.81	0.79	**Benthic Zooplankton**			
Iliacantha sp.			0.79	Phylum Annelida		1.92	1.59
Iridopagurus sp.		0.96		Phylum Nematoda		0.96	0.79
Superfamily Majoidea			0.79				
Macrocoeloma concavum		1.92		**Incidental**			
Palicus sp.		0.96		Algae		5.77	0.79
Parthenope agona			0.79	Anemone		0.96	
Phimochirus sp.		2.88		Rocks	13.04	1.92	
Family Portunidae			0.79	Shark tooth			0.79
Achelous ordwayi			0.79				
Achelous spinicarpus			7.14	**Unidentified crustaceans**	4.35	7.69	8.73
Callinectes similis			1.59	**Class Gastropoda**	8.70	3.85	1.59
Pseudorhombila quadridentata			1.59	***Scyllarus chacei***			0.79
Raninoides louisianensis			0.26	**Squids**	4.35	6.73	2.38
				Tunicates	26.09	30.77	11.90

Percent index of relative importance of 56 prey items for all size classes of red snapper at Jakkula Bright, and East Cameron. Unclassifiable material was not included because contribution to percent index of relative importance cannot be determined.

Prey Type	Jakkula	Bright	East Cameron
Fish			
Unidentified fishes	75.48	68.83	13.00
Family Bregmacerotidae	0.67	0.14	0.01
Gymnothorax moringa		0.33	
Holocentrus adscensionis		0.02	
Family Lutjanidae		0.20	
Family Mullidae		0.01	
Family Ophichthidae		0.10	0.03
Opistognathus aurifrons		0.02	
Family Pomacentridae		0.03	
Prionotus sp.		0.01	
Selene setapinnis		0.03	
Family Serranidae		0.01	0.01
Subfamily Syngnathinae			0.02
Synodus sp.		0.02	
Trichiurus lepturus			0.05
Crab			
Unidentified crabs	0.16	0.06	0.07
Calappa galloides	0.62	0.63	0.01
Iliacantha sp.			0.01
Iridopagurus sp.		0.01	
Superfamily Majoidea			0.01
Macrocoeloma concavum		0.05	
Palicus sp.		0.01	
Parthenope agona			0.01
Phimochirus sp.		0.08	
Family Portunidae			0.01
Achelous ordwayi			0.01
Achelous spinicarpus			0.64
Callinectes similis			0.03
Pseudorhombila quadridentata			0.03
Raninoides louisianensis			0.01
Shrimp			
Unidentified shrimps	0.29	0.04	0.01
Alpheus sp.			0.02
Eucalliax sp.	0.15		
Metapenaeopsis sp.		0.01	
Odontodactylus sp.		0.01	
Rimapenaeus sp.		0.01	
Family Squillidae	0.80	0.01	3.32
Pelagic Zooplankton			
Unidentified zooplankton	0.52	2.44	61.08
Order Amphipoda		0.03	0.68
Phylum Chaetognatha		0.01	0.02
Family Euphausiidae		0.01	
Cavolinia sp.	3.08	8.65	17.65
Heliconoides inflatus	1.21	0.20	0.19
Crab megalopa		0.04	0.32
Order Mysida		0.01	
Benthic Zooplankton			
Phylum Annelida		0.03	0.04
Phylum Nematoda		0.02	0.01
Incidental			
Algae		0.90	0.01
Anemone		0.07	
Rocks	3.66	0.06	
Shark tooth			0.01
Unidentified crustaceans	0.13	0.55	1.18
Class Gastropoda	0.68	0.24	0.02
Scyllarus chacei			0.01
Squids	0.14	0.73	0.07
Tunicates	12.41	15.35	1.43

Percent by weight, percent by number, percent frequency of occurrence, and percent index of relative importance of nice prey items for all size classes of red snapper at McGrail (n=8).

Prey Type	%W	%N	%FO	%IRI
Unclassifiable material	39.41			
Fish				
Unidentified fish	59.44	49.18	62.5	85.60
Holocentrus adscensionis	22.07	6.70	12.5	4.53
Crab				
Unidentified crab	2.80	6.70	12.5	1.50
Parthenope agona	4.36	6.70	12.5	1.74
Shrimp				
Plesionika sp.	3.33	6.70	12.5	1.58
Pelagic Zooplankton				
Order Amphipoda	0.02	10.62	12.5	1.68
Incidental				
Black Coral	1.72	6.70	12.5	1.33
Rock	6.26	6.70	12.5	2.04

Percent dry weight of 56 prey items for size class 4, 5, and 6 red snapper at Jakkula.

Prey Type	4	5	6	Prey Type	4	5	6
Fish				**Shrimp**			
Unidentified Fishes	98.47	40.10	43.91	Unidentified Shrimps		6.28	
Family Bregmacerotidae		16.41		*Alpheus* sp.			
Gymnothorax moringa				*Eucalliax* sp.		0.93	
Holocentrus adscensionis				*Metapenaeopsis* sp.			
Family Lutjanidae				*Odontodactylus* sp.			
Family Mullidae				*Rimapenaeus* sp.			
Family Ophichthidae				Family Squillidae		0.53	
Opistognathus aurifrons							
Family Pomacentridae				**Pelagic Zooplankton**			
Prionotus sp.				Unidentified Zooplankton	0.05	0.00	
Selene setapinnis				Order Amphipoda			
Family Serranidae				Phylum Chaetognatha			
Subfamily Syngnathinae				Family Euphausiidae			
Synodus sp.				*Cavolinia* sp.		0.12	0.69
Trichiurus lepturus				*Heliconoides inflatus*			0.91

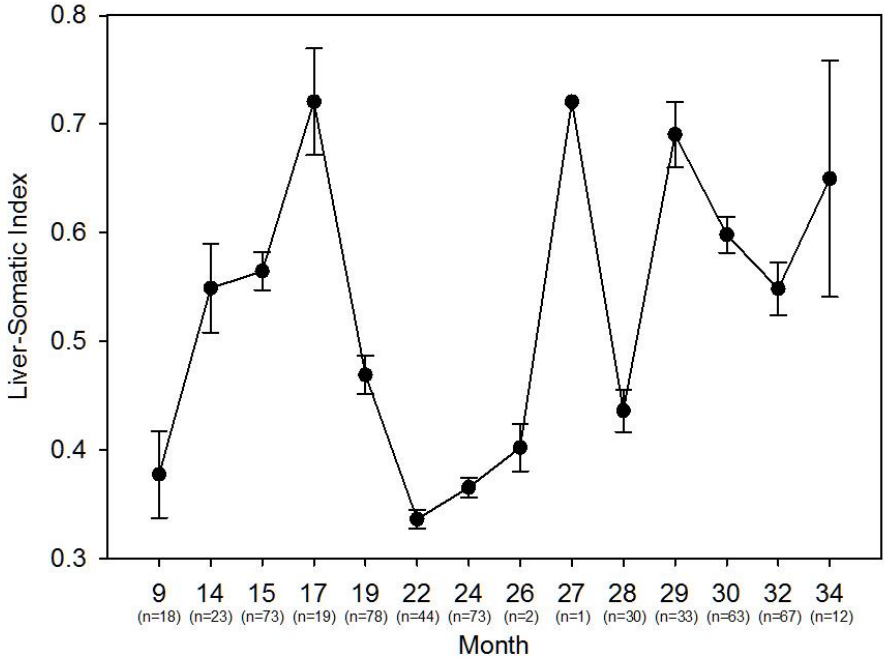
Prey Type	**4**	**5**	**6**	**Prey Type**	**4**	**5**	**6**
				Crab megalopa			
Crab				Order Mysida			
Unidentified Crabs			0.97				
Calappa galloides		19.56		**Benthic Zooplankton**			
Iliacantha sp.				Phylum Annelida			
Iridopagurus sp.				Phylum Nematoda			
Superfamily Majoidea							
Macrocoeloma concavum				**Incidental**			
Palicus sp.				Algae			
Parthenope agona				Anemone			
Phimochirus sp.				Rocks	1.47	6.01	18.03
Family Portunidae				Shark tooth			
Achelous ordwayi							
Achelous spinicarpus				**Unidentified Crustaceans**		0.001	
Callinectes similis				**Class Gastropoda**		0.27	
Pseudorhombila quadridentata				***Scyllarus chacei***			
Raninoides louisianensis				**Squids**		0.23	
				Tunicates		9.54	35.47

Percent dry weight of 56 prey items for size class 4, 5, and 6 red snapper at Bright.

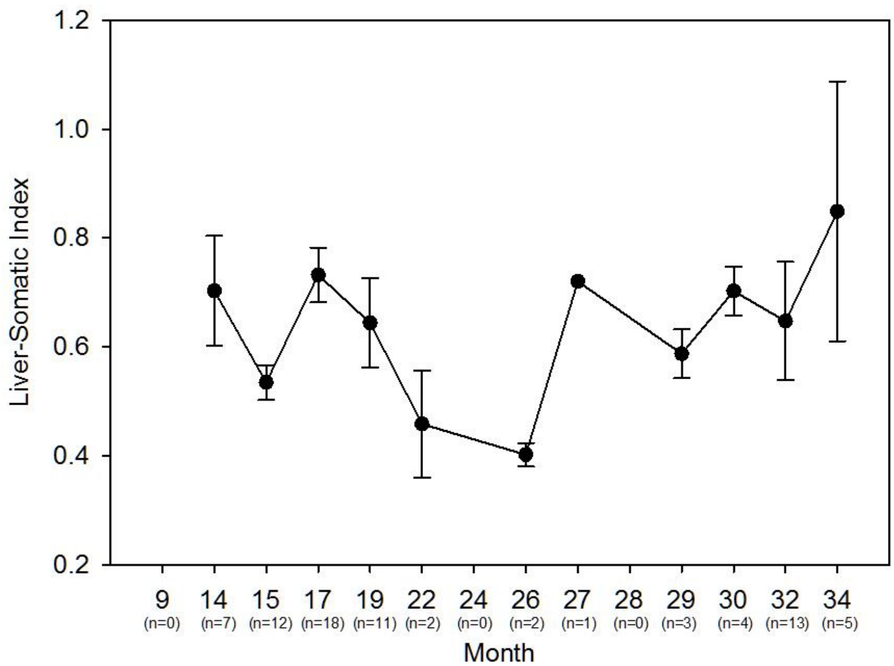
Prey Type	**4**	**5**	**6**	**Prey Type**	**4**	**5**	**6**
Fish				**Shrimp**			
Unidentified Fishes	43.26	40.99	47.98	Unidentified Shrimps	0.04		
Family Bregmacerotidae	2.78			*Alpheus sp.*			
Gymnothorax moringa		8.87	16.24	*Eucalliax sp.*			
Holocentrus adscensionis	3.75			*Metapenaeopsis sp.*	0.32		
Family Lutjanidae	10.31			*Odontodactylus sp.*		0.56	
Family Mullidae		0.28		*Rimapenaeus sp.*		0.70	
Family Ophichthidae		3.70		Family Squillidae	0.01		
Opistognathus aurifrons	3.07						
Family Pomacentridae	5.22			**Pelagic Zooplankton**			
Prionotus sp.	1.15			Unidentified Zooplankton	0.22	0.04	
Selene setapinnis	0.12	0.17		Order Amphipoda		0.002	
Family Serranidae		0.41		Phylum Chaetognatha		0.01	
Subfamily Syngnathinae				Family Euphausiidae	0.01		
Synodus sp.		1.79		*Cavolinia sp.*	0.51	0.54	0.11
Trichiurus lepturus				*Heliconoides inflatus*	0.02	0.07	
				Crab megalopa	0.04	0.004	
				Order Mysida	0.002		

Prey Type	**4**	**5**	**6**	**Prey Type**	**4**	**5**	**6**
Crab							
Unidentified Crabs	0.06	0.05		**Benthic Zooplankton**			
Calappa galloides	5.16	5.35	4.49	Phylum Annelida	0.01		
Iliacantha sp.				Phylum Nematoda		0.05	
Iridopagurus sp.	0.04						
Superfamily Majoidea				**Incidental**			
Macrocoeloma concavum	2.21	0.23		Algae	1.54	4.76	14.00
Palicus sp.	0.08			Anemone		7.32	
Parthenope agona				Rock	0.09		3.60
Phimochirus sp.	1.41			Shark tooth			
Family Portunidae							
Achelous ordwayi				**Unidentified Crustaceans**	0.05	0.0003	2.54
Achelous spinicarpus				**Class Gastropoda**		0.02	7.82
Callinectes similis				***Scyllarus chacei***			
Pseudorhombila quadridentata				**Squids**	0.78	5.51	
Raninoides louisianensis				**Tunicates**	17.78	18.57	3.21

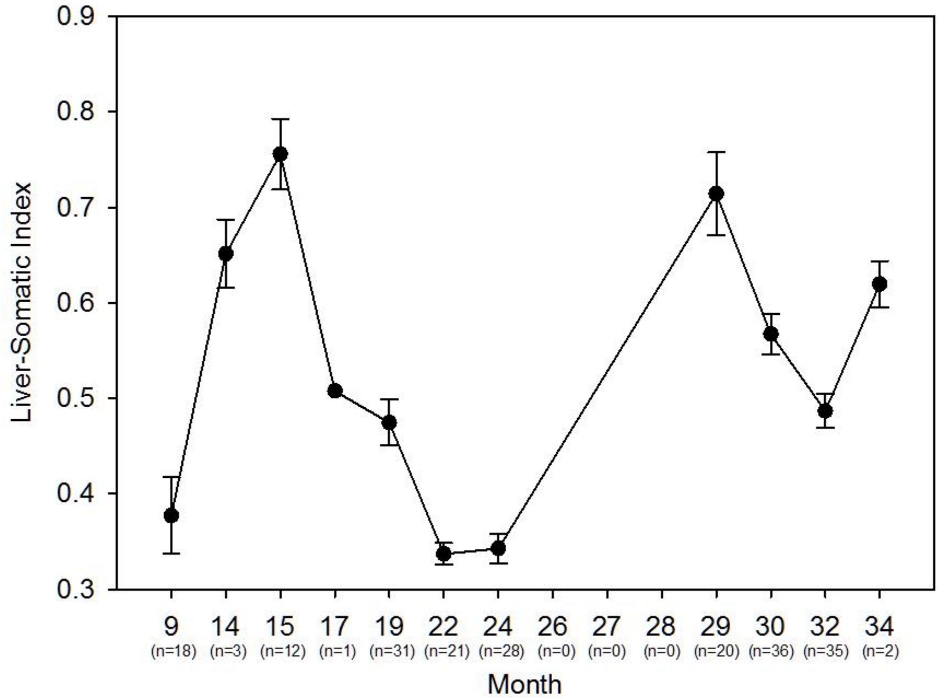
APPENDIX B: CHAPTER 2 SUPPLEMENTARY DATA



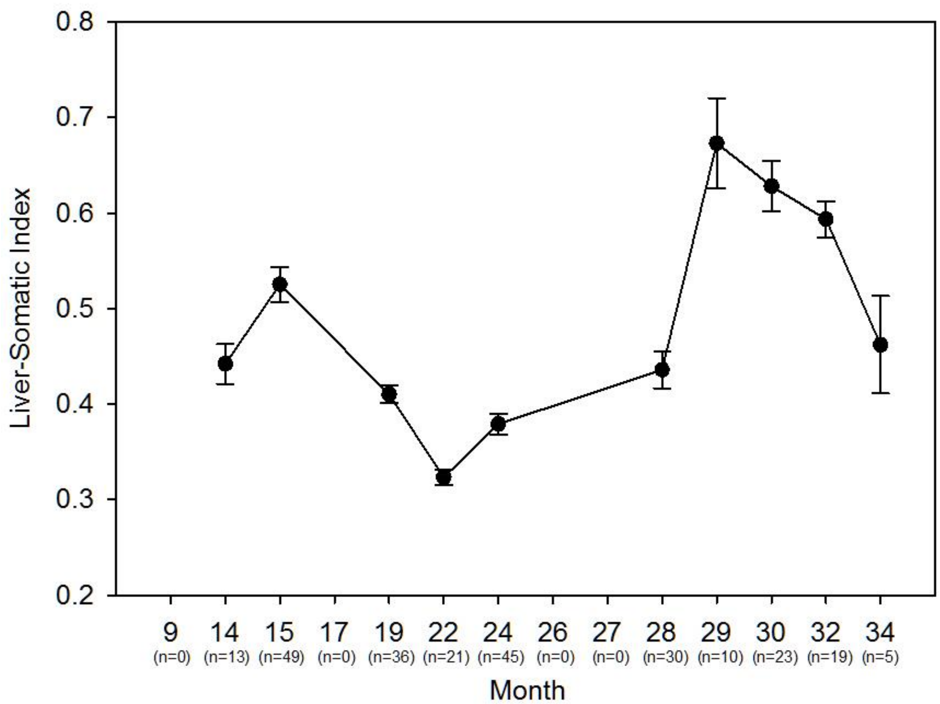
Monthly means for the liver-somatic index of red snapper at Jakkula, Bright, and East Cameron (n=536). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



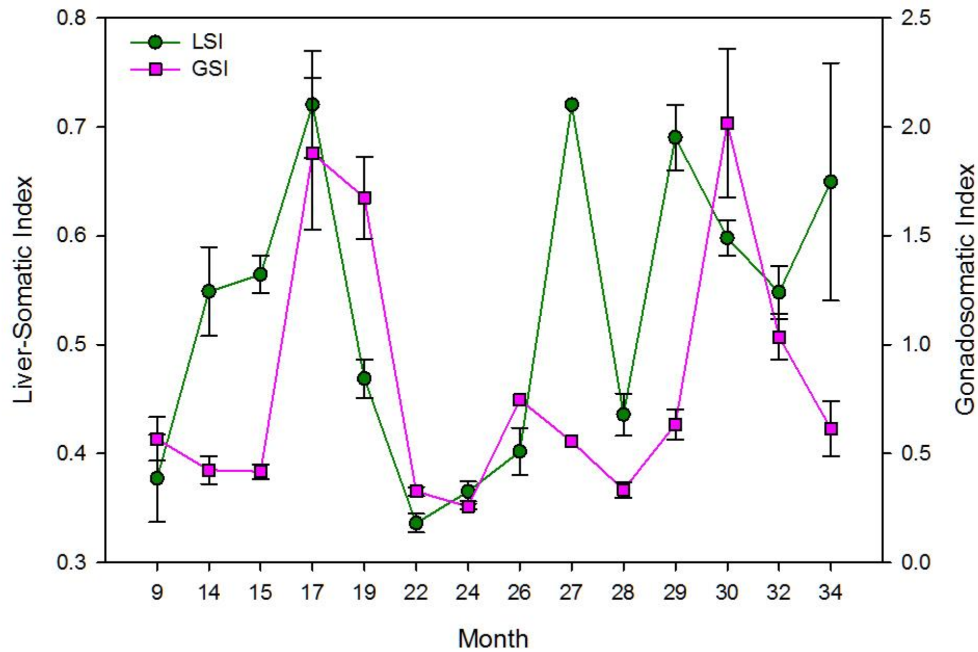
Monthly means for the liver-somatic index of red snapper at Jakkula (n=78). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



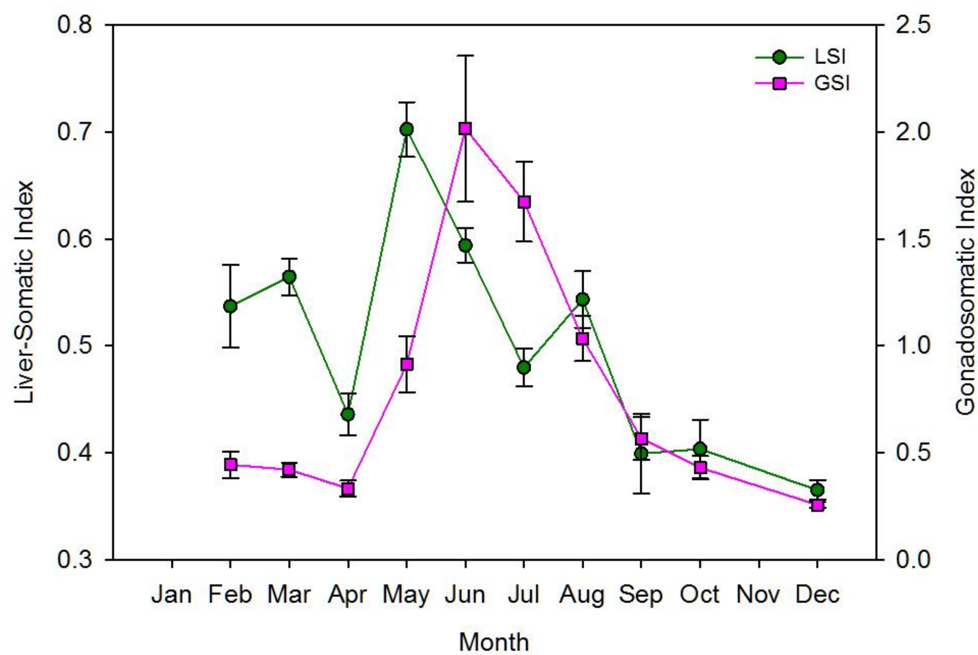
Monthly means for the liver-somatic index of red snapper at Bright (n=207). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



Monthly means for the liver-somatic index of red snapper at East Cameron (n=251). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



Monthly means for the liver-somatic index (n=536; green circles and line) and gonadosomatic index (n=111; pink squares and line) of red snapper at Jakkula, Bright, and East Cameron. Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



The combined monthly means of all years for the liver-somatic index (n=536; green circles and line) and gonadosomatic index (n=111; pink squares and line) of red snapper at Jakkula, Bright, and East Cameron. Vertical lines represent ± standard error of the monthly means.

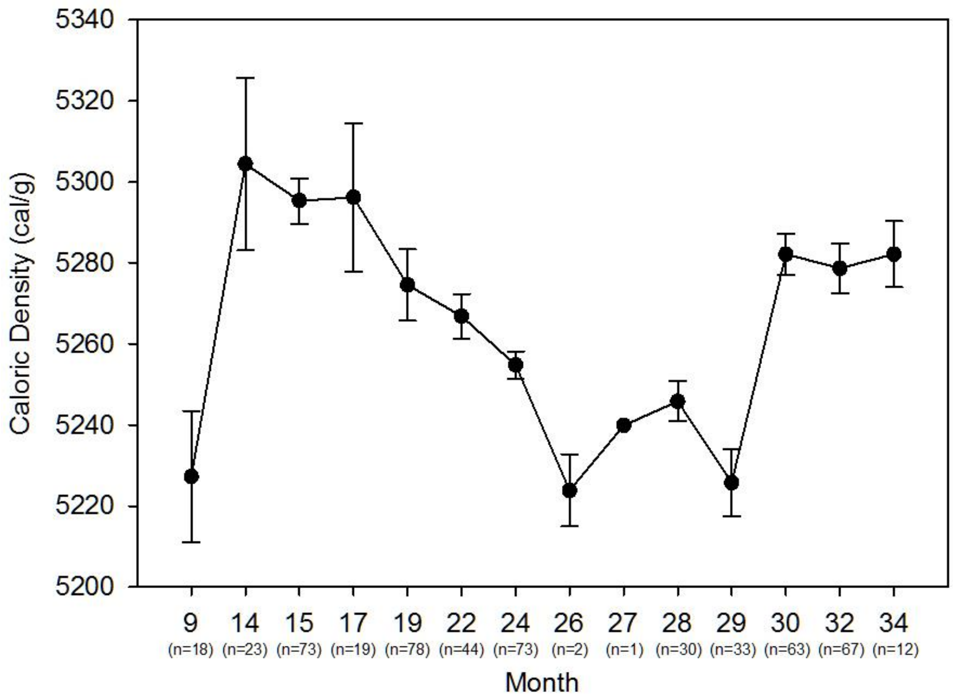
Least Square Means estimates of the liver-somatic index for red snapper at Jakkula, Bright, and East Cameron. SC=Size Class.

Effect	Site	Sex	SC	Estimate	Standard Error	DF	t Value	Pr > |t|
Site	Bright			-0.6352	0.02571	518	-24.71	<.0001
Site	East Cameron			-0.7576	0.01708	518	-44.36	<.0001
Site	Jakkula			-0.7397	0.03916	518	-18.89	<.0001
Sex		F		-0.6214	0.0202	518	-30.76	<.0001
Sex		M		-0.8002	0.02111	518	-37.91	<.0001
SC			4	-0.6699	0.02908	518	-23.04	<.0001
SC			5	-0.7407	0.02072	518	-35.74	<.0001
SC			6	-0.7219	0.02793	518	-25.84	<.0001
Site*Sex	Bright	F		-0.5089	0.03735	518	-13.63	<.0001
Site*Sex	Bright	M		-0.7614	0.02743	518	-27.76	<.0001
Site*Sex	East Cameron	F		-0.7513	0.02501	518	-30.04	<.0001
Site*Sex	East Cameron	M		-0.7639	0.02267	518	-33.69	<.0001
Site*Sex	Jakkula	F		-0.604	0.04458	518	-13.55	<.0001
Site*Sex	Jakkula	M		-0.8754	0.05537	518	-15.81	<.0001
Site*Sex	Bright		4	-0.6718	0.02762	518	-24.32	<.0001
Site*Sex	Bright		5	-0.6799	0.0296	518	-22.97	<.0001
Site*Sex	Bright		6	-0.5538	0.06234	518	-8.88	<.0001
Site*Sex	East Cameron		4	-0.5959	0.03528	518	-16.89	<.0001
Site*Sex	East Cameron		5	-0.8045	0.02635	518	-30.53	<.0001
Site*Sex	East Cameron		6	-0.8723	0.02702	518	-32.29	<.0001
Site*Sex	Jakkula		4	-0.742	0.07766	518	-9.55	<.0001
Site*Sex	Jakkula		5	-0.7376	0.05084	518	-14.51	<.0001
Site*Sex	Jakkula		6	-0.7396	0.05101	518	-14.5	<.0001
SC*Sex		F	4	-0.6014	0.03777	518	-15.92	<.0001
SC*Sex		F	5	-0.6289	0.02777	518	-22.65	<.0001
SC*Sex		F	6	-0.634	0.0378	518	-16.77	<.0001
SC*Sex		M	4	-0.7385	0.03574	518	-20.66	<.0001
SC*Sex		M	5	-0.8525	0.02892	518	-29.48	<.0001
SC*Sex		M	6	-0.8098	0.03564	518	-22.72	<.0001

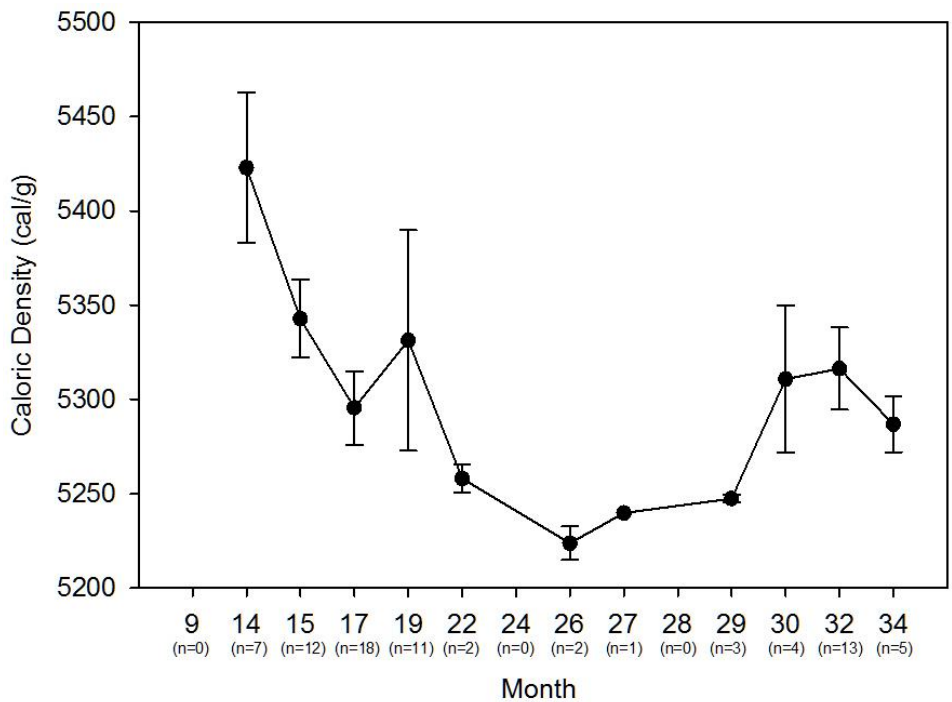
Differences of Least Square Means for the liver-somatic index of red snapper at Jakkula, Bright, and East Cameron. SC= Size Class.

Effect	Site	Sex	SC	Site	Sex	SC	Estimate	Standard Error	DF	t Value	Pr > |t|
Site	Bright			East Cameron			0.1224	0.03121	518	3.92	<.0001
Site	Bright			Jakkula			0.1046	0.04944	518	2.12	0.0349
Site	East Cameron			Jakkula			-0.01786	0.04272	518	-0.42	0.676
Sex		F			M		0.1788	0.02688	518	6.65	<.0001
SC			4			5	0.07079	0.03532	518	2	0.0455
SC			4			6	0.05197	0.03971	518	1.31	0.1912
SC			5			6	-0.01883	0.03358	518	-0.56	0.5752
Site*Sex	Bright	F		Bright	M		0.2525	0.04063	518	6.21	<.0001
Site*Sex	Bright	F		East Cameron	F		0.2424	0.04588	518	5.28	<.0001
Site*Sex	Bright	F		East Cameron	M		0.2549	0.04347	518	5.86	<.0001
Site*Sex	Bright	F		Jakkula	F		0.09513	0.06065	518	1.57	0.1174
Site*Sex	Bright	F		Jakkula	M		0.3665	0.06813	518	5.38	<.0001
Site*Sex	Bright	M		East Cameron	F		-0.01007	0.03715	518	-0.27	0.7864
Site*Sex	Bright	M		East Cameron	M		0.002443	0.03586	518	0.07	0.9457
Site*Sex	Bright	M		Jakkula	F		-0.1574	0.05434	518	-2.9	0.0039
Site*Sex	Bright	M		Jakkula	M		0.114	0.06424	518	1.77	0.0765
Site*Sex	East Cameron	F		East Cameron	M		0.01251	0.03336	518	0.38	0.7077
Site*Sex	East Cameron	F		Jakkula	F		-0.1473	0.05069	518	-2.91	0.0038
Site*Sex	East Cameron	F		Jakkula	M		0.1241	0.06087	518	2.04	0.042
Site*Sex	East Cameron	M		Jakkula	F		-0.1598	0.05037	518	-3.17	0.0016
Site*Sex	East Cameron	M		Jakkula	M		0.1116	0.05979	518	1.87	0.0626
Site*Sex	Jakkula	F		Jakkula	M		0.2714	0.06304	518	4.31	<.0001
Site*SC	Bright		4	Bright		5	0.008131	0.03883	518	0.21	0.8342
Site*SC	Bright		4	Bright		6	-0.118	0.06711	518	-1.76	0.0792
Site*SC	Bright		4	East Cameron		4	-0.07587	0.04436	518	-1.71	0.0878
Site*SC	Bright		4	East Cameron		5	0.1327	0.03829	518	3.47	0.0006
Site*SC	Bright		4	East Cameron		6	0.2005	0.03934	518	5.1	<.0001
Site*SC	Bright		4	Jakkula		4	0.07022	0.0848	518	0.83	0.408
Site*SC	Bright		4	Jakkula		5	0.06584	0.06042	518	1.09	0.2763
Site*SC	Bright		4	Jakkula		6	0.06775	0.06106	518	1.11	0.2677
Site*SC	Bright		5	Bright		6	-0.1262	0.06793	518	-1.86	0.0639
Site*SC	Bright		5	East Cameron		4	-0.084	0.04578	518	-1.83	0.0671
Site*SC	Bright		5	East Cameron		5	0.1246	0.03956	518	3.15	0.0017
Site*SC	Bright		5	East Cameron		6	0.1924	0.04063	518	4.74	<.0001

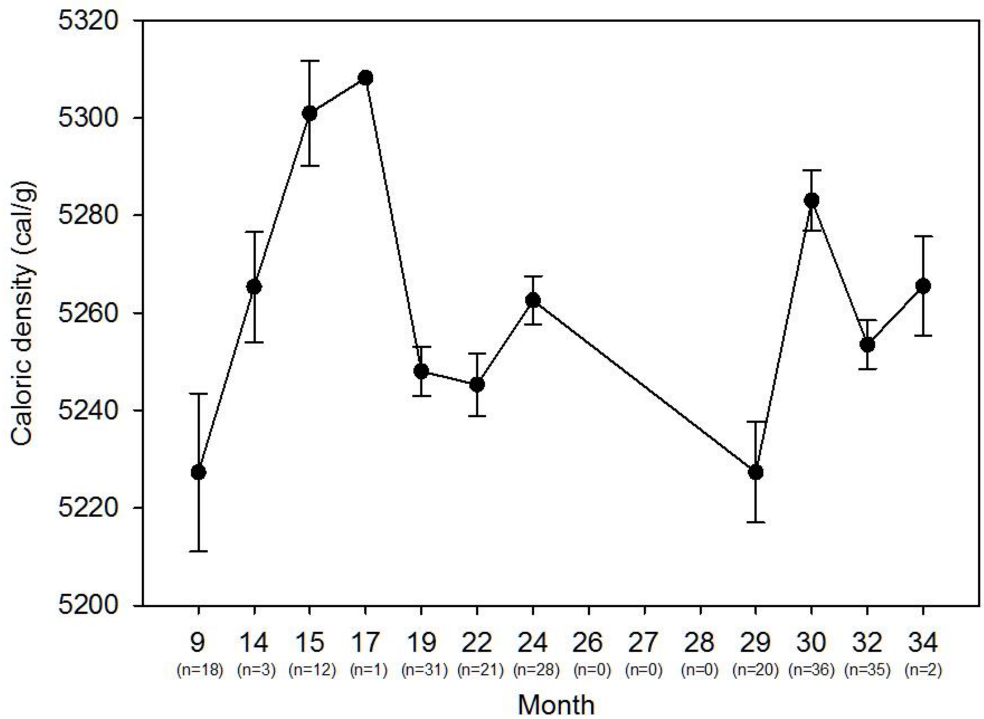
Site*SC	Bright		5	Jakkula		4	0.06209	0.08474	518	0.73	0.4641
Site*SC	Bright		5	Jakkula		5	0.05771	0.06088	518	0.95	0.3436
Site*SC	Bright		5	Jakkula		6	0.05962	0.06109	518	0.98	0.3295
Site*SC	Bright		6	East Cameron		4	0.04216	0.07204	518	0.59	0.5586
Site*SC	Bright		6	East Cameron		5	0.2508	0.06843	518	3.67	0.0003
Site*SC	Bright		6	East Cameron		6	0.3186	0.06792	518	4.69	<.0001
Site*SC	Bright		6	Jakkula		4	0.1883	0.1003	518	1.88	0.0612
Site*SC	Bright		6	Jakkula		5	0.1839	0.0805	518	2.28	0.0228
Site*SC	Bright		6	Jakkula		6	0.1858	0.08208	518	2.26	0.024
Site*SC	East Cameron		4	East Cameron		5	0.2086	0.04435	518	4.7	<.0001
Site*SC	East Cameron		4	East Cameron		6	0.2764	0.04496	518	6.15	<.0001
Site*SC	East Cameron		4	Jakkula		4	0.1461	0.08571	518	1.7	0.0889
Site*SC	East Cameron		4	Jakkula		5	0.1417	0.06208	518	2.28	0.0228
Site*SC	East Cameron		4	Jakkula		6	0.1436	0.06217	518	2.31	0.0213
Site*SC	East Cameron		5	East Cameron		6	0.06778	0.03734	518	1.82	0.0701
Site*SC	East Cameron		5	Jakkula		4	-0.06253	0.08207	518	-0.76	0.4464
Site*SC	East Cameron		5	Jakkula		5	-0.06691	0.05769	518	-1.16	0.2467
Site*SC	East Cameron		5	Jakkula		6	-0.065	0.05786	518	-1.12	0.2618
Site*SC	East Cameron		6	Jakkula		4	-0.1303	0.08155	518	-1.6	0.1107
Site*SC	East Cameron		6	Jakkula		5	-0.1347	0.05699	518	-2.36	0.0185
Site*SC	East Cameron		6	Jakkula		6	-0.1328	0.05728	518	-2.32	0.0208
Site*SC	Jakkula		4	Jakkula		5	-0.00437	0.08872	518	-0.05	0.9607
Site*SC	Jakkula		4	Jakkula		6	-0.00247	0.08805	518	-0.03	0.9777
Site*SC	Jakkula		5	Jakkula		6	0.001909	0.06501	518	0.03	0.9766
SC*Sex		F	4		F	5	0.02758	0.0462	518	0.6	0.5507
SC*Sex		F	4		F	6	0.03265	0.05432	518	0.6	0.548
SC*Sex		F	4		M	4	0.1371	0.045	518	3.05	0.0024
SC*Sex		F	4		M	5	0.2511	0.04928	518	5.1	<.0001
SC*Sex		F	4		M	6	0.2084	0.0528	518	3.95	<.0001
SC*Sex		F	5		F	6	0.005066	0.04606	518	0.11	0.9125
SC*Sex		F	5		M	4	0.1095	0.04528	518	2.42	0.0159
SC*Sex		F	5		M	5	0.2235	0.03868	518	5.78	<.0001
SC*Sex		F	5		M	6	0.1808	0.04547	518	3.98	<.0001
SC*Sex		F	6		M	4	0.1045	0.05027	518	2.08	0.0382
SC*Sex		F	6		M	5	0.2185	0.04683	518	4.67	<.0001
SC*Sex		F	6		M	6	0.1757	0.04772	518	3.68	0.0003
SC*Sex		M	4		M	5	0.114	0.04356	518	2.62	0.0091
SC*Sex		M	4		M	6	0.07128	0.0484	518	1.47	0.1415
SC*Sex		M	5		M	6	-0.04272	0.04361	518	-0.98	0.3277



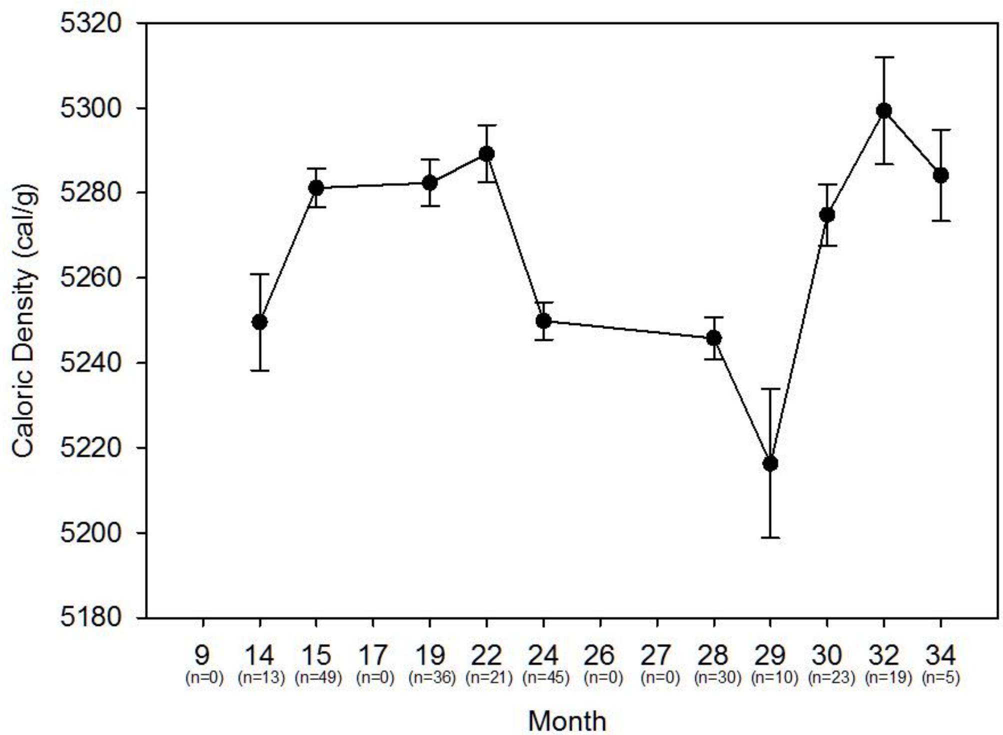
Monthly means for caloric density (cal/g) of red snapper at Jakkula, Bright, and East Cameron (n=536). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



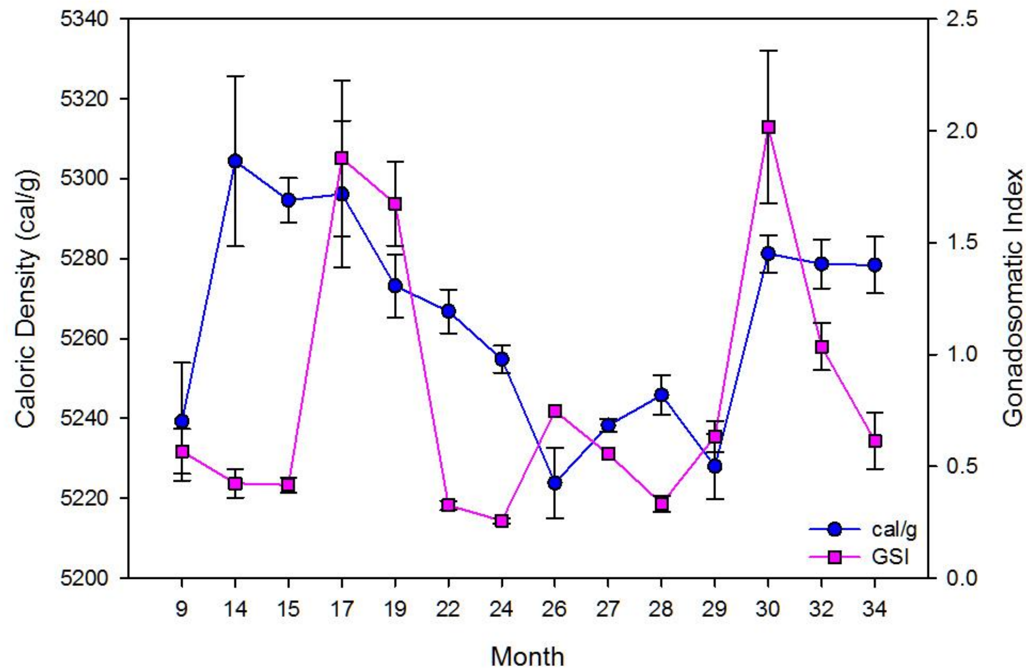
Monthly means for caloric density (cal/g) of red snapper of red snapper at Jakkula (n=78). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



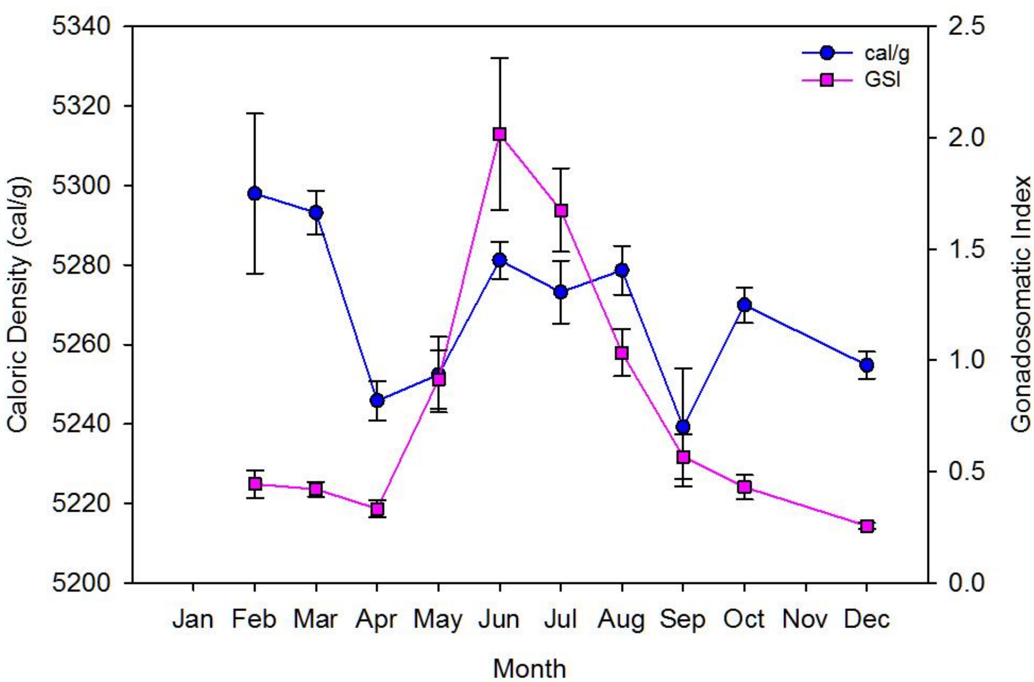
Monthly means for caloric density (cal/g) of red snapper at Bright (n=207). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



Monthly means for caloric density (cal/g) of red snapper at East Cameron (n=251). Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



Monthly means for caloric density (cal/g; n=536; blue circles and line) and gonadosomatic index (n=111; pink squares and line) of red snapper at Jakkula, Bright, and East Cameron. Months are numbered sequentially from 9 to 34 (9 = September 2011; 60 = October 2013). Vertical lines represent ± standard error of the monthly means.



The combined monthly means of all years for caloric density (cal/g; n=536; blue circles and line) and gonadosomatic index (n=111; pink squares and line) of red snapper at Jakkula, Bright, and East Cameron. Vertical lines represent ± standard error of the monthly means.

Least Square Means estimates of caloric density (cal/g) for red snapper at Jakkula, Bright, and East Cameron. SC=Size Class.

Effect	Site	Sex	SC	Estimate	Standard Error	DF	t Value	Pr > |t|
Site	Bright			5261.42	4.9398	518	1065.1	<.0001
Site	East Cameron			5269.04	3.2817	518	1605.58	<.0001
Site	Jakkula			5295.2	7.5245	518	703.72	<.0001
Sex		F		5275.17	3.8816	518	1359.02	<.0001
Sex		M		5275.27	4.0558	518	1300.66	<.0001
SC			4	5258.31	5.588	518	940.99	<.0001
SC			5	5265.46	3.9822	518	1322.27	<.0001
SC			6	5301.89	5.3672	518	987.83	<.0001
Site*Sex	Bright	F		5256.71	7.1769	518	732.45	<.0001
Site*Sex	Bright	M		5266.13	5.2706	518	999.15	<.0001
Site*Sex	East Cameron	F		5263.55	4.8066	518	1095.07	<.0001
Site*Sex	East Cameron	M		5274.54	4.357	518	1210.59	<.0001
Site*Sex	Jakkula	F		5305.25	8.5671	518	619.26	<.0001
Site*Sex	Jakkula	M		5285.14	10.6399	518	496.73	<.0001
Site*SC	Bright		4	5253.47	5.3078	518	989.77	<.0001
Site*SC	Bright		5	5258.38	5.6876	518	924.54	<.0001
Site*SC	Bright		6	5272.4	11.9781	518	440.17	<.0001
Site*SC	East Cameron		4	5276.42	6.7796	518	778.28	<.0001
Site*SC	East Cameron		5	5265.91	5.0631	518	1040.06	<.0001
Site*SC	East Cameron		6	5264.8	5.1917	518	1014.08	<.0001
Site*SC	Jakkula		4	5245.03	14.9222	518	351.49	<.0001
Site*SC	Jakkula		5	5272.1	9.7688	518	539.69	<.0001
Site*SC	Jakkula		6	5368.45	9.8013	518	547.73	<.0001
SC*Sex		F	4	5259.62	7.2568	518	724.78	<.0001
SC*Sex		M	4	5256.99	6.8682	518	765.41	<.0001
SC*Sex		F	5	5266.56	5.3357	518	987.05	<.0001
SC*Sex		M	5	5264.37	5.5562	518	947.48	<.0001
SC*Sex		F	6	5299.33	7.2633	518	729.6	<.0001
SC*Sex		M	6	5304.44	6.8481	518	774.59	<.0001

Differences of Least Square Means of caloric density (cal/g) for red snapper at Jakkula, Bright, and East Cameron. SC=Size Class.

Effect	Site	Sex	SC	Site	Sex	SC	Estimate	St. Error	DF	t Value	Pr > |t|
Site	Bright			East Cameron			-7.6269	5.998	518	-1.27	0.2041
Site	Bright			Jakkula			-33.7786	9.4996	518	-3.56	0.0004
Site	East Cameron			Jakkula			-26.1517	8.2081	518	-3.19	0.0015
Sex		F			M		-0.09945	5.1659	518	-0.02	0.9846
SC			4			5	-7.1569	6.786	518	-1.05	0.2921
SC			4			6	-43.5786	7.6299	518	-5.71	<.0001
SC			5			6	-36.4217	6.4519	518	-5.65	<.0001
Site*Sex	Bright	F		Bright	M		-9.4218	7.8081	518	-1.21	0.2281
Site*Sex	Bright	F		East Cameron	F		-6.8416	8.8164	518	-0.78	0.4381
Site*Sex	Bright	F		East Cameron	M		-17.8339	8.3531	518	-2.14	0.0332
Site*Sex	Bright	F		Jakkula	F		-48.5473	11.6539	518	-4.17	<.0001
Site*Sex	Bright	F		Jakkula	M		-28.4316	13.0923	518	-2.17	0.0303
Site*Sex	Bright	M		East Cameron	F		2.5801	7.1394	518	0.36	0.718
Site*Sex	Bright	M		East Cameron	M		-8.4122	6.8913	518	-1.22	0.2228
Site*Sex	Bright	M		Jakkula	F		-39.1255	10.4425	518	-3.75	0.0002
Site*Sex	Bright	M		Jakkula	M		-19.0098	12.3449	518	-1.54	0.1242
Site*Sex	East Cameron	F		East Cameron	M		-10.9923	6.4105	518	-1.71	0.087
Site*Sex	East Cameron	F		Jakkula	F		-41.7057	9.7403	518	-4.28	<.0001
Site*Sex	East Cameron	F		Jakkula	M		-21.59	11.6962	518	-1.85	0.0655
Site*Sex	East Cameron	M		Jakkula	F		-30.7134	9.6782	518	-3.17	0.0016
Site*Sex	East Cameron	M		Jakkula	M		-10.5977	11.488	518	-0.92	0.3567
Site*Sex	Jakkula	F		Jakkula	M		20.1157	12.1132	518	1.66	0.0974
Site*SC	Bright		4	Bright		5	-4.9136	7.4618	518	-0.66	0.5105
Site*SC	Bright		4	Bright		6	-18.9376	12.8951	518	-1.47	0.1426
Site*SC	Bright		4	East Cameron		4	-22.9554	8.5233	518	-2.69	0.0073
Site*SC	Bright		4	East Cameron		5	-12.4431	7.3573	518	-1.69	0.0914
Site*SC	Bright		4	East Cameron		6	-11.3334	7.5595	518	-1.5	0.1344
Site*SC	Bright		4	Jakkula		4	8.4342	16.2944	518	0.52	0.6049
Site*SC	Bright		4	Jakkula		5	-18.6352	11.6106	518	-1.61	0.1091
Site*SC	Bright		4	Jakkula		6	-114.99	11.7338	518	-9.8	<.0001
Site*SC	Bright		5	Bright		6	-14.024	13.054	518	-1.07	0.2832
Site*SC	Bright		5	East Cameron		4	-18.0418	8.7969	518	-2.05	0.0408
Site*SC	Bright		5	East Cameron		5	-7.5295	7.6015	518	-0.99	0.3224
Site*SC	Bright		5	East Cameron		6	-6.4198	7.8076	518	-0.82	0.4113
Site*SC	Bright		5	Jakkula		4	13.3478	16.2834	518	0.82	0.4128

Site*SC	Bright		5	Jakkula		5	-13.7216	11.6986	518	-1.17	0.2414
Site*SC	Bright		5	Jakkula		6	-110.07	11.7384	518	-9.38	<.0001
Site*SC	Bright		6	East Cameron		4	-4.0178	13.8432	518	-0.29	0.7718
Site*SC	Bright		6	East Cameron		5	6.4945	13.1482	518	0.49	0.6216
Site*SC	Bright		6	East Cameron		6	7.6042	13.0508	518	0.58	0.5604
Site*SC	Bright		6	Jakkula		4	27.3718	19.2779	518	1.42	0.1563
Site*SC	Bright		6	Jakkula		5	0.3024	15.4687	518	0.02	0.9844
Site*SC	Bright		6	Jakkula		6	-96.0483	15.7724	518	-6.09	<.0001
Site*SC	East Cameron		4	East Cameron		5	10.5123	8.5213	518	1.23	0.2179
Site*SC	East Cameron		4	East Cameron		6	11.622	8.6399	518	1.35	0.1792
Site*SC	East Cameron		4	Jakkula		4	31.3896	16.4692	518	1.91	0.0572
Site*SC	East Cameron		4	Jakkula		5	4.3201	11.9284	518	0.36	0.7174
Site*SC	East Cameron		4	Jakkula		6	-92.0305	11.9454	518	-7.7	<.0001
Site*SC	East Cameron		5	East Cameron		6	1.1097	7.1741	518	0.15	0.8771
Site*SC	East Cameron		5	Jakkula		4	20.8773	15.77	518	1.32	0.1861
Site*SC	East Cameron		5	Jakkula		5	-6.1921	11.0851	518	-0.56	0.5767
Site*SC	East Cameron		5	Jakkula		6	-102.54	11.1182	518	-9.22	<.0001
Site*SC	East Cameron		6	Jakkula		4	19.7676	15.6707	518	1.26	0.2077
Site*SC	East Cameron		6	Jakkula		5	-7.3018	10.9509	518	-0.67	0.5052
Site*SC	East Cameron		6	Jakkula		6	-103.65	11.006	518	-9.42	<.0001
Site*SC	Jakkula		4	Jakkula		5	-27.0694	17.0472	518	-1.59	0.1129
Site*SC	Jakkula		4	Jakkula		6	-123.42	16.9192	518	-7.29	<.0001
Site*SC	Jakkula		5	Jakkula		6	-96.3507	12.4928	518	-7.71	<.0001
SC*Sex		F	4		M	4	2.6282	8.6465	518	0.3	0.7613
SC*Sex		F	4		F	5	-6.9373	8.8769	518	-0.78	0.4349
SC*Sex		F	4		M	5	-4.7483	9.4696	518	-0.5	0.6163
SC*Sex		F	4		F	6	-39.7066	10.4372	518	-3.8	0.0002
SC*Sex		F	4		M	6	-44.8223	10.1458	518	-4.42	<.0001
SC*Sex		M	4		F	5	-9.5656	8.6998	518	-1.1	0.2721
SC*Sex		M	4		M	5	-7.3765	8.3697	518	-0.88	0.3785
SC*Sex		M	4		F	6	-42.3349	9.6601	518	-4.38	<.0001
SC*Sex		M	4		M	6	-47.4505	9.3011	518	-5.1	<.0001
SC*Sex		F	5		M	5	2.189	7.4331	518	0.29	0.7685
SC*Sex		F	5		F	6	-32.7693	8.85	518	-3.7	0.0002
SC*Sex		F	5		M	6	-37.8849	8.7375	518	-4.34	<.0001
SC*Sex		M	5		F	6	-34.9584	8.9977	518	-3.89	0.0001
SC*Sex		M	5		M	6	-40.074	8.379	518	-4.78	<.0001
SC*Sex		F	6		M	6	-5.1156	9.1693	518	-0.56	0.5771

VITA

Brittany Dawn Schwartzkopf was born in southern California in January of 1988. She grew up as an only child in Loma Linda, California, where she would spend every summer day swimming in her pool, and soon discovered her love for the ocean from her father. She attended Loma Linda Academy for all 12 years of school and graduated from high school in 2006. She then attended the University of California of San Diego in La Jolla, California, graduating with a Bachelor of Science in Ecology, Behavior, and Evolution in March 2010. During her senior year, Brittany had the opportunity to study abroad in Australia at the University of Queensland, St. Lucia, in the Marine Biology and Terrestrial Ecology Program. It was during this program where she first experienced fisheries research and became instantly hooked. After graduation she worked as a marine science instructor for the Mission Bay Aquatic Center in San Diego, CA. She then went on to do an aquarist internship at Mote Marine Laboratory in Sarasota, Florida. It was at Mote Marine Laboratory where Todd Langland told her about a great graduate school opportunity, and in January of 2011, she entered the masters program in the Department of Oceanography and Coastal Sciences at Louisiana State University, under the supervision of Dr. James H. Cowan, Jr. At LSU she served as Chief Scientist for the research project she and four other graduate students were a part of. She is currently a candidate for the degree of Master of Science in the Department of Oceanography and Coastal Sciences, which will be awarded in August 2014. After graduation, Brittany hopes to peruse her professional career in San Diego, California.