Ecological and Fisheries Management Implications of Competition Between Red Snapper and Vermilion Snapper

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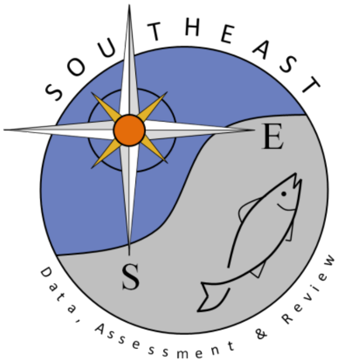
SEDAR45-RD-07

November 2015



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28 April 2014

Acknowledgements

I would first like to express my thanks to Dr. Marcus Drymon. Your guidance has been instrumental in my academic development over the past two years, and your advice and comments regarding this thesis have been invaluable in its completion. Most of all I would like to thank you for your genuine interest in my success and your mentorship both in regards to this thesis and in other aspects of life.

I would also like to thank my advisor Professor Steve Pacala for his thought-provoking comments regarding my thesis and his relaxed attitude towards the thesis process.

I would like to thank Dr. Sean Powers for allowing me access to the resources of his laboratory at the Dauphin Island Sea Lab and giving me the initial idea to study interspecific competition between red snapper and a sympatric reef predator.

I would like to acknowledge all of the members of the Fisheries Ecology Lab for their work in support of this thesis. I would particularly like to thank Aaron Pilnick and Laura Stone for their assistance in completing the trials for my experiment.

I would also like to acknowledge the Princeton University Department of Ecology and Evolutionary Biology, Princeton Environmental Institute, and the Princeton University Office of the Dean of the College for providing funding which made this research possible.

Lastly, I would like to thank my friends and family for their support throughout the thesis process and my undergraduate career. Mom and Dad, thank you for providing me with the best educational opportunities in the world and for encouraging me

whenever Princeton got the best of me. Friends, thank you for being sensitive to the fact that I still had to work after you were finished with your theses.

Abstract

Red (*Lutjanus campechanus*) and vermilion (*Rhomboplites aurorubens*) snapper are two of the dominant species in the northern Gulf of Mexico (GOM) reef fish complex. These two species share similar habitats and diets, but little is known about the way that they interact. It is widely believed among local fishermen that red snapper feed more aggressively than sympatric predators and competitively exclude them from both prey and baits. Thus, there is public concern that the growing red snapper stocks will negatively affect vermilion snapper as well as other species. In this thesis I (1) examined the extent of spatial and dietary overlap between red and vermilion snapper, (2) experimentally compared the feeding behavior of the two species and examined the effects of their feeding interactions, and (3) compared the catchability of the two species. Red and vermilion snapper frequently cohabited reefs in the northern GOM and their diets overlapped with marginal significance despite a lack of samples from smaller red snapper. The experiment results show that red snapper are the dominant forager of the two species, as red snapper fed at a higher rate and more successfully than vermilion snapper. These findings indicate that red and vermilion snapper do compete for prey resources and that increasing red snapper abundance could affect vermilion snapper. Lastly, comparisons of red and vermilion snapper abundance measured using video surveys and catch data revealed that red snapper are indeed more catchable than red snapper. This difference in catchability has immediate implications for catch-based stock assessments.

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Introduction[1]

The natural and artificial reefs of the Gulf of Mexico (GOM) support an ecologically diverse and economically important reef fish population. Two of the dominant species in this reef fish complex are red (*Lutjanus campechanus*) and vermilion (*Rhomboplites aurorubens*) snapper. These two predators are sympatric in the northern Gulf of Mexico and thus share similar habitats and diets. Red snapper is the most economically important fish in the northern GOM, supporting a commercial fishery in excess of $10 million/year and a recreational fishery that has been estimated in value at $3 billion/year (Waters 1996; GMFMC 1999; NMFS, Economics Program). The economic importance of vermilion snapper is similarly high with a commercial fishery in the GOM that has exceeded $8 million/year and a recreational fishery comparable to that of red snapper (NMFS, Economics Program). The vermilion snapper recreational fishery recently has been increasing in importance as red snapper seasons have been shortened (personal communications with charter captains).

Both red and vermilion snapper stocks are heavily exploited. In 2003 the GOM vermilion snapper stock was classified as "overfished" and "undergoing overfishing" (SEDAR 2006). Vermilion snapper stocks have since recovered and are no longer classified as "overfished" or experiencing "overfishing" (SEDAR 2011). Conversely, as of the most recent stock assessment in 2013, the GOM red snapper

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[1] Portions of this section are modified from Davis (2013).

stock remains classified as “overfished.” However, due to increasingly stringent regulation in recent years, “overfishing” of red snapper has stopped in the GOM and the stock is showing signs of recovery (SEDAR 2009; SEDAR 2013).

As red snapper stocks rebuild, red snapper abundance has increased throughout the northern GOM, while vermilion snapper stocks have remained fairly constant (Figure 1). Red snapper stocks are estimated to be at 37% of their target level, and the stock is expected to increase until 2032 when red snapper spawning potential is expected to have reached a sustainable level (SEDAR 2009). As red snapper abundance increases, the potential for interaction with vermilion snapper will subsequently increase; as such, knowing how red and vermilion snapper partition resources, particularly food and shelter, is imperative. It has been widely recognized that ecosystem-level interactions that influence populations of species must be considered in order to improve fisheries management, yet little is known about the way that these two important species interact and partition resources (Browman & Stergiou 2004; NMFS Strategic Plan 2004-2007). The following thesis will focus on one aspect of resource partitioning: how red and vermilion snapper partition food. These species’ interactions and comparative feeding behaviors are not only ecologically important, but also could have important implications for catch-based stock assessments.

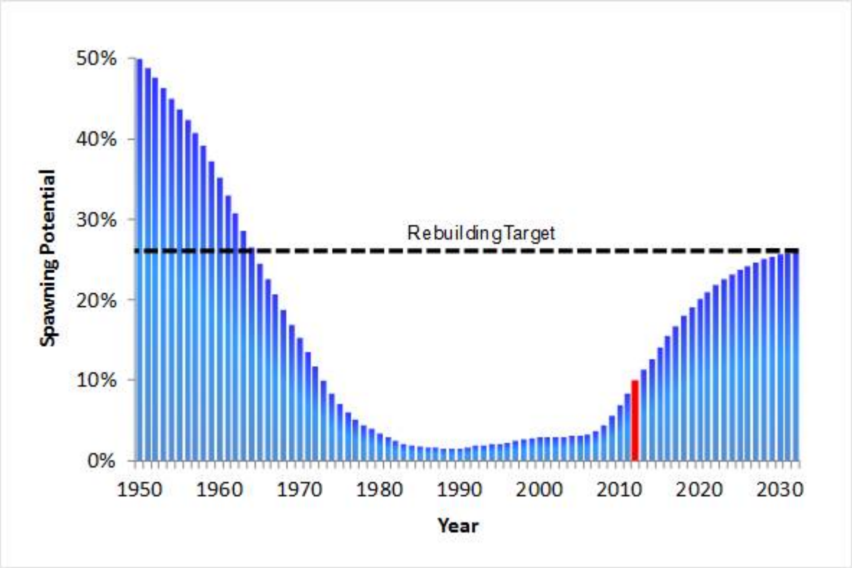

Fig. 1. Past and projected spawning potential of red snapper in the GOM. Spawning potential represents the number of eggs produced by the stock vs. the number that would be produced by an unfished stock. From: NMFS (2013).

Objectives

The objectives of this thesis are threefold:

1) *Examine the extent of competition between red and vermilion snapper for shared food resources*

To determine the extent of competition between these two fish, it is first necessary to establish the degree of spatial overlap between the two species. Dietary overlap between these two species would be irrelevant if they do not usually cohabit reefs. If a high degree of spatial overlap is established, then it is appropriate to examine the extent of dietary overlap between the two species. While diet studies have been conducted for each of these species individually, no work has been published specifically examining the dietary overlap between these species in regions where they co-occur.

2) *Examine how red and vermilion snapper feeding behavior, particularly feeding aggression, compare, and determine if either species negatively affects the other's ability to feed via exploitative or interference competition.*

It is widely believed among fishermen in the northern GOM that red snapper feed more aggressively than sympatric predator species and exploitatively out-compete those other species prey (GMFMC, Public Testimony). Feeding aggression in this context refers to rate of feeding and caution level when approaching potential prey. Due to this perception, there is public concern that red snapper will negatively impact the abundance of sympatric species as red snapper stocks rebuild.

3) *Compare the catchability of each species.*

The aforementioned perception that red snapper are more aggressive than other fish calls into question potential differences in catchability between the two species. Furthermore, many believe that red snapper feed so aggressively that it becomes harder to catch any other species when red snapper are present, as red snapper beat other species to the hook (GMFMC, Public Testimony). Differences in aggression may translate to differences in catchability, as the more aggressive fish would approach baits more quickly and be less cautious to take them. Such differences could subsequently confound stock assessments based on both fisheries-dependent and fisheries-independent catch data. For instance, if red snapper were more catchable than vermilion snapper, then a disproportionate number of red snapper would be caught relative to vermilion snapper at sites they cohabited. As a result, stock assessments for vermilion snapper may be underestimated, or stock assessments for red snapper may be inflated. Furthermore, such differences in catchability could negatively impact commercial and recreational fisheries for the less catchable species. Fishermen may have less success catching the alternative species if the more catchable species is present. This phenomenon would have especially negative impacts in the case of long season closures for the more catchable species, as many fishermen argue is the case with red snapper.

Relevant concepts and literature

The principles of competitive exclusion (Hardin 1960) and resource partitioning (Schoener 1974) are essential to quantifying competition between red and vermilion snapper. According to the competitive exclusion principle, originally known as "Gause's principle" (Gause 1934), vermilion and red snapper could not coexist as true competitors; if either species has any advantage, that species would outcompete and eventually exclude the other, unless the species undergo niche differentiation. Competing species may mitigate competition by shifting into different ecological niches via evolutionary and behavioral processes, thus resulting in resource partitioning among the competing species. The competitive exclusion principle and subsequent niche differentiation are fundamental concepts of evolutionary biology and these phenomena are credited with the causation of most of the world's biodiversity. However, more recent research has indicated that coexistence between competitors is possible under certain circumstances (Armstrong & McGehee 1980; Strong 1982; Gurevitch et al. 2000). Several studies have suggested that interactions between predation and competition may allow for continued coexistence (Gurevitch et al. 2000). The heavily exploited red and vermilion snapper populations may fit these circumstances for coexistence, as heavy fishing, a particularly acute form of predation, may have lowered populations of both competitors to a point well below carrying capacity at which food is not limiting. Almost nothing is known about the distributions of these two species prior to heavy fishing, so it is possible that prior to human disturbance these two species rarely co-occurred or their diets differed significantly.

In the past two decades, experimental studies of predation have revealed that multiple predators sharing a prey resource may have emergent effects. Combined predators may either 1) operate independently, or forage with 2) higher success (facilitation) or 3) lower success (inhibition) than expected based on the success of each predator foraging alone. Sih et al. (1998) termed deviations from predator independence "Emergent Multiple Predator Effects (MPEs)" and concluded that interspecific predator facilitation is uncommon. Rather, Sih et al. concluded that competitive inhibition is common and usually reduces the effectiveness of at least one predator species. Both competitive inhibition and facilitation have been exhibited in freshwater fish and marine invertebrate species (Diehl 1995; Griffen 2006). As of yet, there have been no experiments exploring possible MPEs for large marine predators.

While competition for resources between terrestrial taxa has been well studied, relatively little is known about competition between sympatric fish species. Furthermore, most studies concerning competition between fish have pertained to small freshwater and coral reef associated species. In a review of these studies, Hixon (2002) suggested that both intraspecific and interspecific competition for food can cause density-dependent recruitment in many small coral reef fish. Also, several studies concerning competition among coral reef fishes have found that competition mediates growth and consequently mortality due to predation (Forrester 1990; Hixon & Webster 2002). Interspecific competition has been shown to cause resource partitioning among several temperate reef fishes in California (Larson 1980; Hixon 1980; Ebeling & Laur 1986). The results from these studies are consistent with expected results via the competitive exclusion principle.

Within the last decade there have been comparatively few studies pertaining to intraspecific and interspecific resource partitioning among large reef-associated predators in the Gulf of Mexico. Lindberg et al. (2006) used field experiments to examine intraspecific competition among gag (*Mycteroperca microlepis*). They found that gag were capable of density-dependent habitat selection and prioritized shelter availability over food availability. Gag recruited to reefs offering more shelter at the expense of food availability, indicated by lower growth rates at the more densely populated reefs. Lindberg et al. presume that this discrepancy in growth rates was due to intraspecific competition, as prey abundance was equal among reefs. Interspecific competition could produce similar outcomes. If the inferior forager of two competing species, in this case vermilion snapper, prioritizes shelter quality over prey availability, then the inferior forager may recruit to reefs dominated by the other species despite low prey availability. Such a behavior, as exemplified by gag, could negatively affect the growth of the inferior forager.

Simmons (2008) studied interactions between red snapper and grey triggerfish (*Balistes capriscus*). In both field and laboratory experiments, Simmons found that competition between grey triggerfish and red snapper caused significant reduction in red snapper growth rates. The diets of red snapper and grey triggerfish do not fully overlap, as red snapper are capable of eating larger prey than grey triggerfish due to morphological differences. These results not only show that interspecific competition may significantly effect the welfare of red snapper, but that two competing reef-associated predators do not need to be "complete competitors" to have significant effects on one another. Such a negative effect on growth in particular could be important to consider for fisheries management, as management plans often aim to maximize biomass production of exploited species.

Study organisms

Red snapper

Red snapper inhabit natural and artificial hard bottom areas of the GOM from the west coast of Florida to Texas and throughout the South Atlantic Bight (North Carolina to southern Florida), although they are historically most abundant from the Florida Panhandle to south Texas (Bradley & Bryan 1975). Red snapper spawn from April through September with spawning peaking in June to August (Bradley and Bryan 1975; Collins et al. 1996). The eggs are pelagic and float on the surface until hatching (Szedylmayer and Conti 1999), and remain pelagic during the larval stage, which lasts for 27-30 days (Rabalais et al. 1980; Szedylmayer and Conti 1999). After metamorphosis, juvenile red snapper quickly settle to primarily low-relief structured habitat, usually relic-shell habitat at depths between 18 and 55 m (Szedylmayer and Conti 1999). As they grow they move on to higher-relief reef structures at similar depths, a behavior attributed to a need for larger "hole" sizes for protection from predators (Piko and Szedylmayer 2007). By their second winter (18 months), most red snapper have reached 200 mm TL and begin to recruit to moderate and high relief structures, such as rock outcroppings, artificial reefs (e.g. sunken ships, concrete rubble), and oil platforms (Patterson et al. 2001a; Nieland and Wilson 2003). Beginning the following summer (age 2) at a size usually around 300 mm TL, they reach sexual maturity and recruit to the directed fishery. From age 2-10, they continue to grow rapidly and remain highly associated with natural and artificial reefs (Patterson et al. 2001b; Fischer et al. 2004). Growth slows after approximately 10 years, although maximum age for this species is 50 (Patterson et al. 2001b). Throughout the remainder of their adult life they remain associated with reefs, but they also are known to expand their habitat to open mud and sand-bottom areas, as well (Szedlmayer 2007).

Red snapper are opportunistic feeders whose diet consists of a broad range of fishes, benthic crustaceans, squid, and zooplankton. Their diet is highly variable with ontogeny and displays a general trend of increasing crab and fish consumption with age, while consumption of a variety of small crustaceans, squid, and mysid shrimp decreases with age (Szedlmayer & Lee 2004; Wells et al. 2008). Moseley (1966) conducted the earliest directed study of red snapper diets in the northern GOM and concluded that red snapper were highly opportunistic and ate whatever was available to them. This conclusion has largely been supported by more recent studies. Age 2 and older red snapper have fairly consistently been found to feed on fish, crabs, shrimp, seasonally blooming tunicates, and miscellaneous benthic invertebrates (Bradley and Bryan, 1975; Gallaway et al. 1981; Szedlmayer and Lee 2004; McCawley and Cowan 2007; Wells et al. 2008). In all of these studies fish were the dominant prey source, and larger fish tended to feed more heavily on fish and crabs. In the eastern GOM, red snapper remain opportunists, yet feed more consistently on invertebrates (Beaumariage and Bullock 1976). The relative importance of reef-associated prey species and open sand and mud bottom prey species in red snapper diets is a major point of contention in these studies; however, it is clear that red snapper feed on both reef-associated and open-bottom prey species (Wells et al. 2008, Gallaway et al. 2009).

Vermilion snapper

Similar to red snapper, vermilion snapper are common throughout the Gulf of Mexico and the South Atlantic Bight and are associated with both high and low relief hard bottom habitat including live bottom, rock outcroppings, and artificial reefs primarily at depths between 18-55 m. In the north-central GOM vermilion snapper are generally associated with moderate and low-relief hard bottom areas, but are also commonly found on artificial reefs (SEDAR 2006).

Like red snapper, vermilion snapper spawn from April through September with the highest rates of spawning occurring during the summer months. Vermilion snapper eggs and larvae are pelagic, and the larvae are often sympatric with and indistinguishable from other snapper larvae, including red snapper. Vermilion snapper recruit to reefs very rapidly, as the young-of-the-year associate with reef sites, often schooling above the reef (SEDAR 2006). After recruitment to a reef, vermilion snapper exhibit exceptionally high site-fidelity, often remaining tightly associated with the same reef for years (Fable 1980, Parker 1990). Vermilion snapper grow and reach sexual maturity very rapidly, although they display large spatial variation in size-at-age (SEDAR 2006). Age and growth studies specific to the north-central GOM suggest that most individuals in the region exceed 200 mm

TL in their first year and exceed 300 mm TL by their fifth year (Johnson et al. 2010). Vermilion snapper may recruit to the directed fishery as early as age 1, and all individuals will be expected to have entered into the fishery by ages 4-5. Between ages 5-10 vermilion snapper growth slows, and their typical maximum length is estimated between 400-500 mm TL. Vermilion snapper may live as long as 26 years, but catch-based data indicates that very few individuals exceed 15 years of age (Hood & Johnson 1999, Johnson et al. 2010).

Vermilion snapper have been found to have a highly diverse diet, consisting of a variety of pelagic and benthic invertebrates and small fishes. Johnson et al. (2010) reported that benthic or reef associated amphipods and tunicates were the most important components of vermilion snapper diet in the north central GOM, followed by shrimps, crabs, polychaetes, and small fish. This diet analysis varied significantly from Grimes' (1979) analysis of vermilion snapper diet in the Atlantic. Johnson et al. (2010) reported a larger benthic component of the diet and a smaller pelagic component, whereas, Grimes (1979) reported a larger pelagic component consisting of far more squid and pelagic crustaceans. Johnson et al. (2010) regarded this as unusual, because many benthic tunicates have potent chemical defenses and are difficult to digest. Consumption of benthic tunicates is rare among snappers, although it has been observed for some tropical reef fish.

Overlap in species biology and potential for feeding competition

Immediately after metamorphosis, red and vermilion snapper have little potential for interaction. Young-of-the-year red snapper inhabit low-relief habitats such as relic shell or mud and sand bottom areas, whereas, young-of-the-year vermilion snapper quickly recruit to reef habitats. As such, potential for feeding competition begins only after red snapper recruit to reefs at approximately 18 months. Previous diet studies indicate a high level of dietary overlap, as both species feed upon a similar variety of crustaceans and fish. The potential for feeding competition between red and vermilion snapper seems to be highest for red snapper ages 2-4 (~200-400 mm TL). Young red snapper have been found to feed heavily upon a variety of amphipods and shrimps, staples of the vermilion snapper diet, while older, larger red snapper consume a larger portion of fish and crabs. In addition, larger red snapper likely forage away from the reef (Gallaway et al. 2009). However, it seems that red snapper continue to opportunistically prey upon smaller crustaceans even after shifting to a more piscivorous diet. Johnson et al. (2010) suggested that vermilion snapper and red snapper frequently compete for habitat and prey in the northern GOM and that red snapper were likely the dominant species. Johnson et al. (2010) speculated that red snapper dominance could force vermilion snapper to increase consumption of benthic tunicates, a normally undesirable food, in regions where the two species co-occur frequently.

Methods

Field data collection

The Fisheries Ecology Laboratory, Dauphin Island, AL, performed all collection of field data. The lab conducted three eight-day research cruises from Spring 2011 to Spring 2012. Forty reef sites were sampled three times each, once during each cruise. The sampling sites were distributed evenly from the Alabama – Florida border to Ochlockonee Bay, FL. Half of the sampling sites were artificial reefs and half were natural reefs, with artificial and natural reefs distributed evenly across the sampling area. Before fishing each site, a Seabotix ROV (Appendix 1) was deployed to determine abundances of fish species inhabiting the reef. The ROV recorded 5 minutes of stationary video from the sea floor facing the reef at three separate locations surrounding the reef. The camera was pointed at a 45-degree angle with respect to the sea floor so that the reef and the adjacent water column would be included in the recording. Fish abundances were estimated by taking counts from a single frame from the 5-minute video with the highest abundance of each species observed. The counts from the three replicate 5-minute recordings from each site were averaged to determine abundances. This method is not sufficient to determine absolute abundance of any species on a given reef; however, it does provide a useful tool for estimating relative abundances and species compositions among different reefs (Schobernd et al. 2013). After recording ROV footage, all sites were fished using either vertical longline gear (3 standardized replicates, Appendix 2) or recreational hook and line gear (standardized to 30 minutes). Vertical longline gear is meant to replicate the most common commercial fishing method used for reef fish in the region, while the recreational gear used was identical to that used by the local charter fishing fleet.

Spatial Overlap

The ROV and catch data was analyzed with the goals of determining spatial overlap between the two species and potential habitat preferences. ROV and catch data were combined so that sampling of any red snapper or vermilion snapper by either method indicated the presence of that species. Percentages of sites with neither species, only red snapper, only vermilion snapper, and both species present were calculated for each cruise and for all three cruises combined. Habitat preferences were analyzed by performing paired t-tests for the ROV abundance estimates of red and vermilion snapper at natural reef sites and artificial reef sites separately.

Dietary Overlap

Approximately half of the sites were randomly selected as tag-and-release sites, while at the other sites all fish were kept for stomach content analysis and age/sex assessment. Of these analyses, only stomach contents pertain to this thesis. Stomachs from all retained fish were removed and frozen shipboard. In the lab, stomachs were opened and contents were sieved through a 100μm screen then identified to the lowest possible taxonomic level by examination under a dissection scope. Bait was excluded from the analysis. Each taxonomic group was then weighed to the nearest 0.01 gram. Percent composition by number (%N), percent frequency of occurrence (%O), percent composition by weight (%W), and percent index of relative importance (%IRI) were calculated according to the following equations (Chipps and Garvey 2007):

Eqn. 1: $\%N_\mathrm{i} = \frac{number\ of\ prey\ type\ i}{sum\ total\ of\ all\ prey\ from\ all\ categories} \times 100$

Eqn. 2: $\%O_i = \frac{number\ of\ stomachs\ containing\ prey\ category\ i}{number\ of\ stomachs\ with\ prey\ present} \times 100$

Eqn. 3: $\%W_i = \frac{weight\ of\ prey\ type\ i}{weight\ of\ total\ stomach\ contents} \times 100$

Eqn 4: $IRI_i = (\%N_i \times \%W_i) \times \%O_i$

Eqn 5: $\%IRI_i = \frac{IRI\ for\ each\ prey\ category\ i}{sum\ of\ all\ IRI\ values} \times 100$

Each of these measures of diet composition emphasizes different aspects of the species' diet (Hyslop 1980, Cortés 1997). Percent composition by number tends to emphasize small prey that may be consumed in greater numbers. Conversely, percent composition by weight may over-represent the importance of infrequent, but large prey in a diet. Percent frequency of occurrence provides information regarding how often a particular prey type is consumed, but it provides little information regarding the contribution of that prey type to the overall diet relative to other prey type. Percent index of relative importance is a compound index designed to incorporate aspects of %N, %W and %O, expressed as a percentage (Cortes 1997).

Dietary overlap between red and vermilion snapper was calculated using Schoener's index of diet overlap (Schoener 1970). The index was calculated with respect to %N, %W, and %IRI. Schoener's index was first calculated with stomach contents from all red snapper and vermilion snapper collected during sampling. Overlap was then calculated for the subset of data from sites at which red snapper and vermilion snapper were observed to overlap via ROV analysis. If red snapper and vermilion snapper do compete for prey, then it is expected that diet overlap would be lower where they overlap due to resource partitioning. Previous diet studies of red snapper and vermilion snapper independently of one another suggest that diet overlap may be highest between adult vermilion snapper and red snapper less than 400 mm FL. Ideally, overlap would have been calculated for vermilion snapper and red snapper in this size class; however, too few red snapper less than 400 mm FL were captured.

Catchability

The ROV and catch data from the research cruises was also used for catchability analysis. Relative catchability was examined using general linear models with catch as the response variable and ROV abundance (ROV) and species as predictor variables. The interaction between ROV and species was included in the model. Separate general linear models were then used to analyze catchability of red snapper (RS) and vermilion snapper (VS) separately. For each species ROV abundance, habitat type, gear type, and ROV abundance of the opposite species were examined as factors influencing catch. All first order interactions were included in the models.

Formula 1: $Catch \sim ROV * Species$

Formula 2: $RS\ catch \sim RS\ ROV * Habitat\ type * Gear\ type * VS\ ROV$

Formula 3: $VS\ catch \sim VS\ ROV * Habitat\ type * Gear\ type * RS\ ROV$

Laboratory Experiment

All red and vermilion snapper collected for use in laboratory experiments were captured during five trips in June and July 2013 via hook and line fishing from artificial reef sites located 11-19 km south of Dauphin Island, AL. The target size class was 250-350 mm FL. The fish were collected over shallow depths (19-28 meters) to avoid barotrauma and were handled as little as possible after catch. Fish were transported back to Dauphin Island Sea Lab in a 170.3 L (45 gal.) flow-through livewell. After capture and return to the lab, fish were contained in holding tanks and allowed a two-week acclimation period before being used in trials. All fish were housed in outdoor, shaded tanks with a recirculating pump and filter system. The tanks were 2.44 m (8 ft) in diameter and 1.07 m (3.5 ft) in depth, (filled to approximately 3 ft in depth), translating to a volume of roughly 4100 liters (Appendix 3). Temperature, salinity, and nitrogenous waste levels were monitored daily. Fish were fed a mixed diet of squid (*Loligo sp.*), penaeid shrimp (*Penaeus aztecus*), and mackerel (*Scomber scombrus*) until satiation every 48 hours. Experimental tanks were identical to holding tanks, with the following exceptions.

Experimental tanks contained two hollow concrete cinder blocks to provide shelter, and had sand covering the bottom of the tank. The availability of these small shelters seemed to cause the fish to become more comfortable and acclimate more quickly to the experimental tanks. The sand bottom allowed shrimp to attempt to hide by partially burrowing as they would in a natural environment. Both the holding and experimental tanks were part of the same recirculating system.

The experiment employed a substitutive design and consisted of four treatments: 1) 0 red snapper and 0 vermilion snapper (control), 2) 6 red snapper and 0 vermilion snapper, 3) 0 red snapper and 6 vermilion snapper, and 4) 3 red snapper and 3 vermilion snapper. For all treatments 15 brown shrimp (*Penaeus aztecus*) 90-100 mm TL were introduced to the experimental tank, and the first 30 minutes of feeding after introduction of prey were recording with a pair of GoPro Hero2 cameras in the tank (Appendix 4). Following the trials, the video was viewed and consumption of shrimp and failed predation attempts were enumerated for each species. The time of these predation events was also noted so that feeding rates might be examined. In order to examine feeding rates, time elapsed and species were examined as factors influencing cumulative shrimp consumption. Cumulative shrimp consumption was square transformed to achieve linearity.

The fish were starved for 48 hours before beginning trials to ensure a standardized hunger level. Fish were randomly selected for trials from pools of 8-14 vermilion snapper and 12-18 red snapper. Fish being used in trials were transferred from holding tanks to experimental tanks 24 hours prior to commencing the trial to allow for acclimation and recovery from any stress resulting from transfer. Stress relating to transfer was assumed to be negligible, as the transfer process was very quick and holding and experimental tanks were less than 3 meters apart.

Results

Spatial Overlap

ROV video and catch data analysis showed that red and vermilion snapper frequently cohabited reefs across all three research cruises (Figure 2). The two species overlapped at 74%, 69%, and 58% of sites sampled during the first, second, and third cruises, respectively. However, red and vermilion snapper abundance differed significantly depending upon habitat type (Figure 3). The ROV video survey data for all three cruises combined showed that red snapper were significantly more abundant than vermilion snapper at artificial reef sites (paired t-test, n= 56, p=.003), and vermilion snapper were significantly more abundant than red snapper at natural reef sites (paired t-test, n=60, p=.001.)

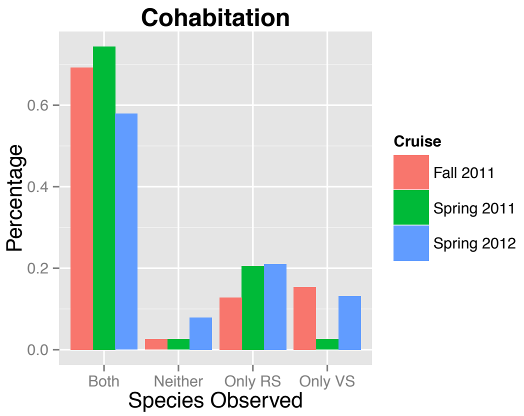

Fig. 2. Percentage of sites where both red snapper (RS) and vermilion snapper (VS) were observed, only red snapper were observed, only vermilion snapper were observed, and neither species was observed.

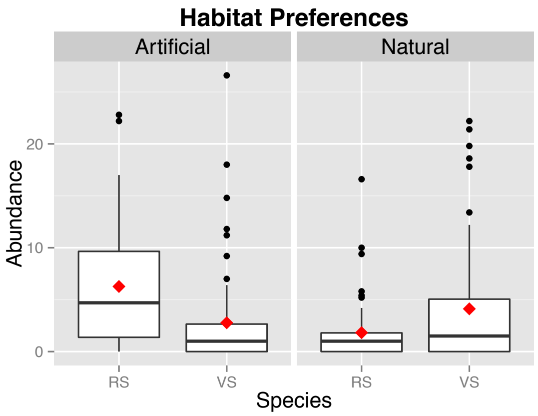

Fig 3. Habitat preferences of red snapper (RS) and vermilion snapper (VS). The boxes represent the interquartile ranges; the horizontal black line is the median; the red diamond indicates the mean. The whiskers indicate the most extreme value within 1.5 × IQR. All black dots are outliers (further than 1.5 × IQR from the median).

Stomach Contents and Dietary Overlap

Stomachs from 154 vermilion snapper and 216 red snapper were examined. Of those, 92 of the vermilion snapper stomachs and 133 of the red snapper stomachs contained identifiable material. Amphipods (Amphipoda), unidentified fish, and unidentified crab were the three largest components of vermilion snapper stomach contents both by percentage of number (%N) and percent frequency of occurrence (%O), and they were the only prey categories to exceed 10% in those measures. For red snapper, unidentified fish, pteropods (Pteropoda), and amphipods (Amphipoda) were the most abundant by %N and %O, and were also the only three categories to exceed 10% in those measures. Unidentifiable material was the dominant category by weight for both species, comprising 80.4% and 76.1% of stomach content mass for vermilion and red snapper, respectively. Unidentifiable material was excluded from %N and %O calculations and subsequently did not contribute to percent index of relative importance (%IRI) calculations. The top three prey categories by %IRI matched those calculated by %N and %O for each species, and the inclusion of all three factors %N, %O, and %W in calculating %IRI emphasized the importance of those prey categories. Amphipods comprised 46.4% of vermilion snapper stomach contents by %IRI and unidentified fish comprised 55.4% of red snapper stomach contents (Figure 4).

Schoener's dietary overlap indices indicate marginally biologically significant overlap. Overlap with respect to %N was .548, and overlap with respect to %O was

.576 (Table 1). These overlap indices are marginally significant as all values greater than or equal to .600 have been suggested to be biologically significant (Pianka 1976). Overlap with respect to %W was .870, a very high value that may largely be attributed to the large contribution of unidentifiable material to each species' stomach contents by weight. Overlap with respect to %IRI was .383 and thus not considered biologically significant. This discrepancy between %IRI and overlap with respect to other measures is largely the result of large differences between red snapper and vermilion snapper stomach contents in the two categories "unidentified fish" and "amphipods" (Figure 4). Vermilion snapper had a much larger %IRI for amphipods while red snapper had a much larger %IRI for unidentified fish; however, each category ranks in the top three categories by %IRI for both species.

Schoener's overlap was calculated for the subset of red snapper and vermilion snapper collected from sites where the two species were observed to overlap via ROV video survey. Overlap was lower than calculated for the complete dataset and was not biologically significant with respect to all measures. Overlap with respect to %N, %O, and %IRI was calculated from stomach contents from 59 and 50 vermilion and red snapper, respectively (Table 1). Overlap with respect to %N was .421 and overlap with respect to %O was .446. Overlap with respect to %IRI was especially low with a value of .247. Very few stomachs from red snapper less than 400 mm FL and zero stomachs from red snapper less than 300 mm FL were dissected.

Consequently, dietary overlap analysis between vermilion snapper and red snapper less than 400 mm FL was not possible.

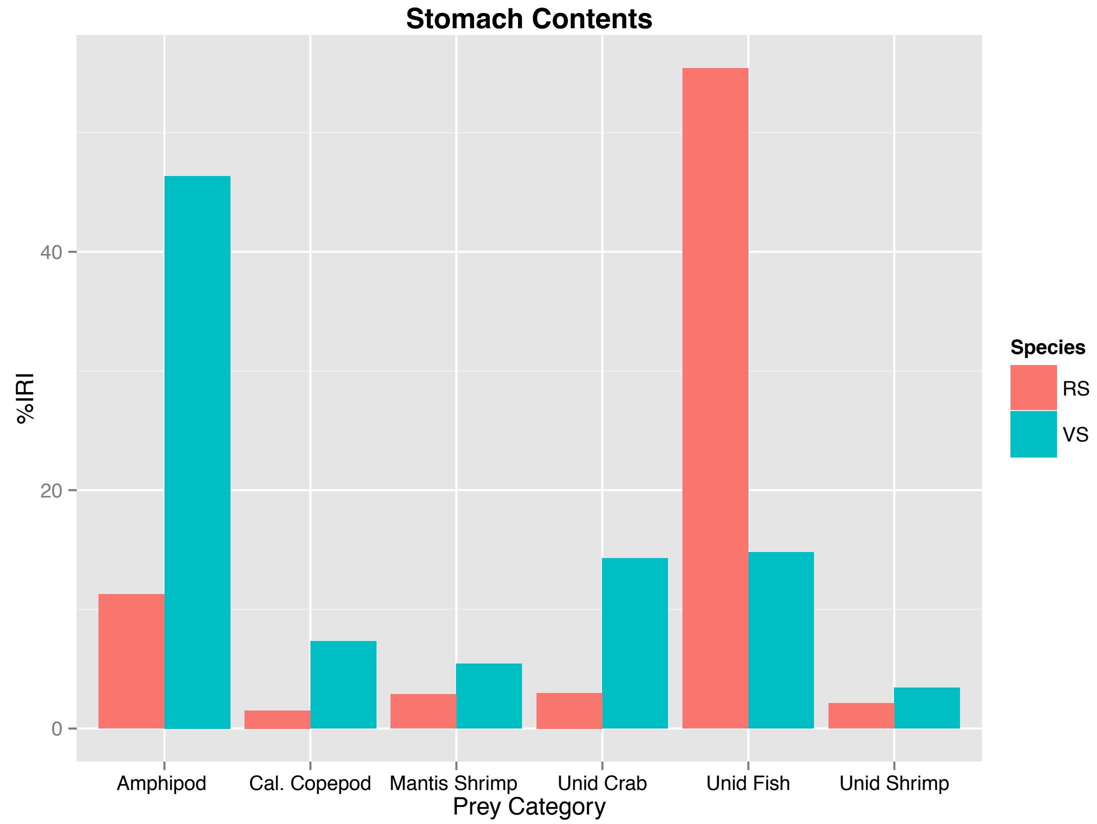

Fig. 4. %IRI of selected prey categories in the stomach contents of red snapper (RS) and vermilion snapper (VS). The selected prey categories are those that were shared among each species' ten most important prey categories by %IRI (Unid is an abbreviation for unidentified).

Schoener's overlap index values

Measurement	All sites	Sites RS & VS Cohabit
%N	0.548	0.421
%O	0.576	0.446
%W	0.871	0.875
%IRI	0.383	0.247

Table 1. Schoener's overlap indices for all stomach contents and only stomach contents from sites where red and vermilion snapper were observed to overlap via ROV survey. The indices for %W are artificially high due to the large contribution of unidentifiable material in each species' stomach contents.

Catchability

The overall model for catch with ROV abundance and species as factors was significant (R^2= 0.47, F=67.9; df=228, 3; p<0.001). The interaction between abundance and species was significant (Figure 5, F=43.0, df=1, p<0.001), indicating that ROV abundance is a better predictor of red snapper catch than it is of vermilion snapper catch.

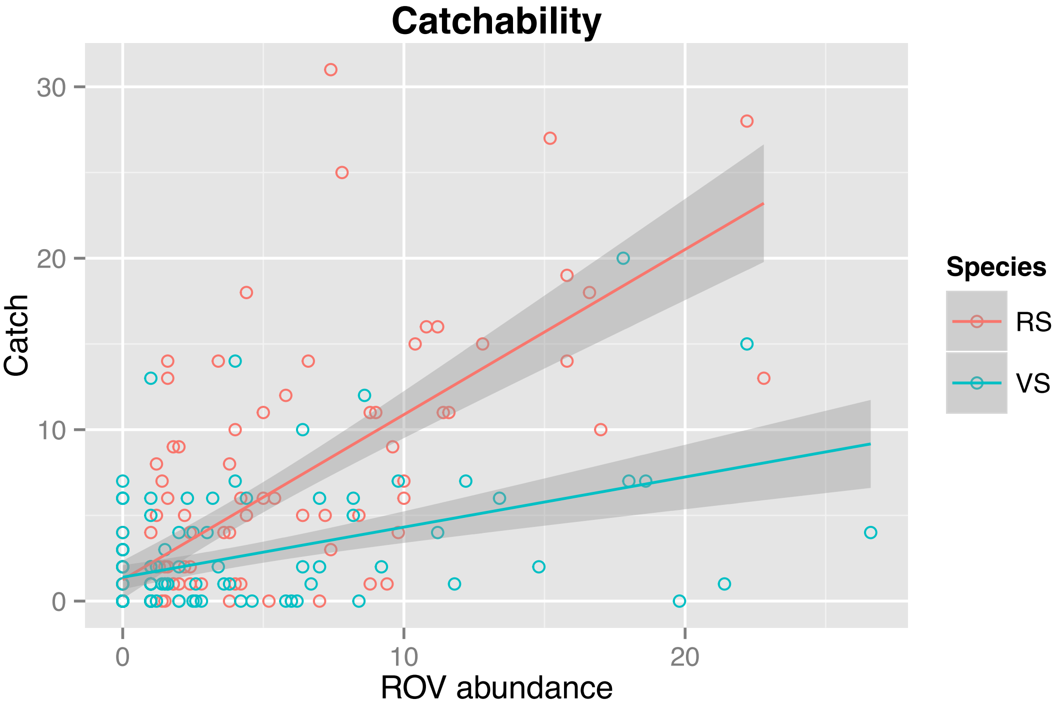

Fig. 5. Catch as a function of ROV abundance for red snapper (RS) and vermilion snapper (VS). ROV abundance of red snapper is a far better predictor of catch than ROV abundance of vermilion snapper. Shaded areas represent 95% confidence intervals.

The model for red snapper catch with the factors red snapper ROV abundance, habitat, gear type, and vermilion snapper ROV abundance was significant (R^2=0.58; F=9.2; df= 15, 100; p < 0.001). The interaction term for red snapper ROV abundance and gear type was significant (Figure 6, F=6.5, df=1, p=0.01). Habitat and vermilion snapper ROV abundance were not significant.

The model for vermilion snapper catch with the factors vermilion snapper ROV abundance, habitat type, gear type, and red snapper ROV abundance was also significant ($R^2=0.52$; F=7.4; df=15, 100; p<0.001). The interactions between vermilion snapper ROV abundance and gear type (Figure 6, F=16.3, df=1, p<0.001) and between vermilion snapper ROV abundance and Habitat (Figure 7, F=11.9, df=1, p=0.001) were significant. Red snapper ROV abundance was not significant.

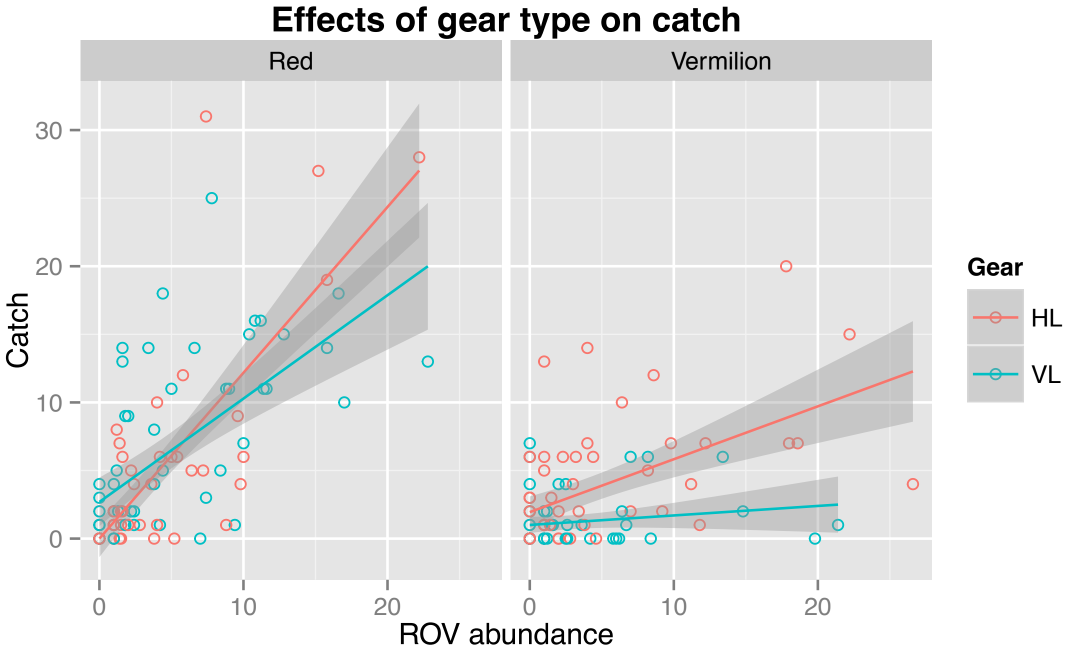

Fig. 6. Catch as a function of ROV abundance for each species, showing the effects of gear type on catch (HL = recreational hook & line; VL = vertical longline). Shaded regions represent 95% confidence intervals. Gear type has little effect on catch in red snapper (RSN), and vertical longline is very ineffective for vermilion snapper (VSN).

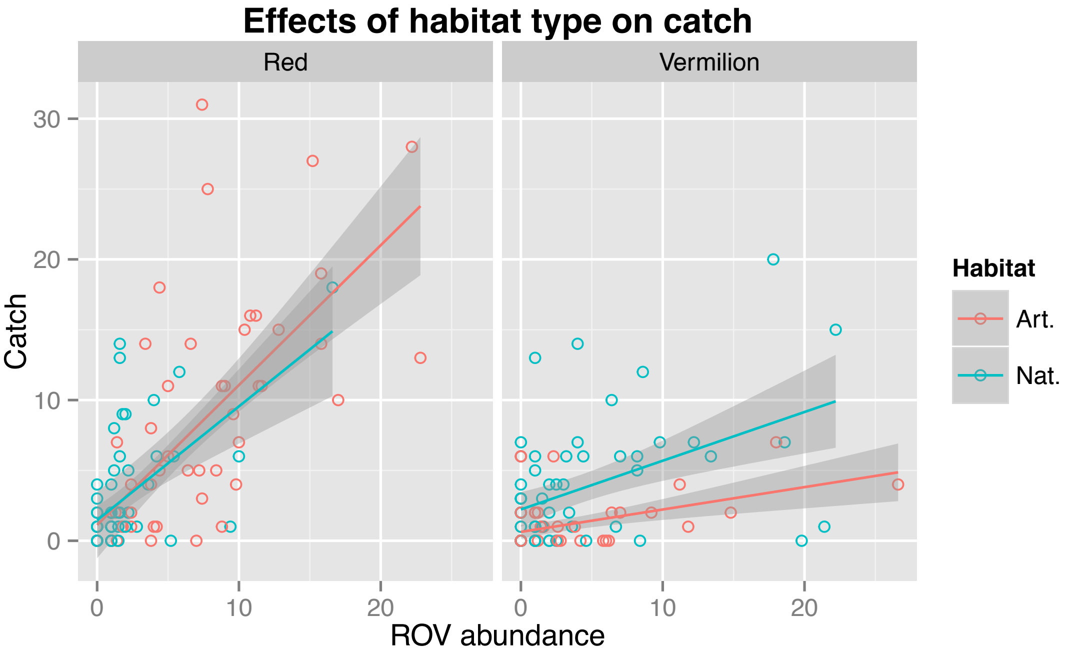

Fig. 7. Catch as a function of ROV abundance for each species, showing the effects of habitat type (Art.= artificial, Nat.=natural) on catch. Shaded regions represent 95% confidence intervals. Habitat has little effect on catch for red snapper (RSN). For vermilion snapper (VSN) ROV abundance seems to be a better predictor of catch at natural reef sites. It appears that this result may largely be due to higher vermilion snapper abundances at natural reefs.

Laboratory Experiment

Eight replicates of the red snapper and vermilion snapper single species treatments were completed; however, only 6 replicates of the mixed species treatments were completed due to fatal error. Red snapper and vermilion snapper used in trials were of similar sizes: mean red snapper length was 273 (±8.57) mm FL and mean vermilion snapper length was 285 (±3.79) mm FL. Red snapper mean mass was 0.36 (±0.035) kg and vermilion snapper mean mass was 0.33 (±0.018) kg.

Red snapper from the single species treatments ate significantly more shrimp per fish than vermilion snapper in both the mixed species treatment (Figure 8a, p=0.02) and single species treatment (p=0.003). Red snapper ate significantly more shrimp per fish in the mixed species treatment than in the single species treatment (p=0.04). Vermilion snapper shrimp consumption per fish did not differ significantly between mixed and single species treatments. Linear regression revealed that shrimp consumption per fish was highly correlated with predation success rate across all treatments ($R^2=0.56$; df=1, 26; F=32.55; $p<0.001$).

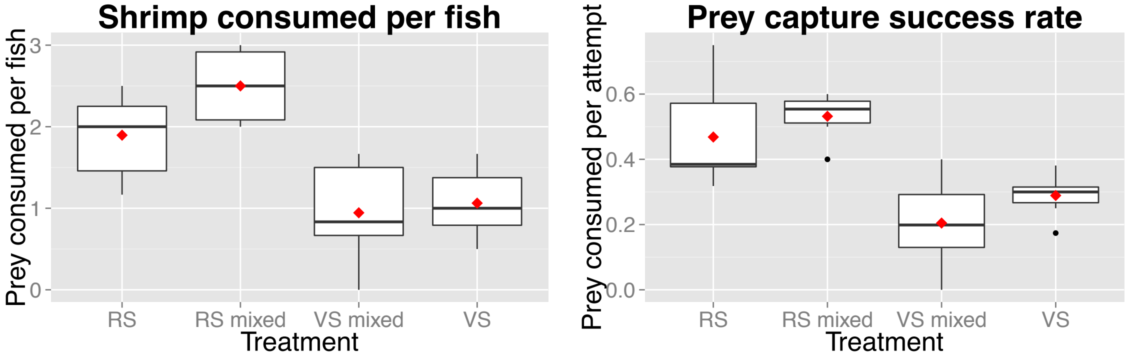

Fig. 8. (A) Shrimp consumed per fish in each treatment group. Shrimp consumption was significantly different among all treatment groups ($p<.05$) except for VS single and mixed species. (B) Shrimp consumed per attempt. Success rates were correlated to shrimp consumed per fish. The boxes represent the interquartile ranges, the horizontal black line is the median, and the red X indicates the mean. The whiskers indicate the most extreme value within 1.5 X IQR. All open dots are outliers (further than 1.5 X IQR from median).

Red snapper fed at a higher initial rate than vermilion snapper in both the single species and mixed species treatments (Figure 9). The overall model for cumulative shrimp consumption with elapsed time and species as factors was significant (R^2=0.50; df=3, 196; F=65.7; p<0.001). The interaction term for time elapsed and species was significant, indicating that time elapsed better predicted cumulative shrimp consumed for red snapper than for vermilion snapper (F=33.7, df=1, p<0.001). Red snapper shrimp consumption also approached a higher asymptotic level than did vermilion snapper shrimp consumption (Figure 10).

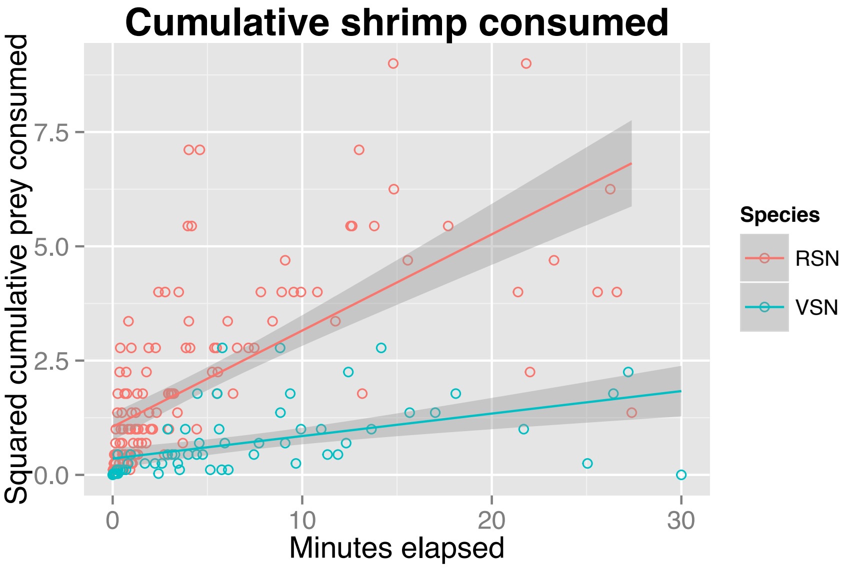

Fig. 9. Squared cumulative prey consumed vs. minutes elapsed in trials. Red snapper (RSN) fed at a higher rate than vermilion snapper (VSN), indicated by the higher slope of the regression line for red snapper. Shaded regions represent 95% confidence intervals.

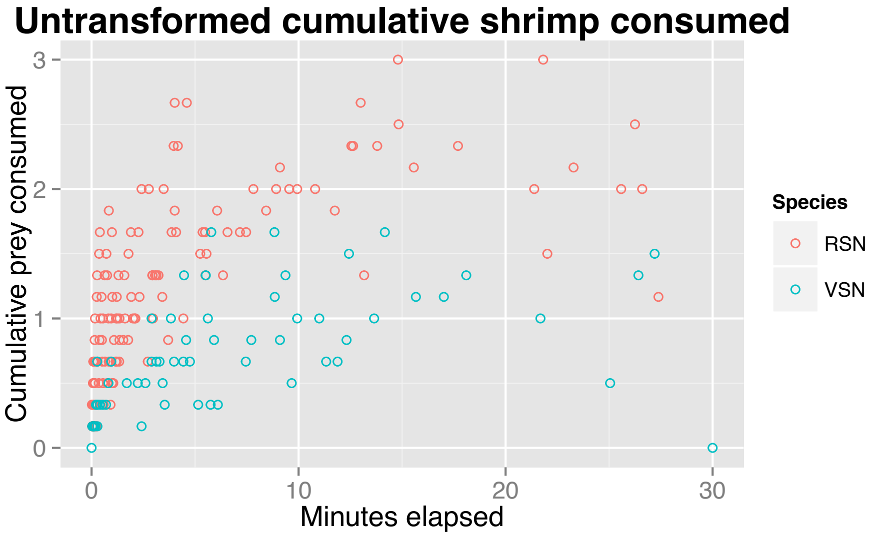

Fig. 10. Untransformed cumulative shrimp consumed vs. minutes elapsed in trials. The shapes of the distributions flatten out at different values of cumulative shrimp consumed for vermilion snapper than for red snapper. This may indicate differing satiation points.

Discussion

Interpretation of results

Red snapper and vermilion snapper frequently cohabit reefs in the northern GOM and rely heavily upon similar prey resources; thus, feeding competition between red and vermilion snapper is probable. While the two species appear to have differing habitat preferences, red and vermilion snapper cohabited the overwhelming majority of reefs sampled. These results indicate the two species' habitat preferences differ only by degree. Likewise, red and vermilion snapper rely heavily upon similar prey resources, although the magnitude of consumption across some prey categories differed. Red and vermilion snapper share ten of their fifteen most important prey categories according to %IRI, and five of their six most important categories by %IRI. Dietary overlap was marginally significant in this study, despite large size discrepancies between the red snapper and vermilion snapper sampled. The primary difference between these two species' diets appears to be the relative importance of fish and amphipods. Yet, each category ranks in the top three most important categories for the opposite species. Previous diet studies have indicated that red snapper smaller than 400 mm FL, which were underrepresented in this study, feed less upon fish and consume a larger proportion of small invertebrates including amphipods (Wells et al. 2008). Consequently, dietary overlap is probably even higher between smaller red snapper and vermilion snapper. Based upon the combination of the results presented here and previous studies, it is reasonable to conclude that dietary overlap between red snapper and vermilion snapper is significant. Furthermore, dietary overlap between red snapper and vermilion snapper was lower at sites they cohabited, a possible indicator of competition and resource partitioning. Given the prevalence of unidentifiable fish remains in the stomachs of both species, further resolution regarding the degree of dietary resource partitioning between species will require additional approaches such as stable isotope analysis or DNA barcoding of stomach contents.

The general linear model analysis of ROV abundance and species as predictors of catch confirms local fishermen's suspicions that red snapper are more catchable than vermilion snapper. Assuming that ROV video survey provides a reasonable measure of relative abundance (Schobernd et al. 2013), red snapper catch increased significantly more than vermilion snapper catch as the abundance of each species rises. Vertical longline gear exacerbates this finding, as ROV abundance was an especially poor predictor of vermilion snapper catch when vertical longline gear was employed. Gear type had some effect on red snapper catch as well. The experimental design for vertical longline sampling probably caused red snapper catch to plateau at a maximum value, as only 3 drops were conducted at every site.

While these findings affirm one of the beliefs of local fishermen, the results also contradict the popular belief that red snapper affect the catchability of other species such as vermilion snapper. The catch models indicate that neither red nor vermilion snapper have any effect on the catchability of the other species. The abundance of red snapper as observed via ROV had no significant effect on vermilion snapper catch. Rather, vermilion snapper abundance and gear type are the primary factors influencing vermilion snapper catch.

Findings from the manipulative laboratory experiments demonstrated that red and vermilion snapper of similar sizes displayed significant differences in feeding behavior. Red snapper fed at a higher rate and consumed more shrimp per fish than vermilion snapper. However, interspecific competition with red snapper did not have a significant effect upon vermilion snapper prey consumption compared to conspecific competition in the single species treatment. So, red snapper did not competitively exclude vermilion snapper from the prey resource in the experiment. However, this result may have been due to the experimental design. Both species were allowed to approach satiation, so prey was effectively not a limited resource in the time period of the trials. In the situation of limited prey, it is expected that red snapper would exclude vermilion snapper from prey as they feed more successfully and at a higher rate.

Total prey consumption was higher when red and vermilion snapper foraged together (mixed species treatment); however, it does not appear that this was indicative of an emergent multiple predator effect. No mechanism of facilitation was observationally apparent in video analysis. Rather, it seems that intraspecific competition among red snapper has a greater effect than interspecific competition with vermilion snapper on the foraging success of red snapper.

Ecological and fisheries management implications

The difference in catchability between the two species has the most immediate implications for fisheries management, as stock assessments rely largely upon catch data. Numerous studies have indicated that catch data do not provide an accurate depiction of species composition and that gear types may select for certain species (Gregalis et al. 2012, Bacheler et al. 2013). This thesis affirms those findings, and it affirms the popular perception that red snapper are more catchable than vermilion snapper. The experimental results corroborate these findings as they may shed light on behavioral differences between the two species that may affect catchability. Since red snapper were shown to feed at a higher rate than similarly sized vermilion snapper, it follows that they may also be caught at a higher rate. This difference in catchability has important implications for stock assessments as catch numbers for vermilion snapper may not be as indicative of absolute abundance as they are for red snapper. Thus, catch-based stock assessments may depict an inflated red snapper : vermilion snapper ratio.

The ecological implications of red and vermilion snapper feeding behavior and interactions are more nuanced. The findings from this study alone indicate that resource partitioning in the prey categories of amphipods and fish may allow for coexistence of red and vermilion snapper. However, evidence from other studies suggests amphipods and other small invertebrates are important in the diets of smaller red snapper. Hence, the two species appear to be in competition for prey, but the question then arises, "how could evolution allow for these two species to be in competition and coexist?" One possible answer is that prior to heavy exploitation, red and vermilion snapper did not overlap spatially. Red snapper appear to prefer sites with more vertical relief such as the artificial reefs that now litter the northern GOM, while vermilion snapper prefer lower relief reefs that are larger in two-dimensional area. It seems plausible that each species was more confined to these preferred habitats prior to population suppression via fishing. Under the heavily exploited condition, it is possible that food resources may no longer be limiting, as predator density is much lower. However, according to historical accounts of the northern GOM red snapper fishery, red snapper were dominant at sprawling low-relief natural reefs in the early years of the fishery (Shipp and Bartone 2009).

Another possible explanation for red and vermilion snapper coexistence despite the apparent likelihood of exploitative competition involves an ongoing debate regarding feeding habits of red snapper. While some studies have contended that red snapper feed heavily upon reef-associated prey (Szedlmayer and Lee 2004), others have argued that red snapper use reefs primarily for shelter and rove the surrounding seafloor to feed (McCawley and Cowan 2007). If the latter is correct, or even if red snapper employ both strategies, an interesting scenario can be envisioned. Red snapper may feed opportunistically upon higher quality prey at the reef site, but once it is depleted they may leave the reef to seek more prey. Vermilion snapper may also feed opportunistically upon the same prey at the reef site but may not exploit those resources as successfully as red snapper. Rather than leave the reef in search of more prey, under this hypothesis vermilion snapper, which are known to have very high site-fidelity, may stay at the reef and feed at a lower rate or upon less desirable prey. These behaviors would also be consistent with their apparent differences in metabolism, as red snapper seem to have a higher satiation ceiling than vermilion snapper of a similar size. Predatory fish with high metabolic rates, such as tunas and larger mackerels, tend to roam constantly in search of high concentrations of high quality food. According to this hypothesis red snapper would employ this strategy, although to a lesser degree, and vermilion snapper might be able feed at a slower rate or consume less desirable prey. Johnson et al (2010) proposed a similar idea, as they found that vermilion snapper in the northern GOM fed heavily upon normally undesirable benthic tunicates.

It is important to recognize the interplay between fisheries management and the ecological implications of competition between these two species. This thesis has established that a high degree of feeding competition between red snapper and vermilion snapper is likely and has proposed mechanisms for the coexistence of the two species. The ecological implications of competition between these two species would not be especially concerning under natural conditions, as the two species evolved to coexist. However, heavy fishing pressure in the GOM has dramatically altered the ecological systems governing the interactions between these two species. Both species are heavily exploited and subject to intense regulation. As red snapper stocks surge in the wake of tightened regulations while exploitation of vermilion snapper remains constant or increases, it may be possible that competition between these two species becomes a cause for concern in the northern GOM. Furthermore, the tremendous number of artificial reefs in the northern GOM may favor red snapper, subsequently supporting red snapper stocks large enough to deplete resources and affect vermilion snapper.

The goals of fisheries management for these two species go well beyond normal conservation concerns and subsequently alter the way interactions between red snapper and vermilion snapper may be treated. Even if red snapper and vermilion snapper have evolved to coexist, simple maintenance of coexistence may not fully meet the goals of fisheries managers. Each of these species is the source of an economically important industry, and thus fisheries managers also have the task of managing the stocks in a manner that maximizes profitability. As it is likely that red snapper are dominant foragers, they may suppress vermilion snapper growth rates even if they do not fully exclude them. Depending upon the relative economic value of these two species, fisheries managers may be more concerned with red snapper or vermilion snapper productivity. Thus, competition between the two species must be taken into account to optimize management.

Recommendations for future research

Dietary overlap between vermilion snapper and red snapper less than 400 mm must be directly examined to gain a more complete understanding of feeding competition and resource partitioning between these two species. As mentioned earlier, the resolution of diet analysis and subsequently dietary overlap could be improved upon by using more advanced methods such as DNA barcoding or stable isotope analysis. DNA barcoding would allow for the highest possible resolution, as small and sometimes indistinguishable prey types (e.g. different families of amphipods) may be identified. Furthermore, unidentifiable material dominated the stomach contents for each species, and DNA barcoding would make it possible to classify these contents by non-visual means.

The most direct approach to studying the effects of competition between vermilion snapper and red snapper would involve comparing growth rates of vermilion snapper and red snapper both when they co-occur and when they do not co-occur. This could be accomplished by comparing size-at-age of vermilion snapper from sites where red snapper are present and not absent. However, such an approach would require significant assumptions regarding the site-fidelity of vermilion snapper and temporal variation in red snapper presence. Alternatively, the effect of coexistence on these species' growth rates could be examined experimentally.

Additionally, the laboratory behavioral experiment presented here could be expanded upon significantly. It may be revealing to repeat the experiment with fewer prey to determine if either species competitively excludes the other from prey. The experiment could also be repeated with a variety of prey types to ensure that the results were not specific to one prey type.

Conclusion

The findings of this thesis demonstrate that there is significant potential for competition between red and vermilion snapper, as the two species overlap spatially and trophically. Red snapper appear to be the dominant forager of the two species, affirming a widespread public perception in the northern GOM. Further dietary overlap research including smaller red snapper will be necessary to better understand how these two species partition resources. Furthermore, the resolution of the ongoing debate regarding the way that red snapper use reefs will also be important for understanding how red and vermilion snapper interact. If red snapper use the reef for shelter and forage away from the reef, then this aspect of their feeding behavior would allow for coexistence with vermilion snapper.

In following with the perception that red snapper feed more aggressively than vermilion snapper, red snapper are indeed more catchable than vermilion snapper. However, the presence of red snapper does not seem to affect the catchability of vermilion snapper, dispelling a widespread belief. These findings regarding catchability have immediate implications for catch-based stock assessments and subsequent fisheries management plans, and they further elucidate the inadequacies of traditional catch-based measures of species composition and abundance.

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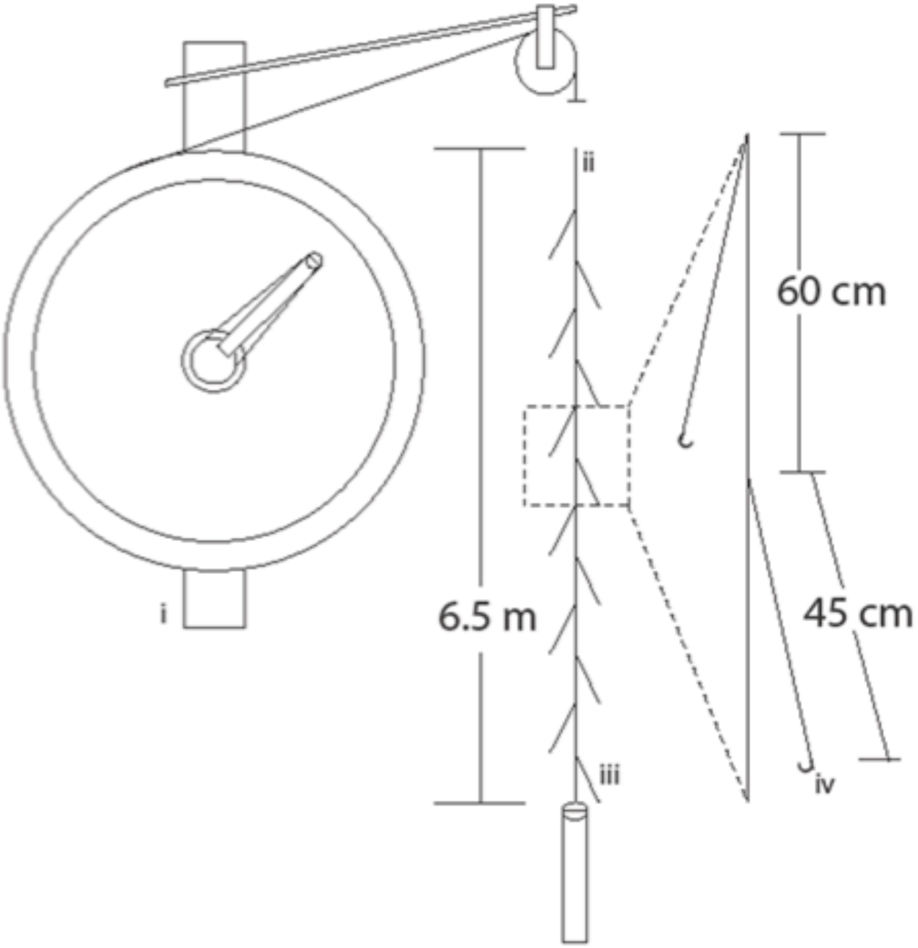
Appendices

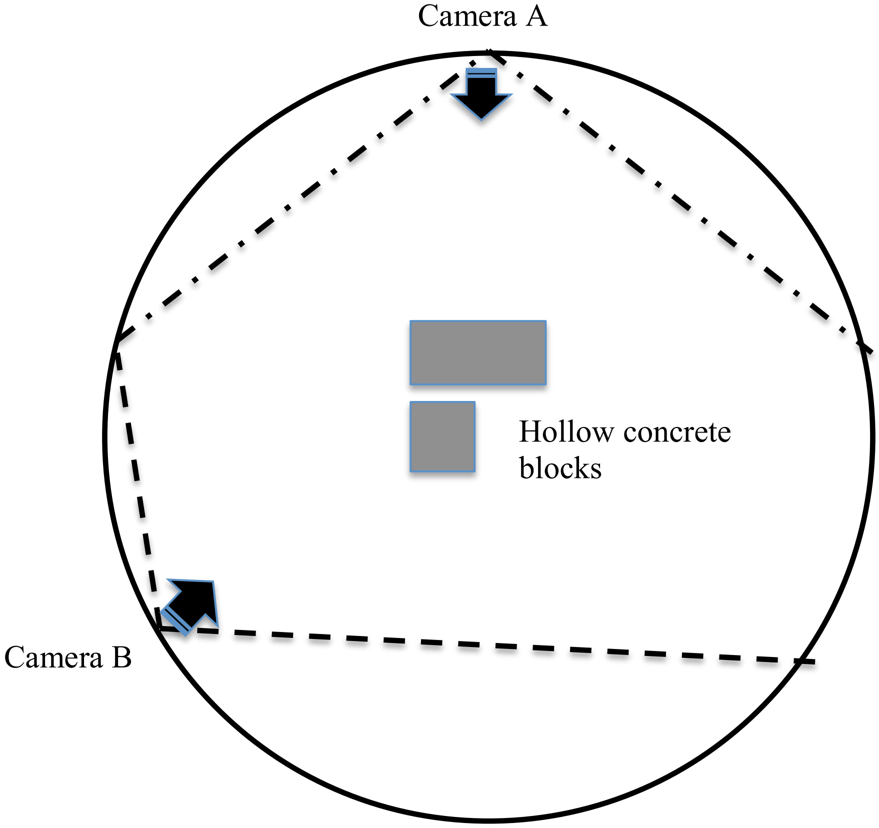
Appendix 1. Seabotix LBV ROV used to determine relative abundances of red snapper and vermilion snapper.

Appendix 2. Schematic diagram of vertical longline gear (i = "bandit" reel; ii = backbone, iii = sash weight; iv= gangion). Adapted from Gregalis et al. (2012).



Appendix 3. The experimental and holding tanks.

Appendix 4. Schematic diagram of GoPro placement in tanks. The cameras have a 170 degree field of view.



Pledge

This paper represents my own work in accordance with University regulations.

William T. Davis