# Evaluation of the Efficacy of the Minimum Size Rule in the Red Grouper and Red Snapper Fisheries With Respect to J and Circle Hook Mortality and Barotrauma and the Consequences for Survival and Movement

by

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## Dedication

This dissertation is dedicated to my family, especially my parents Helen and John Burns, my aunt Ann Burns, and to my good friends Marvin Tinsky, the Tinsky Family and Dr. Bernie Waxman who made my education possible, to Peter Simmons III, Jay Sprinkel and Janet Gannon for their help and encouragement and all the staff ,student-interns and volunteers who worked in the Mote Marine Laboratory Fish Biology Program during the years of my tenure and all the fishers who participated in the research conducted to accomplish this task and to Janet Giles and Linda Franklin for editing this document.

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**Karen Mary Burns**

## ABSTRACT

Although closed seasons, bag limits and quotas are used to manage fishes within the Grouper/Snapper Complex off the southeastern United States, size limits are the cornerstone of fisheries management. Because fishers must release all undersized fishes despite fish condition, this regulation has created a mandatory catch and release system. Inherent in this management strategy is the supposition that these undersized fish survive in sufficient numbers so as to justify this regulation. To satisfy this criteria fish mortality must be low and released fish must also experience minimal sub-lethal effects. Determination of sublethal effects and evaluation of their potential impairment and duration of injury are required to develop effective physiology-based criteria to evaluate the efficacy of the minimum size rule.

The goal of this research was to evaluate some aspects of the efficacy of the minimum size rule in the red grouper and red snapper fisheries off Florida by collecting traditional fisheries data and analyzing it in light of fish physiology, ecomorphology and behavior. Study objectives included 1) determination of the causes for the differences of hook mortality for red grouper and red snapper in the recreational and recreational-for-hire

fisheries by necropsy of acute and latent mortalities, analysis of tag and recapture data for both J and circle hooks, determination of fish dentition and any differences in feeding behavior, 2) examination of the effects of rapid depression from depth on fish survival by inspection and comparison of the red grouper and red snapper swim bladders in both healthy and swim bladder ruptured fish from various water depths, comparison of tag and recapture data, investigation of the effects of fish venting, and laboratory simulations using fish hyperbaric chambers to determine healing and survival from rapid depression trauma, 3) analysis of movement patterns of tagged fish and 4) evaluation of some of the consequences imposed by the minimum size limit based on study results.

# Chapter One: Evaluation of the Efficacy of the Minimum Size Rule in the Red Grouper and Red Snapper Fisheries With Respect to J and Circle Hook Mortality and Barotrauma and the Consequences for Survival and Movement: An Introduction

Red grouper, *Epinephelus morio*, and red snapper, *Lutjanus campechanus*, support important recreational, recreational-for-hire, and commercial fisheries, comprising significant portions of the reef fish catch in the Gulf of Mexico and South Atlantic. According to Coleman et al. (2004), “Marine recreational fishing effort has increased by over 20% in the past 20 years, rivaling commercial fisheries for many fish stocks, including …red snapper.” In 2004, a total of 2,041,530 lbs of red snapper and 3,190,281 lbs of red grouper were landed in Florida by these fisheries (NOAA Fisheries MRFSS, Richard Cody, Florida Fish and Wildlife Conservation Commission, personal communication). Shallow water grouper landings, averaging 10.6 million pounds annually (1985-2001), were responsible for approximately one half of the aggregate reef fish landings in the Gulf of Mexico and of the six grouper species which account for 95%-98% of total Gulf of Mexico grouper landings, red grouper dominated the landings with anywhere from less than five million pounds (1992 and 1998) to almost nine million pounds (1989) (Richard Cody, Florida Fish and Wildlife Conservation Commission, personal communication). With landings averaging 8.3 million pounds annually (1985-2001), snappers represented 38% of the total reef fish catch and of these; red snapper is the most abundant snapper species landed in the Gulf.

Because of their importance, both red grouper and red snapper are highly regulated in both the Gulf of Mexico and South Atlantic. Although there are recreational bag limits for both species in the Gulf and South Atlantic and closed seasons for both species in the Gulf of Mexico, these species, like most reef fish fisheries are primarily regulated by minimum size limits in both state and federal waters throughout the southeastern United States. Size limits have long been the cornerstone of fisheries management in the United States. Minimum size limits are intended to prevent growth and recruitment overfishing by allowing some portion of fish in a cohort to grow and reproduce at least once before dying of natural or fishing related causes. All fishers must abide by the minimum size regulation and release undersized bycatch regardless of location, water depth, fish condition or predators present. The minimum size regulation is enforced by prohibiting the landing of fish below the legal size. Enforcement of the minimum size limit rule has created a mandatory catch and release program for undersized bycatch. Determining the survival of released undersized bycatch in these fisheries, is critical as undersized bycatch comprise a significant percentage of the total catch in the reef fish recreational, recreational-for-hire and commercial fisheries. Undersized releases in the Gulf of Mexico red snapper recreational fishery are estimated to be 40-50% of the catch (Goodyear 1995). Survival of these discards is essential for effective management of these species and critical in determining the efficacy of the minimum size rule

Currently there are insufficient data on the fate of released fishes and survival rates after capture and release. The fate of undersized, released fish depends on a suite of factors contributing to mortality including hook trauma, depth induced mortality, physiological stress from warm water temperatures, handling and increased playing times (Wood et al. 1983, Tomasso et al. 1996, Gitschlag and Renaud 1994, Bruesetwitz et al. 1996, Chopin et al. 1996, Wilson and Burns 1996, Porch 1998, Collins et al. 199, Cooke and Suski 2004, Bartholomew and Bohnsack 2005). Among these, the causes and effects of hook damage and depth of capture on the mortality of undersized red grouper and red snapper in the private recreational and recreational-for-hire fisheries off Florida are of great interest to those responsible for stock assessments and management of these species (Red Snapper SEDAR 2004, Red Grouper SEDAR 2006).

In addition to traditional fishery management practices, the creation of marine reserves has been embraced as an important tool in fisheries management leading to a change from single species management to ecosystem management. Both the President's U.S. Commission on Ocean Policy final report (2004) "A Blueprint for the 21st Century" and the PEW Oceans Commission final report (2003) "America's Living Oceans: Charting a Course for Sea Change" stress the need for ecosystem management to reduce bycatch and protect habitat. One of the strategies to accomplish this goal is the creation of marine reserves to protect marine biodiversity and promote sustainable fisheries (Bohnsack and Ault 1996, Meester et al. 2004). To implement this strategy a suite of scientific disciplines (Bohnsack and Ault 1996) and an understanding of the life history, movements, habitat requirements and spatial-temporal dynamics of the living resources, and spatial arrangement and use of these habitats by living organisms (Meester et al. 2001, Sobel and Dahlegren 2004) are required. In addition to marine reserves, the Pew Oceans Commission (2003) calls for a decrease in bycatch by determining and enforcing bycatch mortality limits for fisheries and rigorous enforcement of regulations of fishing gear that results in high levels of bycatch.

Several avenues of research were pursued during the course of this dissertation toward addressing some of the data needs related to the fishery management issues previously discussed. Chapter Two deals with a discussion of the differences in hook mortality rates for red grouper and red snapper as determined by necropsy of acute and latent mortalities from fish caught during headboat fishing trips. Circle hooks have been touted as the solution for significantly reducing hook mortality. A fish tagging study incorporating fishers from the private recreational and recreational-for-hire reef fish fisheries was conducted to test for differential effects of J versus circle hooks on red grouper and red snapper survival. In addition, differences in dentition, jaw lever ratios and feeding behavior were examined to determine if and how these factors contribute to observed differences in hook mortality between the two species.

Chapter Three addresses depth induced mortality differences between the two species. Topics include differences in swim bladder morphology, the effects of rapid changes in pressure on the swim bladder, the effects of swim bladder rupture on survival of each species, swim bladder healing, and the effects of fish venting on fish survival for red grouper and red snapper caught at various depths. Estimates of survivorship to document swim bladder healing and determination of the interval between swim bladder rupture and healing are important because only then is the fish completely capable of returning to its normal lifestyle. Laboratory studies employing fish hyperbaric chambers to simulate the effects of rapid decompression were used to study the process under controlled conditions. Since fish were held for at least a month before the rapid decompression experiments began, any detrimental effects of hooking during initial capture were eliminated from test results. To verify laboratory results, data were gathered during field studies using a tag/recapture study to determine survival rates of released tagged fish subjected to rapid changes in depth during fishing and the effects of fish venting.

In the next chapter (Chapter Four) movement patterns of red grouper are discussed. Movement data were obtained from tag recapture information collected during the field hook mortality and rapid depressurization studies. Red grouper movements related to size, movements related to ontogeny and the influence of hurricanes were only examined based on data limitations.

The final chapter (Chapter Five) is a brief summary of each of the proceeding chapters and a short discussion of the implications study results provide for management of red grouper and red snapper. Central to this discussion is an evaluation of the consequences imposed by the minimum size limit regulation on undersized red grouper and red snapper based on study results and the importance of including ecomorphology, fish physiology and predation as part of fisheries management for these two species.

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## Chapter Two: Hook Mortality Differences in Red Grouper (*Epinephelus morio*) and Red Snapper (*Lutjanus campechanus*)


### Abstract

To evaluate the efficacy of the minimum size rule for red grouper and red snapper a variety of approaches were undertaken to determine the role hook mortality plays in species survival. The first hypothesis tested was that there was no difference in hook release mortality between red snapper and red grouper. Necropsy results from headboat - client caught fish showed red snapper suffered the greatest acute hook trauma (49.1%), almost equaling all other sources (50.9%) of red snapper mortality combined. Only 20% of red grouper acute mortalities were attributed to hook injuries. Red snapper latent hook mortality (29%) was also much higher relative to red grouper (7%). Tag recaptures were used to test two null hypotheses; first, that there would be no difference in red grouper recapture rates for fish caught on circle and J hooks and second, there would be no difference in recapture rates of red snapper caught on circle versus J hooks. Both null hypotheses were rejected. Circle hooks reduced red grouper but not red snapper hook mortality. Red grouper recaptures were 14.0% (circle) and 7.3% (J) by hook type. Red snapper originally caught on J hooks (12.5%) had a higher recapture rate that those initially caught on circle hooks (8.1%). The next hypothesis tested was that hook mortality differences resulted from disparity in ecomorphology and feeding behavior. Dentition, jaw lever ratios, and feeding type and feeding behavior, including prey residence time in the mouth before swallowing differed between the two species. Red

grouper dentition included rows of small teeth that occurred on the top and bottom of the pre-maxilla, canine teeth on both the upper and lower mandible, and relatively high jaw lever ratios (.17 closing/.24 opening) consistent with jaws required for suction feeding. Red snapper dentition consisted of rows of larger teeth in both the upper and lower jaws with a reduced number of teeth in the bottom jaw and a set of large canine teeth present in the upper mandible but absent in the lower jaw. Red snapper top canine, top fused and depressible as well as bottom jaw tooth length was longer than those of red grouper. Red snapper dentition was indicative of a predator feeding on soft bodied elusive prey. Jaw lever ratios were high (.32 closing/.22 opening) signifying strong jaws. The null hypothesis that there was no difference in prey residence time in the mouth ($\bar{x}$ = red grouper: 6.62 seconds; red snapper: 3.74 seconds and SE = red grouper: 0.419; red snapper: 0.289) before swallowing between the two species was rejected as *t* test mean values were significant ($p =< 0.001$). Red grouper and red snapper demonstrate ecomorphological propensities in feeding morphology that translate into specific feeding behaviors that help clarify differences in J and circle hook mortality between the two species and may prove useful in designing predictive models for determining J and circle hook mortalities for other species.

## Introduction

Grouper landings, averaging 10.6 million pounds annually (1985-2001), were responsible for approximately one half of the aggregate reef fish landings. Of the six grouper species which account for 95% to more than 98% of total Gulf of Mexico grouper landings, red grouper (*Epinephalus morio)* dominated the landings with anywhere from less than five million pounds (1992 and 1998) to almost nine million pounds (1989). In 2004, a total of 2,041,530 lbs of red snapper and 3,190,281 lbs of red grouper were landed in Florida by these fisheries (NOAA Fisheries MRFSS, Richard Cody, Florida Fish and Wildlife Conservation Commission, personal communication). Red snapper (*Lutjanus campechanus)* is the most abundant snapper species landed in the Gulf (NOAA Fisheries MRFSS, Richard Cody, Florida Fish and Wildlife Conservation Commission, personal communication).

The minimum size rule has created a national catch and release program for recreational and commercial undersized fishes (Cooke and Cowx 2004, Bartholomew and Bohnsack 2005). Coleman et al. (2004) found recreational fishing significantly contributed to mortality in a number of marine fisheries including red snapper. Numerous factors can independently or synergistically affect release mortality (Gitschlag and Renaud 1994, Murphy et al. 1995, Chopin et al. 1996, Lee and Bergersen 1996, Nelson 1998, Wilde et al. 2000, Davis and Olla 2001, Neal and Lopez-Clayton 2001, Burns et al. 2002, Lucy and Arendt 2002, Miljard et al. 2003, Burns et al. 2004); however, trauma caused by hooks is the primary determinant of release mortality (Dextrase and Ball 1991, Bendock and Alexandersdottir 1993, Dubois et al. 1994, Render and Wilson 1994, Diggles and Ernst 1997, Malchoff and Heins 1997, Albin and Karpov 1998, Bettoli and Osborne 1998, Bettoli et al. 2000, Julliard et al. 2001, Ayvazian et al. 2002, Lukacovic and Uphoff 2002, Doi et al. 2004, Lindsay et al. 2004, Bartholomew and Bohnsack 2005). To evaluate the efficacy the minimum size rule for red grouper and red snapper a variety of approaches to determine the effects of hook mortality were undertaken. The first was to test the hypothesis that there was no difference in hook release mortality between red snapper and red grouper in the recreational and recreational-for-hire fisheries. To test this hypothesis hook mortality of red grouper and red snapper captured from headboats was assessed by three methods. Acute mortality was determined by necropsy. Direct observation of latent mortality in fishes held and monitored in 3,406 liter laboratory experimental tanks were monitored. Finally, survivorship of shipboard released fishes was evaluated.

In the tag/release portion, hook mortality between species was also assessed by hook type (J versus circle) using tag recaptures as a measure of survival. Circle hooks have been promoted by many within the fishing media and some fishery scientists as the most effective means of reducing hooking mortality. Due to the perception that circle hooks are beneficial for all fish species, they have become very popular in recreational and recreational-for-hire fisheries; however, fish survival varies among species (Cooke and Suski 2004). Results from published hook-type comparisons reveal differential efficacy of circle hooks with dramatically reduced mortality for some species (Prince et al. 2002, Skomal et al. 2002, Trumble et al. 2002, Falterman and Graves 2002), minimal or no benefit for other species (Malchoff et al. 2002, Zimmerman and Bochenek 2002, Cooke et al. 2003a, Cooke et al. 2003b) and severe injury to others (Cooke et al. 2003c). Recapture results were used to test two null hypotheses; first, that there would be no difference in recapture rates for red grouper caught on circle and J hooks and second, that there would be no difference in recapture rates of red snapper caught on circle versus J hooks.

Another part of the approach included examining fish dentition and mandibles of each species, determining jaw lever ratios and documenting differences in feeding behavior to assess whether differences in hook mortality were due to differences in mandible size, shape and dentition resulting in dissimilar feeding behaviors. The relationship of fish dentition and jaw morphology to fish feeding behavior (Motta 1984, Wainwright et al. 2001, Porter and Motta 2004) and its relationship to diet (Wainwright 1991, Mullaney, and Gale 1966, Hernandez and Motta 1997, Ward-Campbell and Beamish 2005) have been well established. Thus, the study approach was to film red grouper and red snapper in the laboratory to reveal and document feeding type and relate feeding behavior to jaw morphology.

## Materials and Methods

### *Acute Mortality*

Monitoring for acute mortality occurred in 1999 and 2003. Moribund red grouper (n=209) and red snapper (n=1,259) caught by hook and line during normal fishing trips aboard headboats fishing off Panama City, Daytona and St. Augustine, Florida were collected, quantified, placed in ice slurries and transported in coolers to the laboratory for necropsy. Fishing occurred at depths ranging 10.4 to 42.7 m.

In the laboratory all major body systems were examined for gross trauma and anomalies including the skin, eyes, fins, gills, heart, liver, spleen, swim bladder, stomach, and urinary bladder. Organ position within the body cavity was noted as well as any gross distortion or discoloration of organ tissues, ruptures or tears in any tissues, presence of gas bubbles, or hemorrhaging. Trauma and any anomalies encountered were noted and documented using a Canon® A20 digital still-camera. Based on necropsy findings, mortality was divided to three categories; hook injury, barotraumas, or "other" causes. The "other "category consisted of mortality caused by improper venting, stress, heat, or unknown causes when cause of death could not be ascertained.

*Latent Mortality - Direct Observations*

Live specimens of red grouper (n=46) and red snapper (n=241) were collected during some of the same fishing trips, transported to the laboratory and held for an observational period of up to one month to address latent fishing mortality. Upon arrival at the laboratory, before being released in holding tanks, fish were placed into 114-liter coolers filled with freshwater treated with 30 drops of 10% buffered formalin for 10 minutes to kill parasites. Fish were removed from the tanks, dipped a second time seven days later and transferred to new quarantine tanks. Fish were subjected to a third dip treatment before being placed in experimental tanks to kill any parasites that hatched from eggs not killed during previous treatments. The fresh dip "bath" water was removed from the coolers after each dip by opening the cooler drain and passing the water through a 202 μ mesh screen. Contents washed off the screen were collected, preserved and later examined under a dissecting microscope for parasites.

Fish were kept in 3,406-liter tanks with a re-circulating filtration system. Filtration included mechanical (filter floss), chemical (carbon), biological (fluidized bed), and ultraviolet (light) components. Water quality was strictly monitored daily to insure proper temperature, pH, salinity, dissolved oxygen, ammonia, nitrate, nitrite, chlorine, and hardness were maintained. A YSI® multi-probe monitor was used in conjunction with wet test kits to check water quality. Daily diet consisted of live shrimp and cut squid and/or fish. Fish were fed to satiety twice daily. A daily log of water quality, quantity of food consumed, fish condition, and any tank treatments such as partial water changes were noted.

*Fish Tagging*

Undersized red grouper and red snapper were caught using hook and line and tagged (red grouper: 1990-2007 and red snapper: 1999-2007) by Mote Marine Laboratory (MML) staff, student interns and volunteers, as well as by charter boat and headboat captains and crew, recreational, recreational-for-hire and commercial fishers throughout the eastern Gulf of Mexico and off the southeastern Florida coast (Figure 2-1). Tags and tagging kits, including instructions were provided. Fishes were tagged using single-barbed Hallprint® plastic dart tags inserted at an angle next to the anterior portion of the dorsal fin (Figure 2-2). Both large and small tags were used; tag size was determined by fish length.

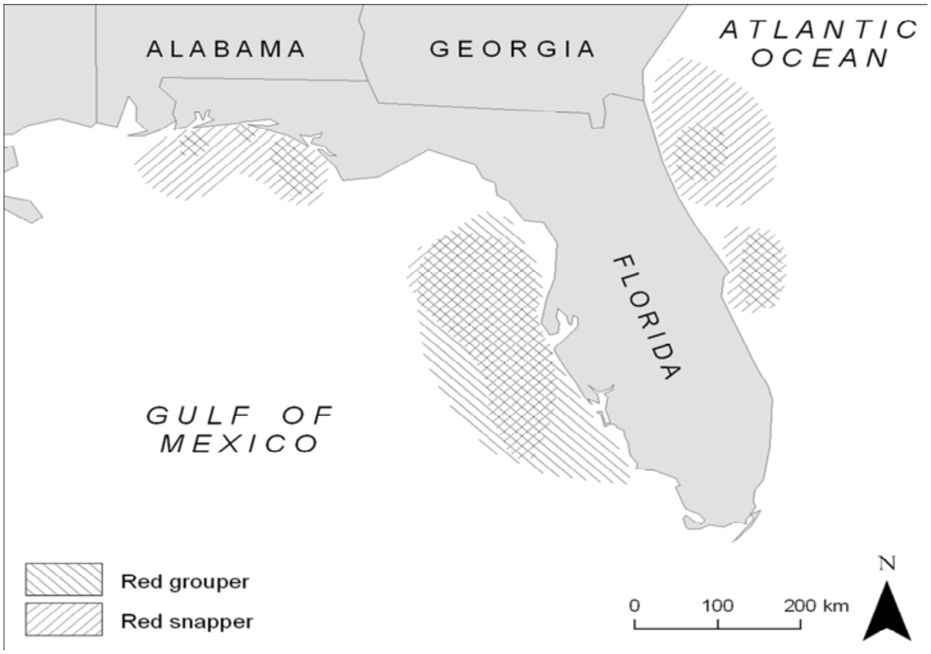


Figure 2-1. Tag and release sites for red grouper *(Epinephalus morio)* and red snapper *(Lutjanus campechanus).*

Figure 2-2. Tagging an undersized red grouper prior to release.

These tags had been used successfully in MML's Reef Fish Tagging Program. Data collected included tagging date, gear type, tag number, time of day, bait used, water depth, fork length in inches, fish condition upon release, amount of time the fish was out of the water, whether or not fish were vented and the capture location to the nearest 1 degree of latitude and longitude.

If fishes were vented before release, a fish venting tool was provided to volunteer fishers. Venting was accomplished by inserting the sharpened tube of a small diameter (e.g., 18-gauge) needle at a 45° angle through the body wall 2.5-5.1 cm from the base of the pectoral fin of the bloated fish. The venting tool was held in place until the majority of the expanded swim bladder gases were released from the fish's body cavity (Figure 2-3).

Figure 2-3. Venting a red grouper.

Tag information included tag number and the 1-800 dedicated telephone number at Mote. The telephone was answered personally during work hours and calls regarding tag return information were recorded on weekends, holidays and evenings by an answering machine. Recapture data including tag number, date of capture, gear type, bait type, water depth, fork length in inches, capture location, overall condition of the fish and of the area around the tag insertion site and whether the fish was kept or released, were recorded.

Data were entered on a PC computer using Paradox® software into a temporary file. Data entered into the temporary file were proofed by a second individual against the original data sheet. If no errors were detected, data were transferred electronically into the permanent reef fish database.

To Increase Recapture Reporting a publicity campaign including MML press releases, presentations at scientific conferences and fishing club meetings and publication of information in various issues of a MARFIN funded Reef Fish Survival Study (RFSS) newsletter, were used to disseminate project objectives and results. Copies of the newsletter were sent to all study participants as well as to fisheries scientists, fishery management agencies, industry representatives, and newspaper “outdoor” writers and fishing magazine writers, who requested them. In addition, a tag lottery was held at the end of each year. The winning tag was chosen from all tags returned during that year. Both the tagger and the person returning the tag each received $100.

A comparison of recapture rates for fish caught on circle versus J hooks was conducted to test two hypotheses. First, that there would be no difference in recapture rates for red grouper caught on circle and J hooks and second, that there would be no difference in recapture rates of red snapper caught by either hook type. Volunteer taggers from South Georgia to Texas were provided with 4/0 and 7/0 zero offset circle hooks either purchased or provided by Eagleclaw®. Other participants supplied their own hooks. Only zero offset circle hooks were used because of reports of trauma inflicted by offset hooks (Prince et al. 2002). An attempt was made to obtain equal numbers of fish by treatment by sending a quarterly newsletter to participants publishing the number of fish tagged by hook type by depth. Recapture data for both species were compared by gear type at various depths and treatments (J versus circle hook). Fish recaptures were used to estimate survival.

*Dentition and Jaw Lever Ratios*

Adult red grouper and red snapper carcasses were obtained from commercial fish houses to describe dentition and collect jaw measurements to determine jaw lever ratios. Adult fish were used because jaws can change during the juvenile stage. These measurements were used to mathematically describe the physical mechanism responsible for observed feeding behavior. Fishes were measured to the nearest mm TL, FL and SL. Gape was measured (mm) in both species by pulling down on the lower jaw until the mouth was open to its maximum width without overextension and using calipers to measure the distance between the jaw joint and the attachment of the adductor jaw muscles between the two coronoid processes on the jaw hinge.

Jaws from adult red grouper (542-691 mm FL) and red snapper (510-870 mm FL) were prepared by dissecting the mandible bones from the head manually removing as much soft tissue as possible. The jaws were soaked in very hot, but not quite boiling water to soften residual tissue. Forceps were used to remove any remaining tissue. Jaws were then soaked in bleach water for an hour. Following cleaning, jaws were dried for six hours at 49°C in a drying oven to desiccate overlying membranes to reveal tooth sockets. Mandibles were processed and tooth counts were made under a dissecting microscope following Weaver (2001).

Closing and opening jaw lever ratios were calculated following Wainwright and Richards (1995). The distance from the quadrato-mandibular joint (QM), or jaw joint to the anterior edge of the dentary (the tip of the front tooth) was measured to determine mandible length which was used as the out-lever measurement for estimating the lever ratios. The closing lever was then calculated as the ratio of the distance from the quadrato-mandibular joint (QM) to the insertion of the adductor mandibular muscle (AMM) divided by the out-lever distance.

$$\text{Closing in-lever} = \frac{\text{distance from QM to AMM}}{\text{Out-lever distance}}$$

The opening in-lever was calculated by dividing the distance from the insertion of the interopercular ligament (IL) to the quadrato-mandibular joint by the out-lever distance.

$$\text{Opening in-lever} = \frac{\text{distance from QM to IL}}{\text{Out-lever distance}}$$

Care was taken with each specimen to ensure measurements were consistent, i.e. taken at the same location for each fish. Observations and comparisons of red grouper and red snapper jaw type (variation in mandible size and shape) and dentition were recorded. Location, size and type of teeth were noted. A Canon® A20 digital still-camera was used to photograph the dentition of each species.

*Feeding Videos*

Healthy, laboratory acclimatized red grouper (8 fishes/group) and red snapper (15 fishes/group) were filmed during feeding experiments in separate 3,406 liter experimental tanks. Only fishes held in quarantine tanks for at least a month and deemed healthy were used. Fishes were kept and tested in groups because captive red snapper remained healthier and acted normally when multiple fish were kept together rather than when kept alone (personal observation). Because unique numbers imprinted on fish tags were too small to be read while viewing the videos, individual fish could not always be identified during the trials raising concerns of pseudo-replication (Hurlbert 1984, Machlis et al. 1985, Eberhardt and Thomas 1991). However, in an attempt to prevent pseudo-replication, individual characteristics, such as small differences in fish size, color, and other physical characteristics (one fish had an enlarged eye), etc., were noted. For consistency 36 large bait shrimp were used during each multiple trial. Fishes were fed to satiety so even less aggressive fishes were filmed feeding. Of the 57 red grouper and 56 red snapper feeding sequences filmed only 14 red grouper and 25 red snapper sequences were complete and used because fish either swam out of the field of view before swallowing or other fish swam in front of the camera obstructing the view.

Two cement blocks, the approximate size of the underwater camera housings, were positioned perpendicular to each other in the tanks and left overnight in the locations where the cameras were to be stationed. The next day, after fish had become accustomed to the cement blocks and ignored them, the blocks were removed and replaced with a SeaViewer Sea Drop® model 650 color camera (lateral orientation) and a Sony VX2000® camera in an Amphibico® housing (head on orientation). Both cameras recorded concurrently and the video feed was viewed simultaneously out of sight of the fish on a laptop computer screen positioned away from the tanks. All video was recorded in mini-DV format. To keep prey within the cameras' fields of view, a live shrimp was tethered to a 1.8 kg diving weight with either 4 lb. monofilament or a rubber band. The weight with the attached shrimp was placed at the intersect point of the recording fields of the two submerged cameras. Color video of both species' feeding behavior was recorded. DVDs of the videos at normal feeding speed and slowed to 1/8 normal speed were made using Turtle Beach Video Advantage® PCI model 1500-1 multi-media video capture software. Footage was used to determine feeding type.

It should be noted that the objectives of these observations were not to measure strike and prey capture kinematics, but rather establish feeding behavior type (ram feeding, suction, biting with oral manipulation, etc.) and determine the length of time prey was kept in the mouth before swallowing. Prey residence time in the mouth was determined by counting the number of frames /sec (based on the established time standard of 29 frames/sec) from prey capture to confirmed swallow while viewing the original videotape with Adobe Premiere Pro 2.0® software. Prey residence time was calculated by capturing and isolating each successful feeding sequence and subtracting the end sequence digital read out from the beginning read out. To provide a more accurate reading, the last part of the read out (the number of frames/sec) was converted to the corresponding fraction of a second based on the 29 frames/sec standard. Only video segments of the entire sequence of capture to confirmed swallow were used. Video of prey capture but no visual swallow or no visual of initial prey capture before confirmed swallow was discarded. Data were entered into an Excel file and a *t* test, using Sigma stat® for Windows® version 3.5 software, was performed on the timed observation data of confirmed swallows to test the null hypothesis that there was no difference between the two species in the time prey remained in the mouth before swallowing.

**Results**

*Acute Mortality*

During 1999 and 2003 when acute mortalities were noted and classified, 191 mortalities were recorded during tagging trips. The 191 fish included 171 red snapper (13.6% of all red snapper caught during this period and 20 red grouper (9.6% of all red grouper captured during this period). Of 171 moribund red snapper collected, J hook damage was the leading source of acute mortality, responsible for 49.1% of fatalities; more than double the J hook acute mortality rate (20%) for red grouper. Depth-related effects (barotraumas) accounted for 13.5% of red snapper mortality. No red grouper acute mortalities were attributed to depth-related effects as fish were caught at shallower depths than red snapper. Mortality in the "other" category claimed 37.4% and 80% of red snapper and red grouper, respectively. Based on necropsy findings, acute mortality was divided into three categories; hook injury, barotrauma, or other causes. Hook injuries included lacerations to internal viscera, gills and/or the esophagus. In severe cases, organs were macerated. In all cases, blood loss was severe. Hook orientation played an important role in determining the site of internal injuries; if oriented upward when swallowed it punctured the aorta or other sections of the heart or severed major blood vessels serving the heart such as the duct of Cuvier (the anterior cardinal vein) (Figure 2-4); if oriented downward it typically punctured or destroyed the liver (Figure 2-5). Depth-related injuries were easily distinguished from hook injuries and

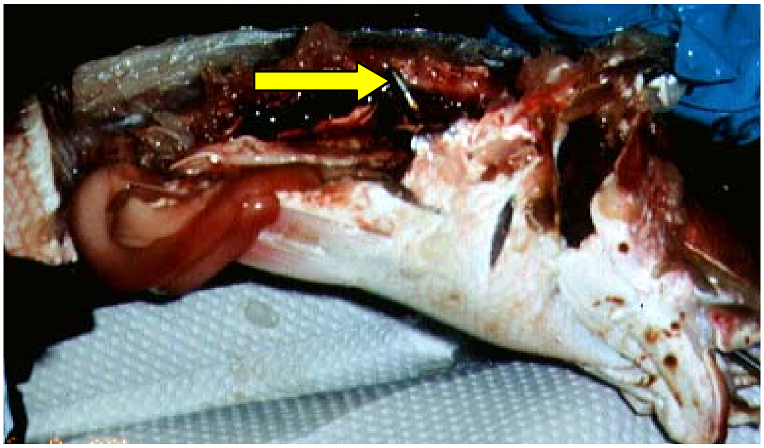

Figure 2-4. Red snapper killed by J hook trauma.

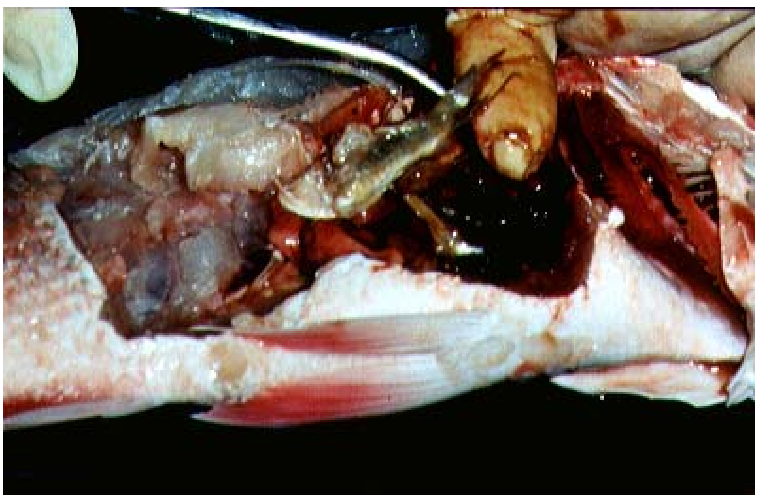

Figure 2-5. Red snapper killed by J hook macerating the liver.

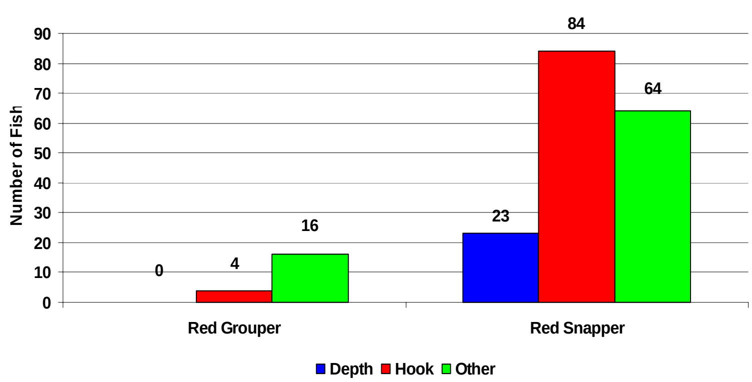


Figure 2-6. Number of red grouper and red snapper acute shipboard mortalities partitioned by cause of death (depth-related, hooking, other).

included severe exophthalmia, visible gas bubbles in the gills, viscera and blood vessels, and profuse hemorrhaging. Another key sign of barotrauma was stomach prolapse and extrusion through the oral cavity, caused by the expansion of swim bladder gases. The "other" category included improper venting, stress, heat, or unknown causes as well as when no determinate cause of death could be found (Figure 2-6).

*Latent Mortality*

Similar to acute mortality rates, red snapper deaths from latent hook mortality (29%) were much higher relative to red grouper (7%). Of undersized red snapper (n=241) caught on J hooks and transported to the laboratory from various fishing trips, 69 were dead upon arrival and 69 died in laboratory quarantine tanks. Trauma was not immediately apparent in the 69 red snapper that died of latent hook mortality. These fishes appeared healthy during transport, acted normally, and fed well the first two days of captivity. On the third day of captivity, they lost their familiar bright red color and ceased feeding and swimming. Death occurred on day five. Necropsies revealed hook damage to vital organs, however, rather than a puncture that caused acute mortality, injuries occurred when a J hook nicked a small area of a vital organ (usually the heart or liver) and "drop by drop", the fish slowly bled to death. Blood from the nicked organ pooled in the ventral coelom (Figure 2-7). Unlike the red snapper, only three of the 45 live red grouper

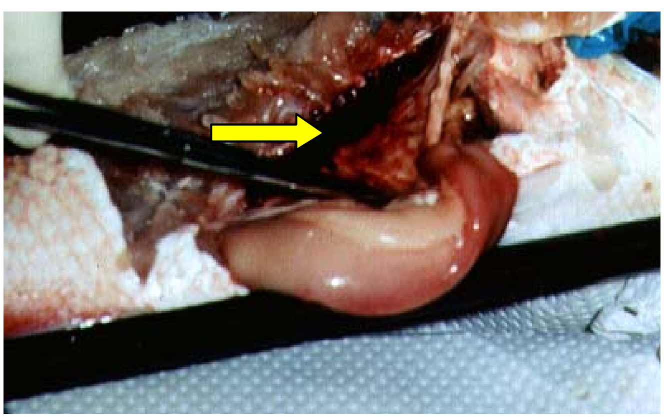

Figure 2-7. Pooled blood in a red snapper that died as a result of latent hook mortality.

caught on J hooks died of similar injuries. The remainder of both species in the absence of hook damage (n=42 red grouper and n=103 red snapper) not only survived, but grew and thrived during captivity.

Another observation of red snapper latent hook mortality was noted when a few emaciated pale sub-legal red snapper were caught during a fishing trip. Necropsies revealed these fish had been previously caught and the hook had longitudinally severed part of the esophagus resulting in the lower esophagus becoming a severed tube of necrotic tissue. Based on lack of blood and the state of the necrotic tissue damage, it was apparent the wound was not recent; however, no estimate of elapsed time between initial trauma and subsequent capture could be made. Another indication that trauma was not recent was the emaciated condition of the fish in the absence of any apparent disease. Damage to the esophagus rendered these fish incapable of feeding as they were unable to swallow. Being caught again demonstrated that although they still attempted to feed, the inability to swallow resulted in their emaciated condition and these fishes were in the process of eventually starving to death or becoming weakened easy prey for predators.

*Tag and Release and Circle versus J Hooks*

Between November 1, 2001 and September 30, 2007, red grouper (n=4,798) and red snapper (n=5,317) were tagged and released at depths ranging ≤ .5 m to ≥ 99 m. Most red grouper were caught at shallower depths ranging 12.5-21.3 m and 21.6 -30.5 m. Red snapper captures were more evenly spread over a broader depth range from 12.5-21.3 m-21.6-30.5 m and 30.8-61.0 m. The majority of red snapper were tagged at 21.7-42.7 m, while most red grouper were caught between 10.4 and 21.3 m.

Although more fish were tagged aboard headboats than recreational vessels, recapture data were lower from headboats than from the recreational fishing sector due to under reporting, rather than lack of recaptures. Only two headboat crews reported recaptures without direct assistance. Some fish tagged aboard headboats were recaptured in other sectors of the fishery.

Some fish were originally caught on J hooks; others on circle hooks (Table 2-1). Of 3,935 red grouper tagged, the recapture rate was 7.3% for J hooks versus 14.0% on circle hooks (Table 2-1; Figure 2-8). With twice as many recaptures of red grouper originally

Table 2-1. Number of red grouper and red snapper tagged and recaptured by hook type.

| **Species** | **J hook tagged** | **J hook recaps** | **% J hook recaps** | **Circle hook tagged** | **Circle hook recaps** | **% Circle hook recaps** | **G test *p* values** |
|---|---|---|---|---|---|---|---|
| Red Grouper | 3935 | 287 | 7.3 | 863 | 121 | 14.0 | $4.49 \times 10^{-8}$ |
| Red Snapper | 2145 | 269 | 12.5 | 3172 | 258 | 8.1 | $2.3 \times 10^{-6}$ |

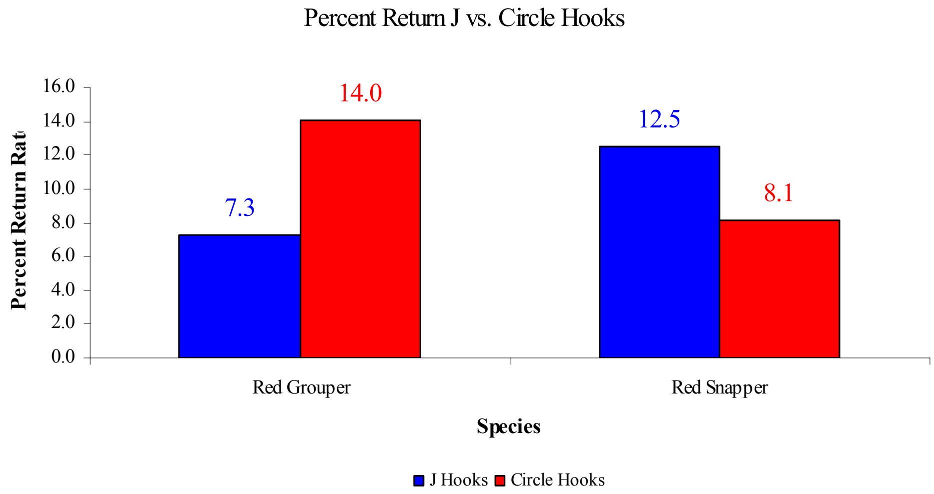


Figure 2-8. Percent return of red grouper and red snapper recaptured by hook type.

caught on circle hooks than on J hooks, red grouper clearly benefited from the use of circle hooks. Results of a log likelihood G –test were highly significant ($p$=5.78 x $10^{-8}$) (Table 2-1). A log likelihood G-test for red snapper returns by hook type was also highly significant ($p$=2.34x $10^{-6}$), but contrasted with those for red grouper (Table 2-1). Red snapper originally caught on J hooks had a slightly better recapture rate that those initially caught on circle hooks (12.5% vs. 8.1%) (Table 2-1; Figure 2-8). Pooled data from the recreational-for-hire and recreational fishing sectors showed no benefits in using circle hooks for red snapper, in spite of 1,027 more red snapper being caught on circle hooks than on J hooks. As one headboat tagged and recaptured a large number of red snapper, a G-test of circle versus J hook data restricted to recreationally caught red snapper was conducted. Results agreed with those reported for all fishing sectors combined; showing no benefit from using circle hooks and increased survival from J hooked fish. Based on these results, both null hypotheses were rejected. Red grouper clearly benefited from the use of circle hooks while red snapper recaptures revealed a slight increase in release survival of J hook captured fish.

Red grouper and red snapper returns by hook type and depth (≤ 27.4 m and > 27.4 m) showed that despite depth, circle hooks continued to enhance red grouper survival. Depth was a factor in red snapper hook recaptures. At shallow depths (≤ 27.4 m) there was only a slight difference in recaptures by hook type. At deeper depths (> 27.4m), twice as many red snapper originally caught on J hooks were recaptured (Table 2-2).

Table 2-2. Red snapper recaptures by hook type and depth.

| **Water** | **Depth** | **≤** | **27.4 m** |
|---|---|---|---|
| Hook Type | Tagged | Recaptured | % Recaptured |
| J | 1,660 | 220 | 13.3 |
| Circle | 1,437 | 185 | 12.9 |
| Water | Depth | > | 27.4 m |
| J | 585 | 49 | 8.4 |
| Circle | 1,765 | 71 | 4.0 |

*Dentition and Jaw Lever Ratios*

Red grouper averaged 526 teeth in the upper jaw and 201 in the lower jaw (Table 2-3). Although tooth size was small, rows of small teeth occur on the top and bottom pre-maxilla, with some pointed inward (Figures 2-9 and 2-10). Red grouper also possess canine like teeth located on the frontal margin of the red grouper upper and lower pre-maxilla (Figures 2-11 and 2-12). They had a larger gape than red snapper at equal body size for all fish measured (Figure 2-13).

Table 2-3. Red grouper specimen lengths, gape size and upper and lower jaw tooth counts.

| Fish | FL (mm) | TL (mm) | SL (mm) | Gape (mm) | Upper Jaw | | | | Lower Jaw | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Count | Canine | Outer Edge | Total | Count | Canine | Outer Edge | Total |
| RG1 | 635 | 662 | 560 | 69.38 | 407 | 2 | 31 | 440 | 142 | 2 | 46 | 190 |
| RG2 | 615 | 646 | 544 | 78.80 | 597 | 2 | 32 | 631 | 166 | 3 | 54 | 223 |
| RG3 | 623 | 654 | 550 | 72.90 | 478 | 2 | 29 | 509 | 132 | 2 | 44 | 178 |
| RG4 | 630 | 660 | 559 | 79.95 | 357 | 2 | 35 | 394 | 150 | 2 | 48 | 200 |
| RG5 | 656 | 685 | 578 | 68.85 | 493 | 2 | 36 | 531 | 177 | 2 | 44 | 223 |
| RG6 | 600 | 629 | 530 | 78.65 | 386 | 2 | 30 | 418 | 154 | 2 | 42 | 198 |
| RG7 | 600 | 632 | 526 | 73.05 | 373 | 2 | 31 | 406 | 140 | 2 | 58 | 200 |
| RG8 | 691 | 723 | 601 | 77.80 | 334 | 2 | 28 | 364 | 168 | 2 | 53 | 223 |
| RG9 | 646 | 677 | 562 | 64.15 | 560 | 2 | 37 | 599 | 137 | 2 | 44 | 183 |
| RG10 | 542 | 570 | 485 | 72.30 | 431 | 2 | 39 | 472 | 132 | 2 | 53 | 187 |

Table 2-4. Red snapper specimen lengths, gape size and upper and lower jaw tooth counts.

| Fish | FL (mm) | TL (mm) | SL (mm) | Gape (mm) | Upper Jaw | | | | Lower Jaw | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | *Count* | Canine | Outer Edge | Total | Count | Canine | Outer Edge | Total |
| RS1 | 640 | 683 | 565 | 59.20 | *587* | 1+2 | 25 | 615 | 79F | 0 | 30 | 109 |
| RS2 | 543 | 581 | 474 | 47.55 | *479* | 1+2 | 20 | 502 | 43F | 0 | 24 | 67 |
| RS3 | 645 | 680 | 563 | 56.10 | *585* | 1+2 | 24 | 612 | 57F | 0 | 33 | 90 |
| RS4 | 870 | 928 | 760 | 77.10 | *869* | 1+2 | 21 | 893 | 52F | 0 | 24 | 98 |
| RS5 | 510 | 548 | 450 | 50.95 | *419* | 1+2 | 23 | 445 | 70F | 0 | 28 | 98 |
| RS6 | 725 | 780 | 625 | 64.30 | *624* | 1+2 | 25 | 652 | 63F | 0 | 31 | 94 |
| RS7 | 819 | 881 | 727 | 80.60 | *712* | 1+2 | 21 | 736 | 53F | 0 | 31 | 84 |
| RS8 | 618 | 665 | 558 | 55.50 | *615* | 1+2 | 24 | 642 | 96F | 0 | 26 | 122 |
| RS9 | 555 | 594 | 488 | 50.65 | *560* | 1+2 | 23 | 586 | 84F | 0 | 32 | 116 |
| RS10 | 550 | 591 | 478 | 52.50 | *535* | 1+2 | 20 | 558 | 64F | 0 | 33 | 97 |
| RS11 | 654 | 705 | 565 | 56.70 | *645* | 1+2 | 21 | 669 | 35F | 0 | 28 | 63 |
| RS12 | 637 | 683 | 556 | 58.75 | *563* | 1+2 | 26 | 592 | 59F | 0 | 26 | 85 |
| RS13 | 589 | 630 | 510 | 52.55 | *478* | 1+2 | 25 | 506 | 55F | 0 | 25 | 80 |

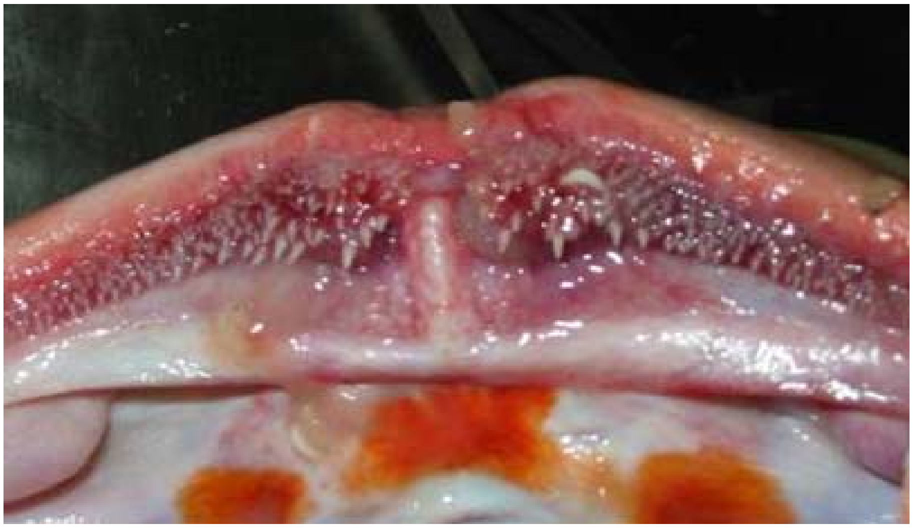

Figure 2-9. Multiple rows of small backward pointing teeth in red grouper top pre-maxilla.


Figure 2-10. Lower jaw dentition of red grouper showing inward pointing teeth.

Figure 2-11. Red grouper front upper dentition featuring canines. Size reference: each square = 5 mm x 5 mm.

Red snapper dentition consisted of approximately 616 teeth in the upper jaw and 93 teeth in the lower mandible (Figures 2-14 through 2-17). A set of large canine teeth was present in the upper mandible but absent in the lower jaw (Figures 2-16 and 2-17). Red snapper top canine, top fused and depressible tooth length was longer than those of red grouper (Figure 2-16 and 2-18). There were a reduced number of teeth in the red snapper bottom jaw (Figure 2-17) and a greater space between bottom teeth in red snapper than those of red grouper (Figure 2-12). Gape was smaller for red snapper than red grouper at comparable sizes (Table 2-4).

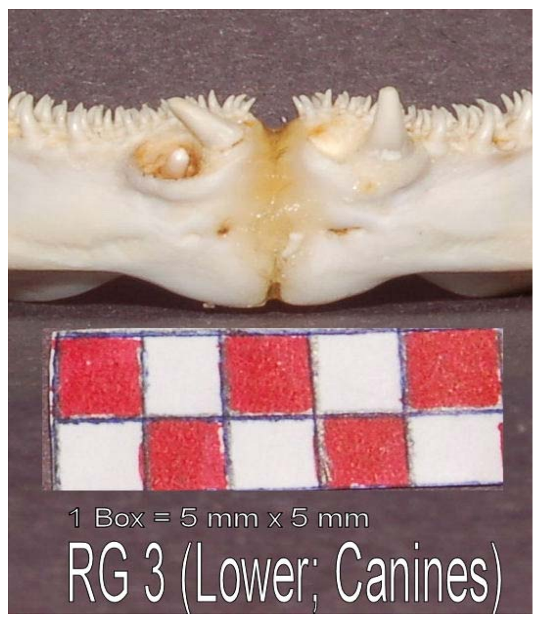


Figure 2-12. Red grouper front lower dentition featuring canines.

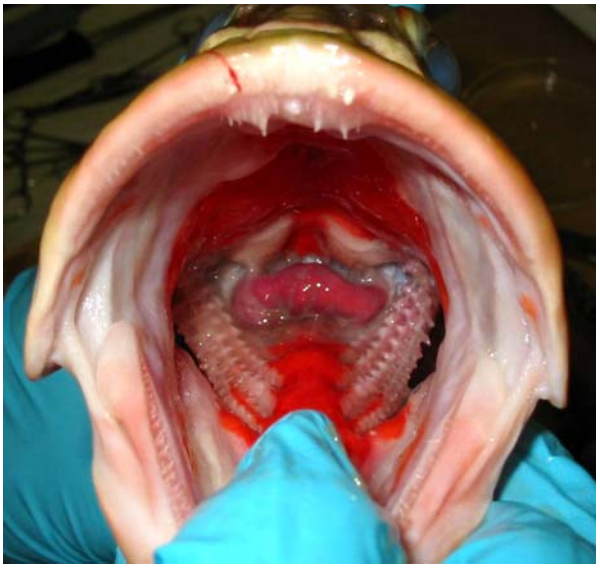

Figure 2-13. Red grouper upper canines and large gape.

Figure 2-14. Rows of sharp conical teeth in both the red snapper upper and lower jaws.

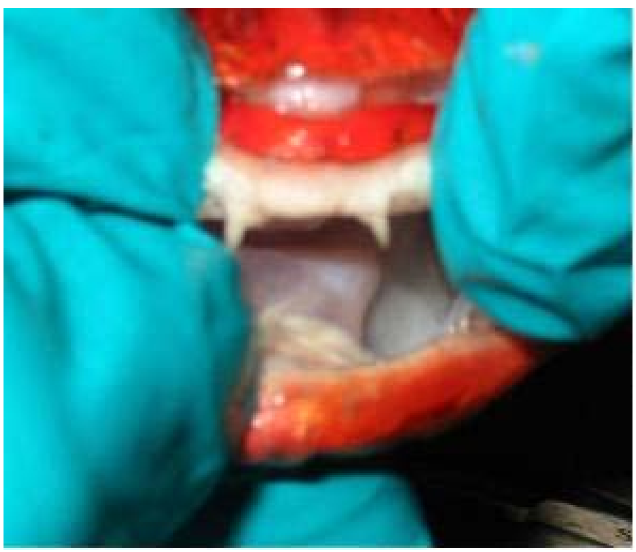

Figure 2-15. Red snapper upper canine teeth.

Figure 2-16. Lateral view of red snapper upper jaw showing canines and conical teeth.


Figure 2-17. Red snapper lower jaw frontal view showing the reduced number of conical shaped teeth in the lower mandible.

Figure 2-18. Lateral view of red grouper upper jaw showing canines and conical teeth.

Red grouper jaw lever ratios (0.17 closing/0.24 opening), were high. Red snapper jaw lever ratios were also high (0.32 closing/0.22 opening). Although both species had high jaw lever ratios, mandibular shape varied between the two species. The rear margin of the red grouper dentary was greatly extended because of the increased height of the ascending process and an extension of the posterioventral region creating a wide mandible. The red snapper ascending process was shorter and narrower (Figures 2-19 and 2-20).


Figure 2-19 Lateral view of red snapper lower jaw. Yellow arrow shows location of ascending process.


Figure 2-20. Lateral view of red grouper lower jaw. Yellow arrow shows location of ascending process.

*Feeding Videos*

Although both red grouper and red snapper were aggressive feeders, taped footage of the two species revealed marked differences in feeding behavior. Differences included the manner prey was approached, captured and consumed. Since the objective was to understand the effect feeding had on hook mortality, only observations of predator orientation, prey capture, and time prey remained in the mouth before swallowing were recorded.

Species differed in the manner prey was approached. All red grouper in the tank showed interest in prey when introduced but dominant fish (lighter colored fish) fed first and often guarded prey preventing those lower within the hierarchy from feeding. To circumvent this, dominant red grouper were segregated from lower ranking individuals after they fed to allow all fish in the tank to be filmed while feeding. Unlike the hierarchal feeding seen in red grouper, when prey was introduced into the tank, red snapper formed together in a tight school hesitating to approach the introduced prey until one fish began to approach the prey, at which point all fish swam toward the prey.

Video analyses revealed red grouper were ambush suction feeders. They approached prey, examined it and then enveloped it by expanding their large buccal cavity (Figure 2-21). Prey was orally manipulated (mouthed) and swallowed whole. Unlike red snapper, which immediately swam away from the prey capture site following prey acquisition, red grouper either remained at the site or slowly swam away mouthing captured prey. Other red grouper would attempt to steal an expelled shrimp or scan the immediate area for additional prey, but unlike red snapper, never tried to remove prey from the successful grouper's mouth. At times, tethered shrimp were expelled from the

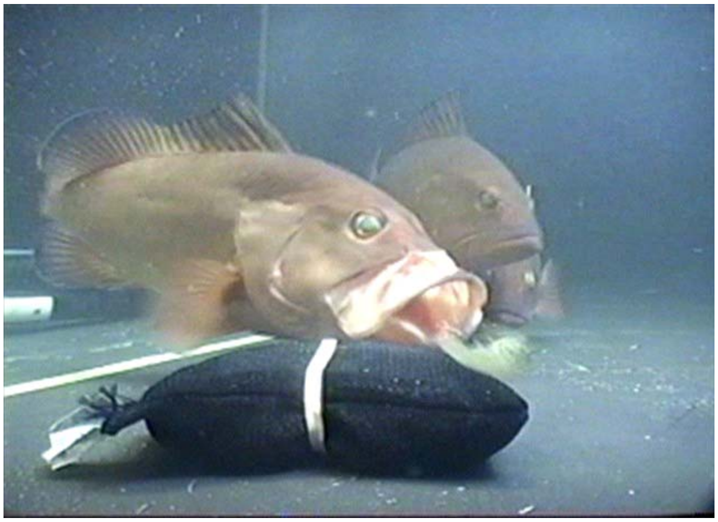

Figure 2-21. Red grouper exhibiting ram suction feeding. Note full buccal extension as the entire shrimp is drawn into the fish's mouth.

grouper's mouth because the fish's teeth did not sever the monofilament tether. In these instances, expelled shrimp were observed to be alive, completely unharmed, and if not for the tether, capable of escape indicating oral teeth were not involved in prey processing. However expelled shrimp were recaptured by either the original fish or by a nearby fish, especially if the other fish was of higher rank.

Figure 2-22. Red snapper exhibiting biting feeding behavior caught in the process of biting a shrimp in half before swallowing it.

Red snapper exhibited biting feeding behavior, approaching prey via high velocity lunges with open mouths using their canine teeth to sever the monofilament tether and bite the prey (tethered shrimp), often severing the shrimp into two parts (Figure 2-22). When this occurred, the first snapper took part of the prey; a second immediately took what remained of the shrimp carapace. Other red snapper tried to steal any piece of the prey protruding from the successful fish's mouth. This observation explained the behavior that immediately following prey acquisition, the successful fish swam away to escape surrounding conspecifics that mobbed it, trying to steal prey from its mouth.

On average, red snapper handled prey far less time than red grouper (red snapper $\bar{x}$=3.74 seconds, red grouper $\bar{\mathbf{x}}$=6.62 seconds) (Figure 2-23). The null hypothesis that there was no difference between the two species in prey residence time within the mouth before swallowing was rejected ($p$<0.001). Data passed the normality test ($p$=0.157) and the equal variance test ($p$=0.489). The difference was-2.373 and t = -4.339 with 37 degrees of freedom ($p$=< 0.001) with a 95% confidence interval for difference of means: -3.481 to -1.265.

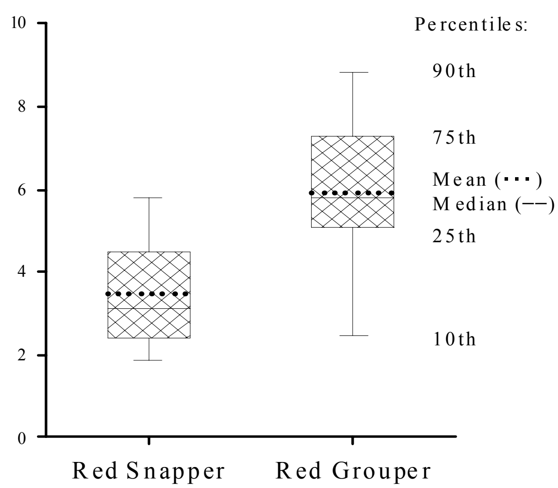


Figure 2-23. Difference in prey residence time in the fish's mouth before swallowing between red snapper and red grouper.

## Discussion

*Acute Mortality*

Red grouper did not show the severe obvious signs of hook mortality seen in red snapper. Necropsies of acute mortalities caught from headboats showed hook trauma was the leading cause of death for red snapper. Red snapper mortalities were highest at depths ranging 27.7-42.7 m (depth range where most fish were captured); however hook trauma not barotraumas caused most mortality (49.1%). Overall, hooking injuries were found to account for the largest overall percentage of red snapper mortalities. Comparing overall mortality rates between species showed 64.3% of the total red snapper catch died from hook trauma, almost double the 35.7% of red grouper that succumbed to hook mortality. It appears hooking injuries are far more common and harmful to red snapper than red grouper at depths ranging 27.7-42.7 m and that hooks have a much larger impact on red snapper survival than depth related effects at these depths.

*Circle Hooks*

Although circle hooks have become popular and are perceived by many to be an effective tool in significantly reducing hook mortality in all species, results from numerous hook survival studies are mixed showing some species benefit greatly from circle hooks, some moderately, while others show no survival difference between J and circle hooks and for a few species circle hooks have been shown to be detrimental (Cooke et al. 2003a, Cooke et al. 2003b, Cooke et al. 2003c, Cooke and Suski 2004). Some of the species which greatly benefit from being caught on circle hooks include juvenile bluefin tuna, striped bass, Atlantic and Pacific sailfish, yellowfin tuna, and Pacific halibut (Falterman and Graves 2002, Lukacovic and Uphoff 2002, Prince et al. 2002, Skomal et al. 2002, Trumble et al. 2002). Red grouper also benefited from circle hooks based on higher recapture rates. However, red snapper results agree with those of Zimmerman and Bochenek (2002) and Malchoff et al. (2002), for summer flounder, who reported that circle hooks were not more effective than J hooks in reducing hooking mortality. Rather, more red snapper originally captured on J hooks were recaptured.

Cooke and Suski (2004) wrote "Though much of the current literature shows the benefits from using circle hooks, the data are somewhat limited, and, in many cases, are somewhat conflicting". Although their meta-analysis results demonstrated, circle hooks reduced hooking mortality rates by roughly 50% versus J hooks for some species; they also reported that circle hooks were responsible for increased tissue damage in others. Circle hooks vary by whether or not the hook is offset and by the degree of offset. Malchoff et al. (2002) reported "hook offset may have negated the normal jaw hooking only pattern" typically observed with circle hooks. This is corroborated in the sailfish fishery where highly offset circle hooks were associated with significantly more deep hooking than minor offset (4%) and non-offset hooks (Prince et al. 2002). Although zero offset circle hooks were used in this study, there was a difference in survival in favor of J hooks for red snapper caught at shallow depths where barotrauma was not a factor. Red snapper appear to be one of the species, like summer flounder, where circle hooks do not provide increased survival over J hooks (Jon Lucy, Virginia Institute of Marine Science, personal communication); despite J hooks being the leading cause of red snapper mortality as determined by necropsy.

*Dentition and Jaw Lever Ratios*

Dentition differed dramatically between the two species as did variations in jaw morphology reflecting important differences in feeding methodologies. Prey type, disposition and feeding behavior are consistent with fish dentition and jaw morphology (Mullaney and Gale 1966, Wainwright and Richards 1995, Hernandez and Motta 1997, Porter and Motta 2004, Ward-Campbell and Beamish 2005). For example, Wainwright (1991) found that morphology could be used to predict comparative prey shell crushing ability in labrids.

Red grouper teeth were small and consisted of rows of teeth in the dentary and premaxilla that were caudally rotated, indicating these inward pointing teeth are used for grasping and holding during initial prey capture rather than piercing or slashing prey thus serving to prevent captured prey from escape before swallowing. Red grouper use their oral jaws for initial prey capture and their pharyngeal jaws for prey processing which are swallowed whole (Burns and Parnell in prep.). Stomach contents of wild caught red grouper showed most prey was swallowed whole but somewhat macerated. Adult red grouper feed on many different species of fishes and octopods, as well as a variety of crustaceans, including portunid, and *Callapa* crabs, shrimps, stomatopods, and palinurid and scyllarid lobsters (GMFMC 1981b). Weaver (1996) found crustaceans dominate the juvenile red grouper diet, while the adult red grouper diet consists of 50% fishes and 50% crustaceans.

The red snapper diet differs markedly from that of red grouper. Red snapper have larger teeth in both mandibles and fewer fixed teeth in the lower mandible. Many piscivorus species frequently have large teeth in the upper jaw and fewer fixed teeth in the lower jaw (Weaver 2000). This tooth spacing in the lower mandible strengthens tooth penetration into soft bodied prey. Although shrimp are the most common prey of juveniles, red snapper become more piscivorus after age one. Adult red snapper are characterized, as carnivores since their usual prey are fish and squid (GMFMC 1981b). According to Weaver (2001), increased tooth size, fewer teeth, probably increase capture success of elusive, soft-bodied prey, especially, fishes and squid as soft-bodied prey require less oral manipulation than those with hard shells or a carapace. Stomach content analyses of hook-and-line caught wild red snapper, revealed that although some food (small prey) was swallowed whole, there were often pieces of prey in red snapper stomachs. These results are in keeping with observed rapid lunging at prey and the use of canine teeth for slashing and biting prey, captured on the feeding videos.

Wainwright et al. (2001) reported on variation of prey approach by a variety of cichlid species as a result of differences in feeding behavior. This agrees with laboratory observations of taped red snapper and red grouper feeding behavior. Red snapper fed as a school with several individuals rapidly approaching a single prey item simultaneously. Their large canines were used to slash prey that was quickly swallowed. Often prey was cut in half by the first snapper to reach it, leaving the remainder to be snapped up by a conspecific. Unlike the rapid lunging and biting behavior observed during red snapper feeding, red grouper acted individually and exhibited suction feeding behavior appearing to examine the shrimp before creating a strong suction force to draw it into the mouth by extending its large buccal cavity and completely engulfing prey.

The teleost jaw operates as a system of two opposite lever devices, one for opening; the other for closing the mouth (Wainwright and Richards 1995, Westneat 1995). Mandibular dimensions and the associated biomechanical properties they determine have been studied for other fish taxa (Wainwright and Richards 1995, Westneat 1995, Albertson et al. 2005, Huber et al. 2005). Results show jaw shape is a major factor in determining biomechanical processes that govern a species' jaw functioning and feeding behavior. Lower jaw depression begins buccal expansion responsible for prey capture. A high lever closing ratio translates into decreased velocity of jaw opening but increased jaw strength. A high lever opening represents increased velocity (Wainwright and Richards 1995). Jaw level ratios were relatively high for both species but ratios showed they represented two feeding types. Red grouper are suction feeders; red snapper are biters.

As suction feeders, red grouper draw prey into their mouths via hydraulic pressure produced by buccal cavity expansion and the simultaneous expulsion of water through the opercula. The production of hydraulic pressure requires impressive jaw strength (Wainwright and Richards 1995, Westneat 1995). However with a lever ratio of 0.17 closing/0.24 opening, red grouper have jaws strong enough for suction feeding, but with a capacity for greater velocity for jaw opening and closing required for producing a rapid increase of buccal cavity volume while expelling water through the operculum to forcefully draw in entire prey. Red snapper (biters) have a jaw lever ratio of 0.32 closing/0.22 opening. The 0.32 closing ratio translates into greater biting force necessary for deep penetration of the large sharp canines in the upper jaw to grip and immobilize prey combined with the fewer farther spaced teeth in the lower jaw that enhances tooth penetration to bite prey into pieces easily (Weaver 2000).

Mandibular shape also varied between the two species. The rear margin of the red grouper dentary was greatly expanded through the height of the ascending process and an expansion of the posterioventral region creating a wide mandible. The longer the ascending process the greater the increase in added force transmitted to the jaw by the mandibular muscle (Wainwright and Richards 1995, Weaver 2000).

*Feeding Videos*

Different feeding behavior predicated on dentition and jaw ecomorphology appears to be a major factor responsible for differences in hook mortality between red grouper and red snapper. Although both species are aggressive feeders, video showed not only a marked difference in feeding behavior but also different prey residence times within the mouth. This is not unexpected as red grouper draw entire prey into their mouths and orally manipulate "mouth" it, before swallowing it whole whereas red snapper quickly caught, bit and swallowed pieces or small entire prey.

*Fish Ecomorphology and Hooks*

The divergent patterns seen in red grouper and red snapper dentition, jaw shape and the other morphological features determining feeding behavior appear to provide insights into factors responsible for J and circle hook mortality. How these species approach wild prey appears to parallel the manner in which they deal with bait on J and circle hooks. Although both are predators, red grouper and red snapper have evolved to fill different ecological niches feeding on dissimilar prey. Fishing with J hooks requires the angler to set the hook. Based on this premise, longer prey residence time within the oral area, allows more time for an angler to set a J hook before bait is swallowed. Red snapper, with a briefer prey residence time in the mouth before swallowing exhibited far higher acute and latent J hook mortality than red grouper that kept prey in the mouth and pharynx longer to orally manipulate it before swallowing. Red grouper use their oral jaws for initial prey capture and their pharyngeal jaws for prey processing (Burns and Parnell in prep.). It is during prey processing by the pharyngeal jaws that the angler feels the pressure or tug on the line and sets the J hook. Setting the J hook during prey processing in the pharyngeal jaws jerks the baited hook out of the pharyngeal jaws where it becomes lodged in the mouth or jaw. This process would explain the observed reduced hook mortality found for red grouper (Burns and Parnell in prep.).

Following this reasoning, red snapper, with a smaller prey residence time in the mouth, should have higher J hook mortality than red grouper. Once red snapper bite, prey are rapidly swallowed quickly passing through the pharyngeal jaws that are covered with sharp, fragile, canine teeth that serve to keep prey moving down the esophagus (Burns and Parnell in prep.). This modification of the pharyngeal jaws prevents prey or hooks from easily exiting them and reversing movement toward the mouth (Burns and Parnell in prep.). Tugging on the fishing line would more often result in gut hooked fish or other serious lacerating trauma to the esophagus, pharyngeal jaws and potentially the heart, liver or other internal organs (Burns and Parnell in prep.). This feeding mode appears to be occurring *in situ* because red snapper necropsy results of acute and latent mortalities caused by J hooks are consistent with injuries caused by J hooks being set while or after the fish swallowed the hook.

Fish feeding behavior based on ecomorphology may govern not only differences in J hook mortality but also the disparity with which species benefit from circle hooks. Study results comparing hook mortality among gag, scamp and red porgy (Overton and Zabawski 2003) showed a 24% J hook release mortality for gag and scamp, both picivores as adults, (Randall and Bishop 1967, Weaver 1996, 2000) versus 5% for red porgy, that feed primarily on invertebrates (Randall and Bishop 1967, Manooch 1977, Castriota et al. 2005). Gag recapture results by hook type in the MML database closely resembled those for red snapper (13.1% on J hooks and 9.9% on circle hooks; G-test: $p$=0.036939). Since both species share similar dentition and diets (Weaver 2001), this may explain J and circle hook results for these species were analogous but very different from red grouper results based on the ecomorphology.

Additional research on various species is needed to confirm that J and circle hook mortality is heavily dependent on ecomorphology and fish behavior rather than phylogeny. Variation resulting from ontogenetic and inter-specific differences in jaw strength and velocity may be species specific as species within the same family can occupy diverse niches as a result of differentiation in dentition and jaw lever ratios, leading to different feeding behavior. It may be that ecomorphology can be applied to traditional fishery management tools used to develop models to predict hook mortality susceptibility and determine the level of benefit a species would derive from the use of circle hooks and J hooks. Regulations used to manage fisheries are commonly applied to multi-species complexes and while beneficial to some species these regulations may either have no effect or be detrimental to others. However, ecomorphology could be a useful tool in ecomanagement not only in understanding how fishing affects a fish species' ecology, but by providing insights into predicting hook mortality estimates for other species commonly caught in the fishery. While MPAs are an important part of environmental management, insight into morphological features species have evolved to adapt to their ecological niches in the marine environment may allow for the development of methodologies to enhance survival by the ability to develop predictive models of mortality by hook type and provide new management strategies for these species in fished areas.

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## Chapter Three: Differences between Red Grouper (*Epinephelus morio*) and Red Snapper (*Lutjanus campechanus*) Swim Bladder Morphology and How These Differences Affect Survival during Rapid Depressurization


### Abstract

Depth induced mortality caused by trauma during rapid decompression acutely impacts survival of undersized reef fish discarded in compliance with minimum size regulations (Render and Wilson 1994, Gitschlag and Renaud 1994, Render and Wilson 1996, Collins et al. 1999). Although red grouper and red snapper suffered injuries caused by rapid decompression, mortality varied between species based on anatomy, physiology, and behavior. If not allowed to return to depth immediately, red grouper (*Epinephelus morio*) died from rapid decompression at shallower depths than red snapper (*Lutjanus campechanus*). Although Wilson and Burns (1996) have shown red grouper, gag, and scamp can potentially survive decompression in sufficient numbers to justify a minimum size rule if fish are rapidly allowed to return to the corresponding habitat depth, differences in morphology influence survival. This study tested multiple hypotheses which included: 1) red grouper were more susceptible to depth-induced mortality than red snapper at shallower depths, based on swim bladder size, thickness, and number and arrangement of rete mirabile and gas gland cells within the swim bladder; 2) smaller red grouper (< 30.5 cm) survive rapid decompression better than larger (> 38 cm) fish based on changes in swim bladder structure with fish length between 30.5-38 cm; 3) venting red grouper and red snapper is harmful to fish and does not enhance fish survival; 4) that

there is no difference in survival by gear type; 5) ascent rate does not affect red grouper survival from depth in fish traps, and 6) that in addition to pressure changes, other factors influence fish survival during rapid decompression. Objectives were accomplished by combining morphological and histological examinations to assess the general appearance of swim bladders, gas glands, rete mirable, and comparison of tissue hemorrhages from necropsies of red grouper and red snapper acute mortalities from fish caught off headboats. Results were compared with data from laboratory depth simulation experiments in fish hyperbaric chambers, a fish tagging study using tag returns as a proxy for survival and examining red grouper caught by commercial long-lines and fish traps. Red grouper had larger (in relation to body size), thinner swim bladders than red snapper. Red snapper swim bladder ruptures were smaller than those of red grouper. Red grouper > 38.1 cm FL had developed a star-shaped area of tissue on the posterior swim bladder ventral wall, absent in red snapper that incorporated some rete and a greater number of gas gland cells that aid in gas absorption and secretion. Beginning vascularization in this area was first visible under a dissecting microscope when red grouper length reached 31.8 cm. Overall red snapper survived rapid decompression better than red grouper because of a smaller quantity of gas in the swim bladder and less tendency to hemorrhage, especially in smaller fish. Swim bladders of both red grouper and red snapper ruptured with rapid pressure changes of 1 atm of pressure (10 m). In the laboratory both red grouper and red snapper easily survived rapid decompression from 21 m; however, 50% of red grouper suffered trauma at 27.4 m; red snapper did not. Differences in ability to tolerate rapid decompression increased with depth. Red snapper (40%) suffered mortality or sub-lethal effects during rapid decompression from 42.7 m.;

the remainder survived at 1 atm pressure. At the same depth red grouper mortality (75%) was much higher. At 61 m, 45% of red snapper died, but vented red snapper survived at 1 atm of pressure when vented. Red grouper never survived rapid decompression from 61 m to 1 atm pressure for more than 30 minutes, even when vented because emboli developed when fish could not return to simulated depths in holding tanks (Burns et al. 2004). Results of these investigations were compared with data from red grouper and red snapper fish tagging studies. Red grouper and red snapper caught off Florida were quantified and measured and tagged and released from recreational-for-hire, private recreational and commercial vessels by Mote Marine Laboratory (MML) staff, student interns, and volunteer taggers. At sea, red grouper survival from this depth and deeper occurred only if red grouper immediately returned to habitat depth. This difference in survival demonstrates that morphological and physiological differences between the two species described in this chapter determine the ability to adjust to rapid depressurization. Some red grouper caught on commercial long-line gear, tagged, released and vented were recaptured up to 2,172 days of freedom. Red grouper caught in commercial fish traps at depths of 61 m were less likely to suffer severely ruptured swim bladders. Swim bladders were intact and inflated or if ruptured, swim bladders had a smaller linear or pinhole wound rather than the large swim bladder rupture found on red grouper caught on hooks at any depth. Some trap-caught red grouper did not show the common external symptoms of rapid depressurization. However, necropsies revealed some fish with damaged swim bladders did have gases escape into the body cavity and exhibited torqued internal organs.

## Introduction

Trauma resulting from swim bladder rupture caused by rapid decompression from depth during fishing is a major factor contributing to mortality for physoclistic fishes (Burns and Restrepo 2002, Burns et al. 2004, Collins et al. 1999, Koenig 2001, Marshall 1970, Wilson and Burns 1996). The extent of internal trauma is depth dependent and intensifies as pressure increases. Internal trauma is characterized by external symptoms including stomach prolapse, exophthalmia, intestine prolapse and body bloating. Body bloating results in inability to return to habitat depth since fish are unable to control buoyancy. Floating at the surface, fish are subject to predation by seabirds, marine mammals and predatory fishes and are exposed to the elements. This highly visible loss of discarded live fish has been the source of much debate by fishers, scientists and fishery managers both nationally and internationally. Various techniques, such as fish venting (removing swim bladder gases from the fish's body cavity) and the rapid release rig (attaching a lead weight and a barbless hook upside down to fishing line, hooking the fish's jaw with the inverted barbless hook and quickly transporting the fish to the bottom) are just two methods used to return fish to habitat depth (Queensland FMA 1989, Collins et al. 1999, Burns 2001a, Shipp 2001, Burns and Restrepo 2002, Burns et al. 2004, Theberge and Parker 2005).

It was unknown if these techniques were merely cosmetic and sank fish or if they improved survival. Other unknowns included the fate of fishes with ruptured swim bladders, if a ruptured swim bladder healed, healing duration, if swim bladder rupture caused the same amount of trauma in all species, critical survival depths and effects of different gear types. Answers to these questions are critical because swim bladder rupture occurs with a change of 1 atm (10 m) and trauma intensity increases with depth. Although some fishing occurs at 10 m, most takes place at much deeper depths and fishers must comply with the minimum size law that mandates all undersized fishes must be returned to the water, regardless of condition. To be effective, a substantial portion of released fish must survive. This regulation has created an enormous national catch and release program whose merits continue to be debated (Bartholomew and Bohnsack 2005, Rummer and Bennett 2005, Wilde 2009). Investigations comparing survival of red grouper and red snapper at various depths and under a variety of conditions were conducted to address the efficacy of this regulation with regard to effects of barotraumas on these species. Results are provided in this chapter.

Like most marine teleosts, red grouper and red snapper have physoclistic (closed) swim bladders. Causes and implications of depth induced trauma in these two species were investigated using various methodologies including comparisons of acute mortality, swim bladder gross morphology and histology, laboratory depth simulations using fish hyperbaric chambers, a tag and release study in the eastern Gulf of Mexico and the South Atlantic off the state of Florida, a small fish trap study conducted in the eastern Gulf of Mexico and necropsies of commercial trap caught red grouper.

Investigation of how fishing gear and practices affect the fish swim bladder requires an understanding of swim bladder elements and their role in the normal functioning of the swim bladder operating under homeostatic conditions. The function and features of this hydrostatic organ have been described by various fish physiologists (Jones and Marshall 1953, Fange 1966, Marshall 1970, Pelster 1997). Morphologically, the fish swim bladder can be described as a gas-filled, ellipsoid sac located in the upper body cavity below the backbone and kidneys that develops as an outgrowth of the roof of the foregut. It is defined as open or physostome, if the link (pneumatic duct) with the foregut remains in adult fish. However, most (at least two-thirds) teleost swim bladders are closed (physoclistic). In some, the pneumatic duct is only present during larval stages, used to fill the developing swim bladder with swallowed air before it degenerates. In others, gas is formed by gas gland cells within the swim bladder (Marshall 1970).

The fish swim bladder evolved early and was common in many ancient fishes. Some ancient tassel-fins may have used them as a buoyant scuba tank as do modern lung-fishes that collect and store air swallowed at the surface. Although some teleosts, also utilize their swim bladders for sound production or as a hydrophone through connections with the ears, its main function is that of a hydrostatic organ. Some fishes, such as sharks, rays, mackerel and cobia lack swim bladders however for those species which have them, they conserve energy and allow the fish to remain neutrally buoyant with little effort even while stationary. To provide neutral buoyancy swim bladder capacity of marine fish must be approximately 5% of its body volume (Marshall 1970).

A marine species' swim bladder must not only be kept inflated at 5% of the fish's body volume but at a pressure equal to that of the surrounding water. Swim bladder volume follows Boyle's law making pressure and volume changes with changes in hydrostatic pressure. Pressure at the water's surface is 1 atm and increases by 1 atm, or 14.7 pounds per square inch, per each 10 meters of descent. A fish swimming near the surface is only subject to the pressure of 1 atm. At 10 meters the pressure increases to 2 atm, compressing the swim bladder to half its original surface volume. The fish becomes heavier than water allowing descent. To return to the surface and retain neutral buoyancy, the swim bladder must be inflated to its original volume, because returning to the surface decreases pressure in the swim bladder by half. The swim bladder expands as pressure decreases therefore the fish must deflate it to prevent over buoyancy inhibiting controlled movement (Marshall 1970).

Physostomes can quickly deflate their swim bladders by removing swim bladder gases during ascent by releasing gas through the pneumatic duct as bubbles through the mouth or gills. Physoclists are incapable of rapid deflation. They rely on diffusion of swim bladder gases via a dense network of bundles of arterial and venous blood capillaries called rete mirable housed within the swim bladder walls. They adjust resorption or secretion as needed. Swim bladder gases, often nitrogen, oxygen and carbon dioxide, diffuse into the rete as long as gas pressure within the swim bladder is greater than that in the capillary blood. Although difference in gas pressure varies with water depth, deflation rate is proportional to the area and complexity of the rete and to circulation speed. In many physoclists, gas absorption occurs in the oval, a distinct thin-walled area on the dorsal wall of the swim bladder that is in contact with the rete. The oval contains circular and radial muscles that open and close it. Contraction and expansion of these muscles, which are under neural control, either expose or limit rete contact with the swim bladder gases.

Although some physostomes can rapidly inflate their swim bladders, within one to two hours, by swallowing air forced down the pneumatic duct into the swim bladder, most physostomes and all physoclists obtain gases needed for swim bladder inflation through the gills and inflate the swim bladder by a slower method via gas secretion through gas gland cells that receive gas via the blood through the rete mirabile. This close association between gas gland cells and rete (Figure 3-1) is essential for swim bladder gas production

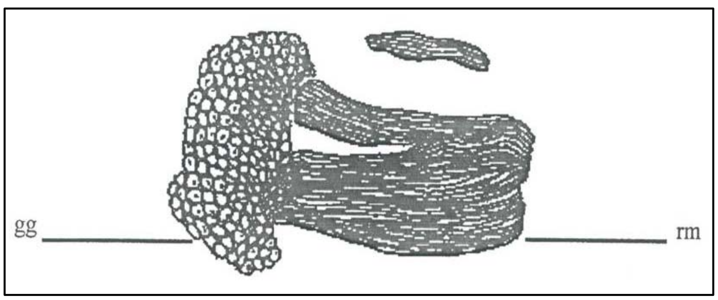


Figure 3-1. Illustration of the close association of the gas glands (gg) and the rete mirable (rm) in the red grouper swim bladder ventral wall.

not only to create gas pressures required to inflate the swim bladder but also to maintain gases within it. The tightly packed arterial and venous capillary bundles that compose the rete mirable system are arranged parallel to each other in a countercurrent arrangement providing an extensive contact surface area for gas exchange between arterial (ingoing) and venous (outgoing) capillaries that transport blood to and from the gas gland.

In the absence of this counter current, the swim bladder would lose gas through outgoing blood flow. This loss would not only prevent gas pressure maintenance but also inhibit swim bladder inflation because each of the swim bladder gases must be produced at a pressure greater than that already within the swim bladder. To inflate the swim bladder, the rete and gas glands must produce gas pressures at concentrations individually greater than the combined pressure of the gases within the swim bladder. Since the combined pressure of gases dissolved in water is equal at most to 1 atm increased pressure is achieved through a counter-current multiplication of gas retrieved from venous flow and carried back to the gas gland via the arterial capillaries ensuring the pressure of any gas eventually becomes greater than the combined pressure of the gases within the swim bladder.

To concentrate gases from the outgoing venous blood in the rete, the gas gland produces acidic metabolites, including lactic acid and carbon dioxide. These acidic metabolites reduce gas solubility in the venous capillaries and release some of the oxygen bound to hemoglobin. This increases gas pressure in the venous blood where it becomes greater than that in the arterial blood. This extra pressure results in gas diffusion from venous to arterial capillaries transporting gas to the gas gland, where it is concentrated and multiplied.

Gas deposition and secretion maintain the swim bladder at proper buoyancy keeping the fish neutrally buoyant. Both processes are under neural control as the swim bladder is innervated by the autonomic nervous system through branches of the vagus nerves. Excitation of appropriate nerves results in the correct response of gas deposition or secretion. However, fish with closed swim bladders, brought to the surface from depth during fishing, are unable to decompress rapidly enough to compensate for the fast pressure changes responsible for swim bladder rupture.

When the swim bladder ruptures, swim bladder gases are immediately released into the fish's body cavity causing internal trauma. Trauma severity is dependent upon the quantity of gas released (depth dependent) and fish physiology. External signs of trauma include various degrees of body bloating, stomach prolapse, exophthalmia, gill hemorrhage and intestine protrusion from the anus. There is much debate if fishes survived this trauma and what the lasting effects might be for survivors. Like most marine teleosts, red grouper and red snapper have physoclistic (closed) swim bladders. Causes and implications of depth induced trauma in these two species were investigated by approaching the problem using various methodologies including comparisons of acute mortality, swim bladder gross morphology and histology, laboratory depth simulations using fish hyperbaric chambers, a tag and release study and comparison of gear types (hook-and-line, commercial long-line and commercial reef fish traps). Six hypotheses were tested. They included 1) red grouper are more susceptible to depth-induced mortality than red snapper based not only on swim bladder size and thickness, but also on the number and arrangement of bundles of rete mirable and gas gland cells within the swim bladder; 2) smaller red grouper (< 30.5 cm) survive rapid decompression better than larger (> 38 cm) red grouper because of changes in swim bladder structure with size (between 30.5-38 cm); 3) venting red grouper and red snapper is harmful to fish and does not enhance fish survival; 4) survival rates for fish caught at the same water depth were unaffected by gear type; 5) ascent rate does not affect survival from depth in fish traps, and 6) other factors in addition to pressure changes influence fish survival during rapid decompression.

**Methods**

*Acute Mortality*

Moribund red grouper and red snapper caught on hook-and-line that were landed dead or died on deck during normal fishing trips aboard headboats fishing off Panama City, St. Petersburg, Sarasota, Venice, Ft. Myers, Daytona and St. Augustine, Florida and the Dry Tortugas, were collected, quantified, placed in ice slurries and transported in coolers to the laboratory for necropsy. In the laboratory all major body systems were examined for gross trauma and anomalies including the skin, eyes, fins, gills, heart, liver, spleen, swim bladder, stomach, and urinary bladder. Fish were also checked for any changes in the position of organs within the body cavity, gross distortion, discoloration, ruptures or tears in any tissues, presence of gas bubbles, or hemorrhaging. Trauma and any anomalies encountered were documented using a Canon® A20 digital still-camera. Mortality was divided to three categories based on necropsy findings: hook injury, barotraumas, or “other” causes. The “other” category consisted of mortality caused by improper venting, stress, heat, or unknown causes when cause of death could not be ascertained.

*Swim Bladder Differences*

Swim Bladder Collection and Processing:

To collect information on swim bladder structure, a relatively small number of fish were selected spanning the size range (under permitted trips where fish could be retained regardless of size). Upon arrival at the laboratory, specimens were logged in to continue documenting chain of custody. Fish were measured and examined for external and internal signs of barotraumas, disease or abnormalities. Swim bladders were examined for inflation or rupture and to assess the general appearance of the bladder before measurement to determine the approximate size ratio of red grouper and red snapper swim bladders in relation to fish length. Excised fresh swim bladders were fixed, preserved in 10% formalin and placed into labeled jars. Swim bladder gross morphology was examined under a dissecting microscope and a comparison made between the two species. Sections of the swim bladder were embedded in paraffin, sectioned at 4 micrometers and stained in hematoxylin and eosin to examine gas glands, rete mirabile and any hemorrhaging. Intact, ruptured and histological sections were examined and photographed. Swim bladder and trip data were entered on a PC computer using Excel spreadsheets.

*Laboratory Simulations of Depth Effects Using Fish Hyperbaric Chambers*

Live Fish Collection and Fish Sanitation Protocol

Before experiments were conducted, red snapper were brought into the laboratory to determine water quality parameters necessary to maintain excellent health over time. Red snapper not maintained under the strictest water filtration and water quality protocols were prone to parasite infestation, disease and ill health irregardless of fish density and fish care. When tested in the hyperbaric chambers fish not maintained under very strict sanitation protocols sustained more sever injuries and fewer fish survived. To ensure healthy fish, seawater was subjected to numerous filtrations. Seawater brought in through intake pipes in Sarasota Bay passed through a course sand filter on its way to ozination and storage. From the storage tanks, water was passed through a fine sand filter, biological filter, fluidized bed and finally through UV light filtration before reaching tanks. Each tank was its own system (each tank had its own biological filter, fluidized bed and 4-bulb UV light filter) and isolated from all other tanks. All equipment associated with each tank (nets used to add or remove fish, beakers to collect water quality, etc.) were labeled and used exclusively for that tank.

Undersized red grouper and red snapper were captured by hook- and-line aboard headboats and held in 208-liter coolers or in shipboard live wells. Fish were transported to the laboratory in 946-liter tanks equipped with oxygen and kept at capture water temperatures. Upon arrival, fish were placed in other 208-liter coolers for a 5-minute freshwater dip treated with Formalin solution (2 drops 37% Formalin/3.8 liters of water) to remove ectoparasites and gill trematodes. Fish were also dipped 7, 14 and 21 days after the first dip treatment to kill any ectoparasites that hatched after the first dip. Fish received a final dip, on day 28, before being transferred from quarantine tanks to experimental holding tanks. Following each dip, dip water was filtered through a 202 μ mesh sieve. Sieve contents were collected and viewed under a dissecting microscope to identify any parasites. Fish were quarantined for one month to identify any health or parasite problems, to eliminate the possibility of complications from latent hook mortality, and to acclimate fish to handling and laboratory surroundings. Fish were fed chunks of fresh fish and live shrimp daily until all fishes were sated. Food quantities were monitored. Tanks and filters for each tank were cleaned and water chemistry checked daily. Following quarantine, fishes were divided into different experimental groups and well fed before being placed in the hyperbaric chambers.

*Laboratory Pressure Experiments*

Year 1

Hyperbaric chambers (described in Wilson and Burns 1996, shown as Figure 3-2), were used to produce laboratory simulations of pressure changes red grouper and red snapper

Figure 3-2. Series of fish hyperbaric pressure chambers situated over a 1,000 l tank, used in the pressure simulation experiments.

would experience during capture from depths of 21.3, 27.4, 42.7 and 61.0 m (31 *psi*, 40 *psi,* 63 *psi* and 90 *psi*, respectively). Depths were chosen to match important capture depths in the fish tagging study. Four chambers were used simultaneously, providing four replicate samples. After fish were acclimated to conditions within the chamber, observations of gauge pressure and fish behavior/orientation within each chamber were made and recorded every 30 minutes. Observations of fish behavior were made through an acrylic view plate (Figure 3-3). Acclimation was confirmed when fish became neutrally buoyant and achieved an upright (vertical) orientation within the chamber following initial tendency to list or lie on its side at the bottom of the chamber. Pressure within the chambers was increased in a step-wise manner until experimental depth simulation was achieved. When acclimation was confirmed, hydrostatic pressure within the chamber was rapidly decreased (rate approx. 2-3 m/sec to ambient at 1 atm),

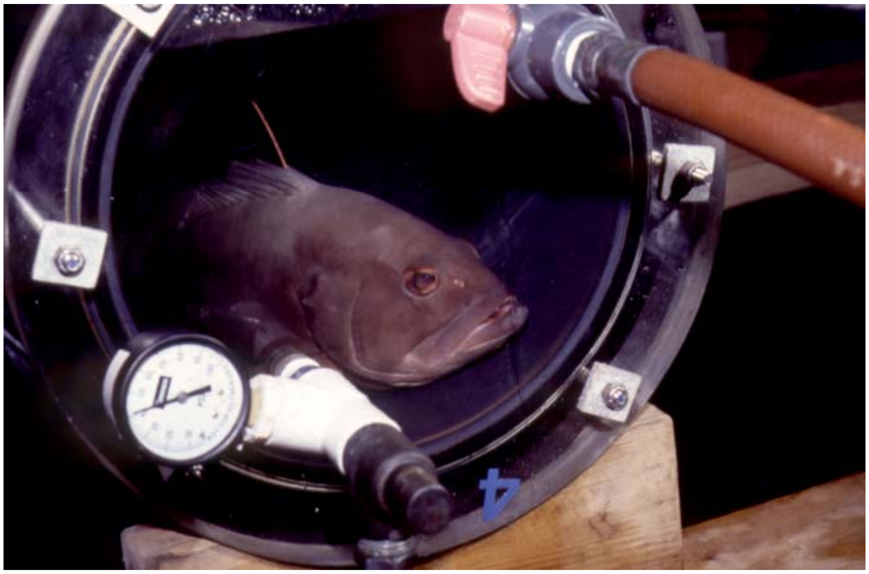

Figure 3-3. Red grouper in one of the fish hyperbaric chambers as observed through the acrylic view plate. Tags with unique numbers identified each experimental fish.

whereupon the fish was removed from the chamber as quickly as possible. During the first year, all chambers were depressurized simultaneously. During year two, each chamber was depressurized individually so fish in each chamber were unaffected by pressure changes occurring in another chamber during recompression. A stopwatch was used to time handling time for each fish and all times were recorded. Timing began when the pressure gauge reached 0 *psi* (1 atm ambient) and ended when the fish was released from the chamber.

Upon removal from the chamber, fish were vented and released into holding tanks. Immediately following venting, one fish from each experiment was anesthetized with

MS222, sacrificed and necropsied to determine the extent of internal trauma sustained from that depth simulation. The remaining fish were released into holding tanks to heal. A second fish was sacrificed 2-4 days after being removed from the chamber and a third after seven days to document healing. During year two, the fourth experimental fish was kept for long-term (1-2 months) observation. After all experiments were completed, this last group of fish was divided by species. The red grouper were sent to the Florida Aquarium in Tampa and the red snapper were moved to the large exhibit tank at Mote Aquarium.

All major body systems were examined during necropsy for any gross trauma or anomalies that could have been caused by rapid depressurization. The skin, eyes, fins gills, heart, liver, spleen, swim bladder, stomach and urinary bladder of each fish were examined. Observations included organ position within the body cavity, gross distortion or discoloration of organ tissues, gas bubbles, ruptures or tears in any tissues and hemorrhaging. A digital still-camera was used to document any trauma and anomalies found.

Year 2

During the second year, an additional pressure experiment using the hyperbaric chambers was conducted to examine fish acclimation times during controlled ascents from simulated depths of 21.3, 27.4 and 42.7 m. Red grouper and red snapper were acclimated to depth as in all other experiments; however, depressurization was initiated in stepwise increments allowing the fish to acclimate to each new depth (pressure) before continuing the next incremental decrease in pressure. Chamber pressure was decreased gradually until the fish exhibited symptoms of depth related stress, such as increased buoyancy, downward oriented swimming, or bloating, at which time the amount of pressure within the chamber was maintained. The *psi* on the pressure gauge was recorded at each stopping point. Fish remained at this stopping point until acclimation was affirmed when the fish exhibited neutral buoyancy. Once neutral buoyancy was achieved, *psi* within the chamber was decreased further until outward symptoms of depth related stress again manifested. Fish were then held at this new pressure until acclimation was confirmed. This stepwise decrease in chamber pressure carried out in increments continued until fish were at ambient pressure (1 atm) at which point, fish were removed from the chambers. Acclimation times were recorded. Necropsies were performed using the same schedule as above to determine if any trauma took place during controlled ascents.

*Fish Tag and Release*

Fish Tagging

Undersized red grouper and red snapper were tagged by MML staff, student interns and volunteers, as well as by charter boat and headboat captains and crew, private recreational and commercial fishers throughout the eastern Gulf of Mexico and off the southeastern Florida coast (Figure 3-4). Undersized red grouper were also tagged and released by MML staff and a trained observer in the southeastern Gulf of Mexico, aboard various commercial reef fish long-line vessels out of Madiera Beach, Florida. Tags and tagging kits including instructions were provided to all.

All fish were tagged using single-barbed Hallprint® plastic dart tags inserted at an angle next to the anterior portion of the dorsal fin. Both large and small tags (for juveniles) were employed. These tags have already been used successfully in MML's Reef Fish

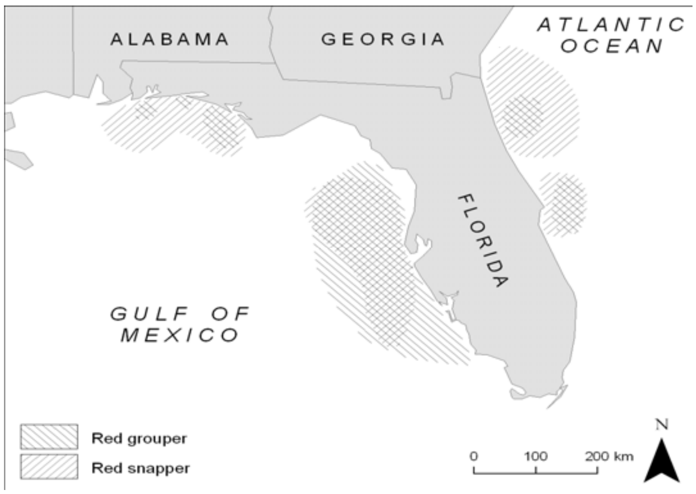


Figure 3-4. Study area where red grouper and red snapper were tagged.

Tagging Program. Data collected included tagging date, gear type, tag number, time of day, bait used, water depth, fork length in inches (converted to metric in the lab for analyses), fish condition upon release, amount of time the fish was out of the water, whether or not fish were vented and the capture location to the nearest one degree of latitude and longitude.

To determine if fish venting was harmful two treatments were employed. 1) Over a 10-year period (1997-2007), Mote staff, student interns and volunteers aboard recreational-for-hire and private recreational vessels released captured tagged fish; 2) the other half were also vented before release. Venting instructions were provided in tagging kits, in Florida Sea Grant brochures, in copies of newsletters provided to fishers and through a Mote website video produced to teach proper venting techniques. Half of the captured fish were tagged and released, the other half were also vented before release. If fishes were vented before release, a fish venting tool was provided to volunteer fishers. Venting was accomplished by inserting the sharpened tube of a small diameter (e.g., 18-gauge) needle at a 45° angle through the body wall 2.5-5.1 cm from the base of the pectoral fin of the bloated fish. The venting tool was held in place until most of the expanded swim bladder gases were released from the fish's body cavity. Fish were subject to both treatments regardless of depth. In deeper waters (> 27 m) fishes were vented to test venting as a tool to enhance survival from barotrauma. In shallow waters (< 21 m) fishes were vented to determine if venting in and of itself was hazardous to fish health, by introducing pathogens into the fish's body from the venting tool or by causing damage to internal organs.

Tag information included tag number and the 1-800 toll-free dedicated telephone number at Mote. The telephone was answered personally during work hours and calls regarding tag return information were recorded on weekends, holidays and evenings by the answering machine.

Return data including tag number, date of capture, gear type, bait type, water depth, fork length in inches, capture location, overall fish condition and of the area around the tag insertion site and whether the fish was kept or released were recorded. Data were entered on a PC computer using Paradox® software into a temporary file. A second individual proofed the entered data against the original data sheet. If no errors were detected, data were transferred electronically into the permanent reef fish database. Recapture data for both species were compared by gear type at various depths and treatments (vented vs. not vented).

Fish recaptures were used to estimate survival. Evaluation of survivorship was accomplished by comparing study results with those of other Mote studies, as well as by integrating the new data into MML's ongoing long term reef fish tagging program (discussion in Schirripa et al. 1993, Wilson and Burns 1996), as these data have proven very reliable (Schirripa and Burns 1998).

To increase recapture reporting a publicity campaign including MML press releases, presentations at scientific conferences and fishing club meetings and publication of information in various issues of a MARFIN funded Reef Fish Survival Study (RFSS) newsletter, were used to disseminate project objectives and results. Copies of the newsletter were sent to all study participants as well as to fisheries scientists, fishery management agencies, industry representatives, and newspaper “Outdoor” writers and fishing magazine writers, who requested them. In addition, a tag lottery was held at the end of each year. The winning tag was chosen from all tags returned during that year. Both the tagger and the person returning the tag each received $100 funded by MARFIN projects.

*Fish Trap Study*

Six commercial reef fish traps were deployed during two offshore fishing trips off the commercial long-line vessel *Bold Venture* out of Madiera Beach, Florida to compare trap caught fish condition with fishes caught on commercial long-line at comparable depths as part of CRP Project # NA03NMF4540417. To determine if trap ascent rate affected survival of commercial trap caught fish, two treatments were employed. Traps were deployed off a commercial long-line vessel and after a 4-hour soak time (at one station soak time was 14 hours due to weather conditions), were hauled to the surface either by hand or by the winch used to deploy and retrieve the long-line cable. Trap recovery by treatment alternated among traps. If the first trap was hauled to the surface by hand, the second was retrieved by winch. Ascent rates for both treatments at all depths fished were timed with a stopwatch and recorded. Data were entered into an Excel spreadsheet after the trip.

Six study sites were chosen based on water depth and because red grouper had been captured at these locations previously during regular long-line fishing trips (Figure 3-5). Site coordinates were recorded to the nearest 1-minute of latitude and longitude to prevent reporting exact fishing locations. Traps were baited with mackerel and squid and fished for four hours with the exception of one site that was fished for 14 hours due to weather. Six sites were fished using multiple traps (5-6 per site). Site depths ranged 52.4-115.8 m.

Fish behavior during trap retrieval was filmed by sliding a SeaViewer® underwater color camera with a 46 m video cable down the buoy line so fish within the trap could be videotaped during ascent. The camera cable was attached to a shipboard Sony®GV-D 900 digital video recorder to provide real time viewing of trap ascent, allowing for

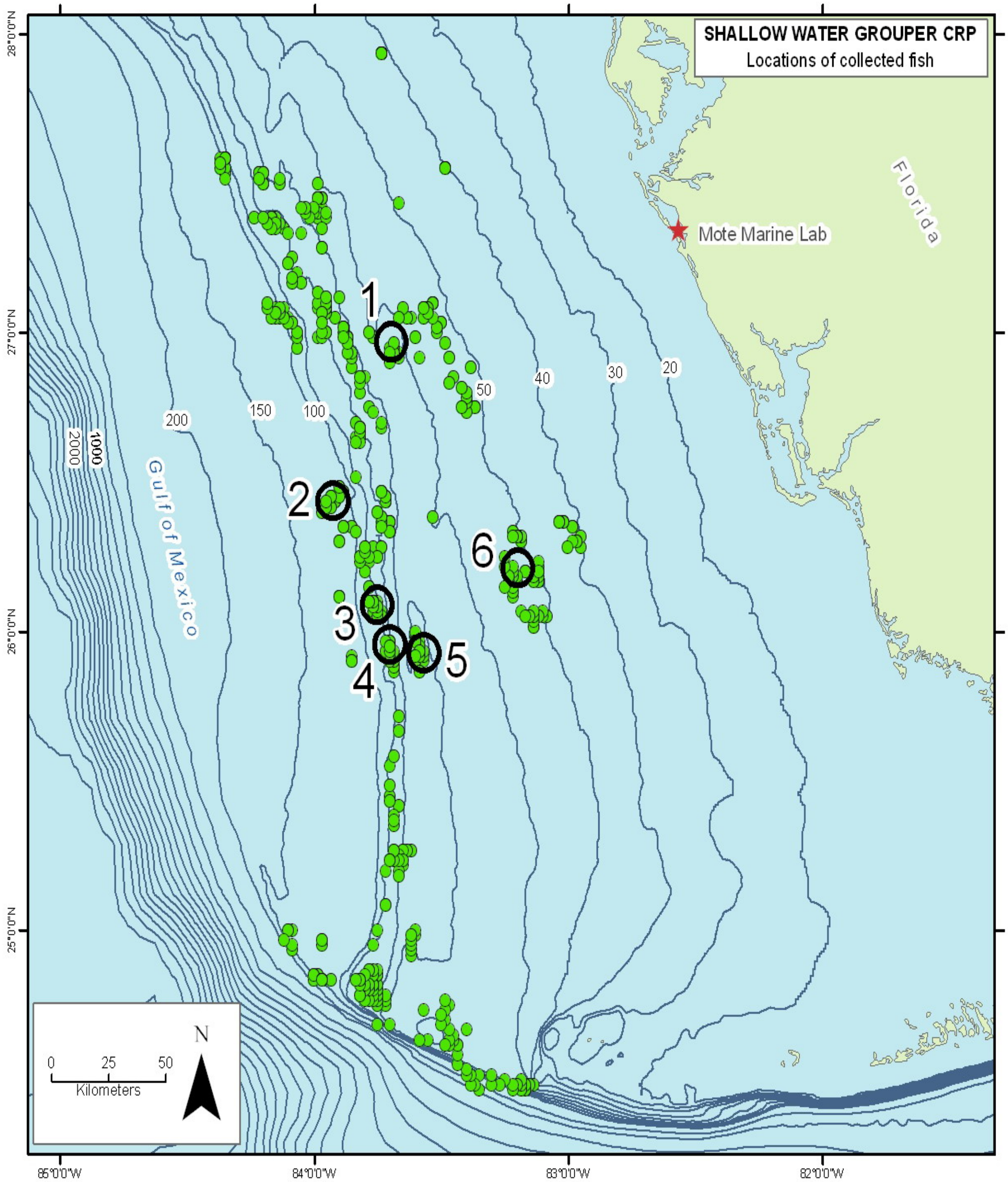


Figure 3-5. Fish trap study sites. Water depths are in meters. Distance is in km.

observation of behavior and condition of captured fish within the traps. As traps were hauled to the surface, video data were stamped with the time, date, and GPS coordinates. After traps were recovered, filming focused on the fish within the recovered traps on deck and after their removal from the traps. All fish caught were identified, counted and their condition noted. Most fish, regardless of condition, were released with release condition (swam straight down, swam down slowly or floated) noted. Only red grouper were tagged with Hallprint® plastic dart tags before release. A few red grouper specimens were kept to determine the condition of the swim bladder and internal organs. No red snapper were caught in the traps.

*Red Grouper Purchased from Commercial Fish Trappers*

Ten legal sized red grouper were purchased from commercial fish trappers (depths ranging 55-61 m) to determine if these commercially caught fishes showed common external and/or internal symptoms of rapid depressurization and to compare fish condition caught by commercial fish trappers during a normal fishing trip and fish caught during the previously described fish trap experiment. Necropsies were conducted because commercial trap fishers asserted that most red grouper caught in traps, even at deeper depths (62 m) survive and show little or no external signs of depth-induced trauma, including swim bladder rupture.

Since fish are normally landed gutted, fish purchased were landed whole by special agreement with the captain. The agreement stated that the purchased grouper were not only to be whole, but were to be the last fishes caught before returning to the dock; ensuring fish were as fresh as possible. Commercially caught red grouper were brought back to the laboratory in a cooler filled with ice slurry, examined for any outward appearance of depth-induced injuries and photographed. Following external examination, fish were necropsied to detect any signs of trauma to internal organs. Photos of internal organs were taken during necropsy.

## Results

### *Swim Bladder Differences*

Gross Anatomy

Swim bladders from more than 140 red grouper (20.5-76.6 cm FL) and 62 red snapper (12.3-67.4 cm FL) caught on hook-and-line off headboats were examined. Red grouper possess a more capacious (in relation to total body size) swim bladder than red snapper and thus the capacity to contain a larger volume of swim bladder gases than red snapper (Figures 3-7 and 3-8). Red grouper swim bladder tissue was thinner than that of red snapper and red grouper swim bladder ruptures were always much larger (approximately $^{1}/_{3}$-½ the length of the swim bladder) than those in red snapper for hook-and-line caught fish (Figures 3-9 and 3-10).

Red grouper were prone to bi-lateral cranial hemorrhaging from escaped swim bladder gases that traveled to the head and both eyes if fish are unable to reacclimate to depth rapidly (Figure 3-11). In contrast, red snapper did not show the same proclivity to cranial hemorrhaging as red grouper following rapid decompression at depths ≤ 62 m, especially when vented. During laboratory depth simulations, some red snapper experienced exopthalmia in one or both eyes at 42 m and deeper but in all these fishes, the brain appeared unaffected. Fishes with one eye affected remained with the rest of the school and acted and fed normally in holding tanks. In the holding tanks, blind red snapper were able to maintain upright orientation, detect food, feed and respond to sounds indicating

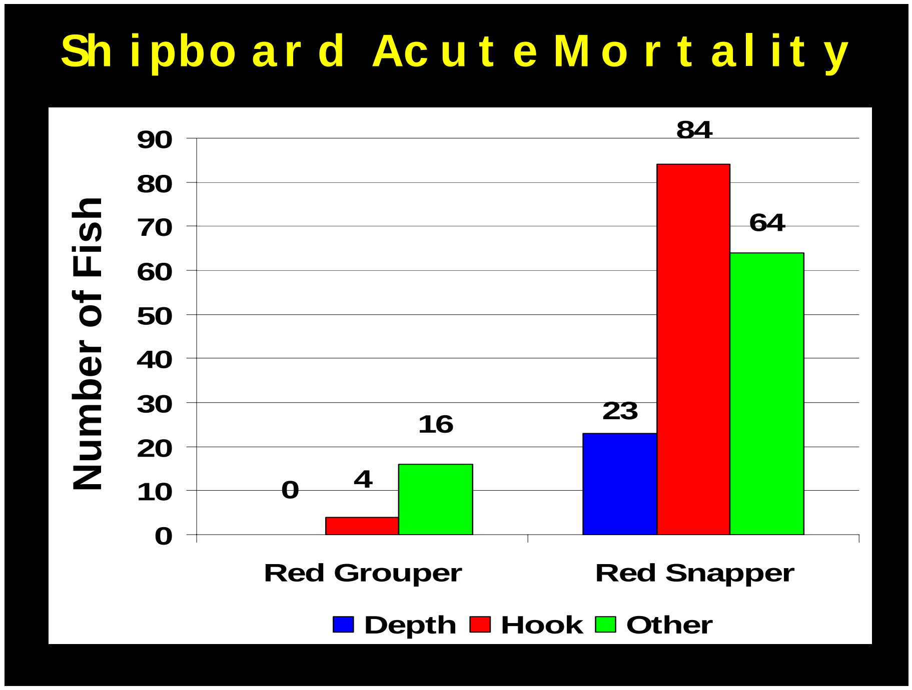


Figure 3-6. Acute shipboard mortality partitioned by cause of death (depth-related, hooking, other).

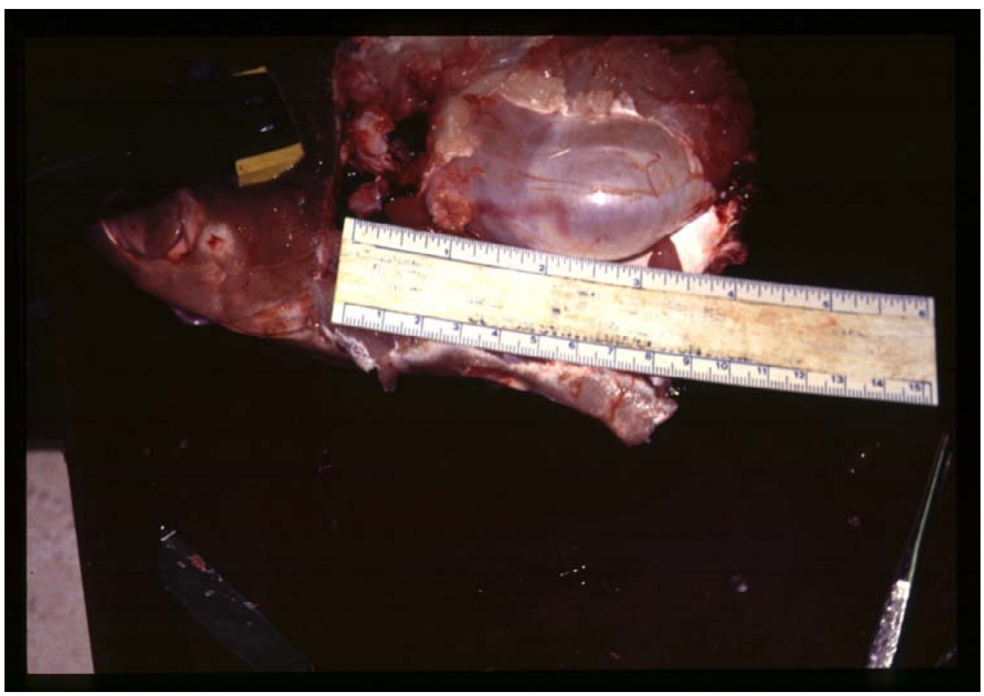

Figure 3-7. Inflated red grouper swim bladder showing swim bladder size in proportion to total body size.

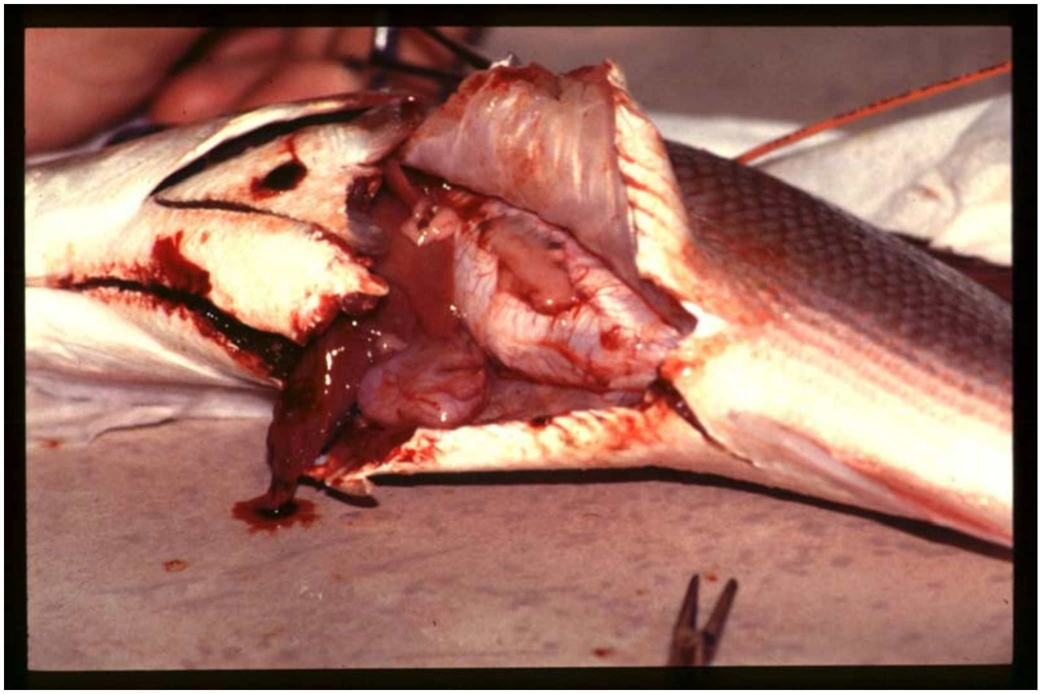

Figure 3-8. Inflated red snapper swim bladder showing swim bladder size in proportion to total body size.

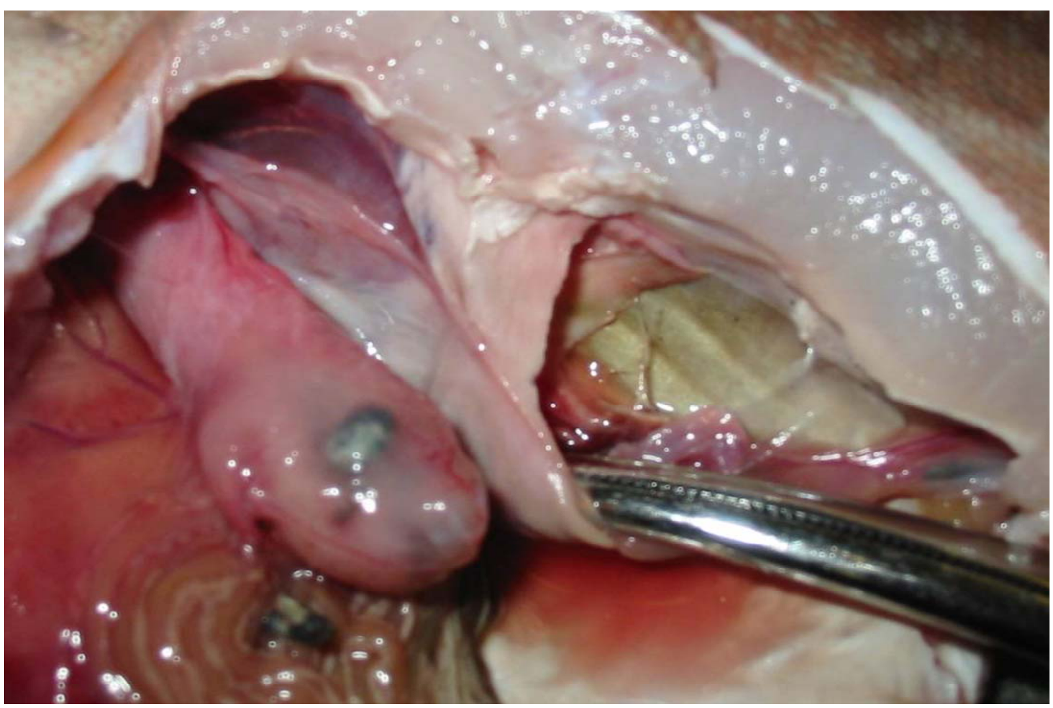

Figure 3-9. Initial rupture in a red grouper swim bladder.


Figure 3-10. Initial rupture in a red snapper swim bladder.

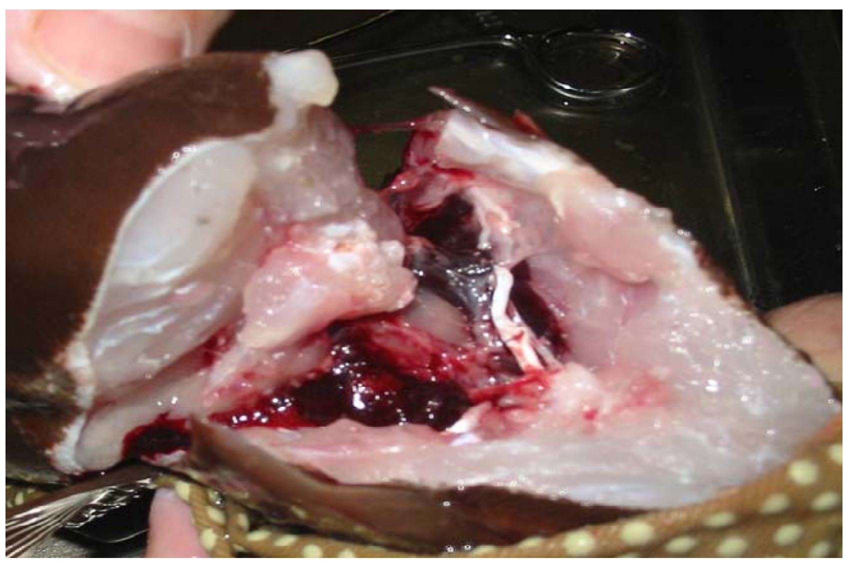

Figure 3-11. Bilateral post-cranial hemorrhages in red grouper rapidly decompressed from 21.3 m.

normal brain function. These fishes survived for months and had to be humanely euthanized at the end of the study.

Although rete mirable and gas glands responsible for gas absorption, secretion and resorption were located in the inner ventral wall of the anterior portion of the swim bladder of both species, size and shape of this anterior gas controlling portion of the swim bladder differed. In addition, 71 out of 140 red grouper were > 38.0 cm FL and all had a secondarily less vascularized star-shaped area on the posterior ventral wall of the swim bladder visible with a dissecting microscope absent in red snapper of any size (Figure 3-12). Under a dissecting microscope, this posterior area also appeared absent in small (< 30.5 cm FL) red grouper.

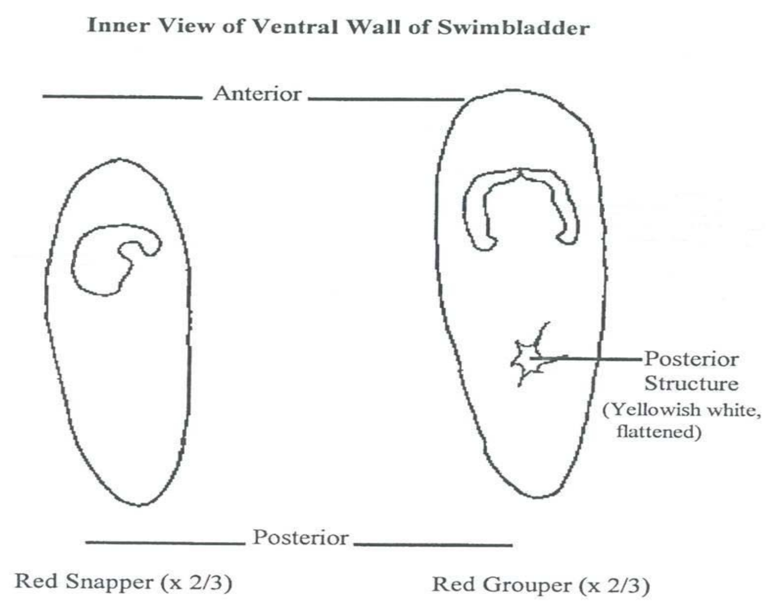


Figure 3-12. Inner view of the ventral wall of a red snapper and red grouper swim bladder showing the differences in areas of gas absorption and resorption and the secondary structure in the red grouper posterior portion of the swim bladder.

*Laboratory Simulations of Depth Effects Using Fish Hyperbaric Chambers*

Barotrauma Effects of Rapid Decompression from Simulated Depths

In depth simulation experiments red grouper exhibited higher susceptibility to barotrauma mortality than red snapper. Although similar percentages of red snapper (39%) and red grouper (40%) died from decompression injuries, significant differences between species were apparent. Red snapper mortality was 40% for fish decompressed from 42.7 m and 45% for fish from 61.0 m. For red grouper 75% of the fish tested at 42.7 m died. Red grouper mortality at 42.7 m was so high during the first trial that no 61.0 m simulation experiments were attempted (Table 3-1). In previous studies, red grouper exhibited 50% mortality at 27.4 m while red snapper had 0% mortality in trials at this depth (Joakim Malmgren, personal communication). Acute mortality caused by barotraumas in red grouper accounted for 100% of all red grouper mortality, while 71% of red snapper mortality was acute (Table 3-2).

Table 3-1. Red snapper and red grouper mortalities during hyperbaric chamber tests. Data include number of mortalities for each depth, % of all fish tested by species, % of all fish tested at depth by species, and % of all mortalities by depth.

| | | Depth (m) | | | | |
|---|---|---|---|---|---|---|
| | | 21.3 | 27.4 | 42.7 | 61.0 | % of species |
| Red snapper | # of mortalities | 0 | 0 | 8 | 9 | 39.0 |
| | % by depth | 0 | 0 | 40.0 | 45.0 | - |
| | % of all RS mortalities | 0 | 0 | 47.1 | 53.0 | - |
| Red grouper | # of mortalities | 0 | 2 | 6 | - | 40.0 |
| | % by depth | 0 | 50.0 | 75.0 | - | - |
| | % of all RG mortalities | 0 | 25.0 | 75.0 | - | - |

Table 3-2. Acute and delayed mortalities of red snapper and red grouper from hyperbaric chamber tests.

| | Acute | Delayed | Total mortalities | % acute | % delayed |
|---|---|---|---|---|---|
| Red snapper | 12 | 5 | 17 | 71.0 | 29.0 |
| Red grouper | 8 | 0 | 8 | 100.0 | 0.0 |

Signs of trauma and fish behavior during and following the hyperbaric chamber studies

Both red grouper and red snapper that had been acclimated to a simulated depth of 42.7 m and rapidly decompressed exhibited some external signs of depth induced trauma including distended abdomens, intestine protrusion out of the anus and stomach prolapse (Figure 3-13) when removed from the chambers mirroring those seen in fish caught during normal fishing at this depth. In addition, red grouper exhibited bilateral pressure-induced exophthalmia (Figure 3-14) that was unique to red grouper throughout the course of these experiments.

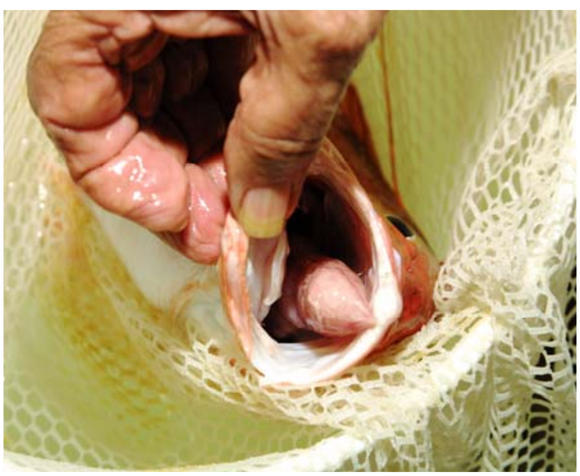

Figure 3-13. Red snapper exhibiting stomach prolapse caused by swim bladder gas expansion following swim bladder rupture.

Another difference between red grouper and red snapper was that most vented red snapper released into holding/recovery tanks immediately swam to the bottom and remained in the upright position on the bottom and behaved normally and behaved normally. Venting had enabled them to acclimate immediately to 1 atm of pressure despite the *psi* they had been acclimated to during the experiments in the chambers. However, red grouper, especially those acclimated to

42.7 m repeatedly dove straight down, bounced off the tank bottom and slowly floated to the surface exhibiting increasing external signs of barotraumas such as exopthalmia and bloating over time until they died in approximately 30 minutes.


Figure 3-14. Pressure induced exopthalmia in a red grouper.

There were also differences in internal trauma. Necropsy results showed red grouper suffered much more extensive internal trauma than did red snapper. Although all fish regardless of species, suffered ruptured swim bladders when rapidly decompressed from 42.7 m or deeper, red grouper exhibited profuse internal hemorrhaging, even in some red grouper decompressed from 27.4 m. Hemorrhaging included bilateral clots in the post-cranial area and thoracic cavity. In contrast, red snapper exhibited some visceral displacement and torsion, especially in those rapidly decompressed from 61.0 m; however, much less hemorrhaging was detected.

*Esophageal Ring*

Both red grouper and red snapper exhibited stomach prolapse caused by rapid decompression. Force produced by swim bladder gas expansion propelled the stomach through the esophagus with such strength; it created a ring-like bruise formed when doubling over of the esophagus caused capillaries in the esophagus to burst (Figure 3-15). This ring-like esophageal bruise was an important discovery because it provided a physiognomic feature indicative of recent swim bladder rupture and stomach prolapse caused by depth-related trauma. The “esophageal ring” remained for several days post swim bladder rupture and viewing the bruise was a tool to gauge the magnitude of depth-related trauma since it only occurred in response to stomach eversion into the oral cavity.

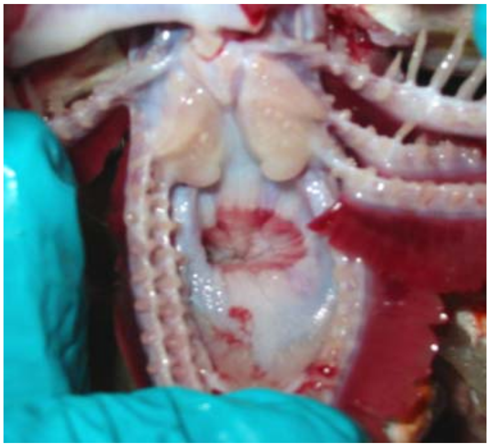

Figure 3-15. Esophageal ring bruise caused by stomach prolapse in red snapper decompressed from 61 m.

*Simulated Depths and Controlled Step-wise Decompression*

All red grouper and red snapper survived the slow controlled incremental step-wise decompression experiments within hyperbaric chambers from the simulated depth of 42.7 m, but there were differences in both the number of pressure increments required to acclimatize fish back to ambient surface atmospheric pressure and decompression times between the two species. Red grouper needed five pressure increments (63, 50, 35, 20

Table 3-3. Results of incremental step-wise decompression experiments in fish hyperbaric chambers to determine the number of pressure increments (number of stops) needed for red grouper and red snapper to acclimate to surface pressure (1 atm) after acclimation to a simulated depth of 42.7 m (4.3 atm).

| | **Pressure Increments *(psi)*** | **Time (hrs)** |
|---|---|---|
| Red Grouper (n=8) | 60 50 35 20 5 | 76.5 |
| Red Snapper (n=8) | 63 40 25 15 | 104.0 |

and 5 *psi*) to acclimate to 1 atm of pressure, red snapper only required four (63, 40, 25 and 15 *psi*) (Table 3-3). Despite requiring an additional stop, red grouper spent less cumulative time (76.5 hours) becoming acclimated to the various simulated ascent depths than red snapper (104 hours). Fish handling time averaged 51 sec (standard deviation 21.9 sec) for all trials and all chambers, although some fish became trapped within the chamber by the inward opening chamber doors, resulting in longer handling/struggle times. Total handling time ranged 9-103 sec.

Another difference was red grouper depressurization occurred at increasing greater increments of pressure (20, 30, 43, and 75%) from the previous pressure whereas red snapper depressurization occurred in approximately equal increments of 39, 37, and 40% decreases from the previous pressure. Initial acclimation time to the simulated depth of 42.7 meters (63 *psi)* also differed. Red grouper took 71 hours to acclimate to depth while red snapper acclimated faster (52 hours). Finally, although red snapper needed more time to reacclimatize after each decrease in pressure, they were capable of handling larger pressure changes per increment than red grouper.

*Swim Bladder Healing*

Despite differences in severity of internal trauma, in all fish that survived, regardless of species and simulated depth, swim bladder ruptures showed signs of healing within 24 hours with tissue on both sides of the rupture tenuously connected along its entire length. All fish swim bladders healed enough to be functional within 2-4 days after removal from the chambers. Even extensive ruptures in both species healed within this time period. The inner layer (submucosa) (Figure 3-16) healed first allowing the swim bladder to hold gas. Newly healed tissue was nearly transparent and became increasingly opaque over time as the other layers, the muscularis mucosa (middle smooth muscle layer) and tunica externa (outer layer of connective tissue) (Figure 3-17). At the end of one month, the only visible sign of rupture was a line of scar tissue that persisted over time providing a physiognomic indicator of previous ruptures in caught and released fish (Figure 3-18).

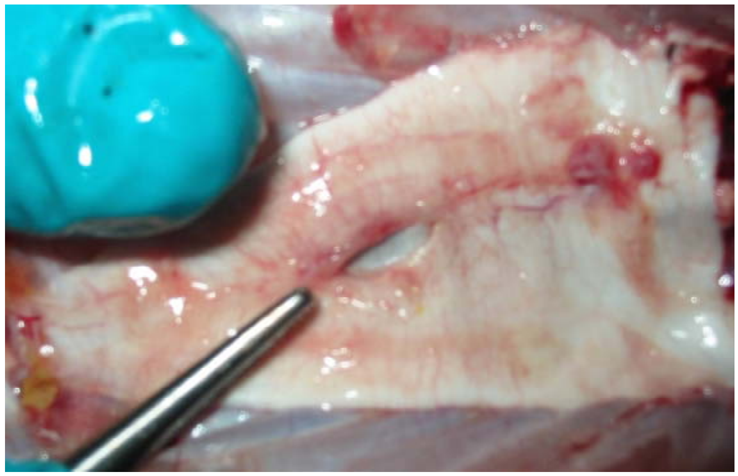

Figure 3-16. Red snapper swim bladder rupture site showing healing in a fish sacrificed 2 days after rapid decompression from the simulated depth of 62 m in hyperbaric chambers.


Figure 3-17. Red snapper swim bladder rupture scar 3 days after rupture in 62 m hyperbaric chamber rapid decompression experiment. Rupture is healed sufficiently to be functional.

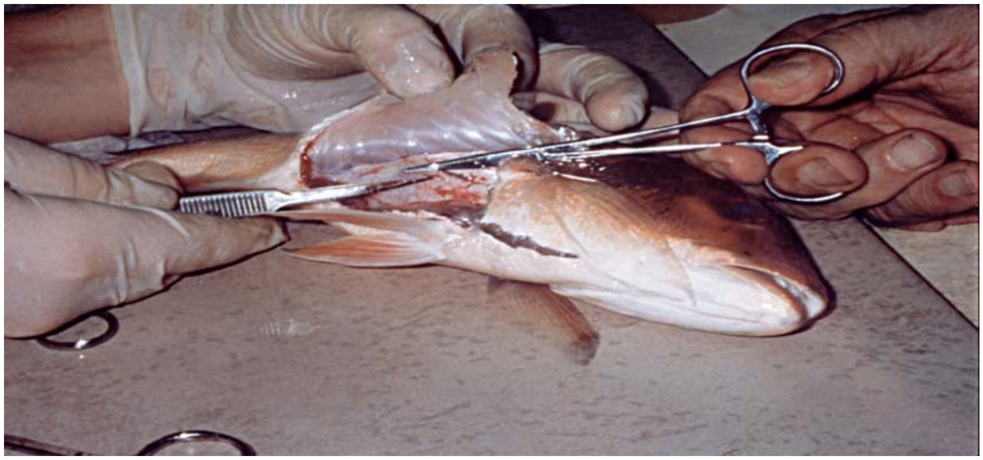

Figure 3-18. New swim bladder rupture from depth simulation of 21.3 m (tip of forceps) and healed scar (tip of scissors) from rupture at 21.3 m during capture one month previously.

New ruptures did not occur in areas previously ruptured. It may be that the thicker scar tissue is more resistant to new injury than areas without scar tissue.

*Stomach Prolapse and Feeding*

One of the most common external signs of swim bladder rupture was stomach prolapse. As long as stomach muscles were not severed by the force of released swim bladder gases following swim bladder rupture, stomach muscles of vented fish pulled the stomach back into place within one hour. Red snapper that survived decompression from 42.7 m fed aggressively within four hours after being removed from the chambers; red grouper within 12-24 hours. In contrast, red grouper rapidly decompressed from simulated depths of 27.4 m and 21.3 m, fed within two hours after removal from the chambers (Figures 3-19 and 3-20). No fish within the control groups used in the hyperbaric chamber step-wise acclimatization/decompression experiments exhibited stomach prolapse. All fish within both groups fed within 1-2 hours following removal from the chambers.

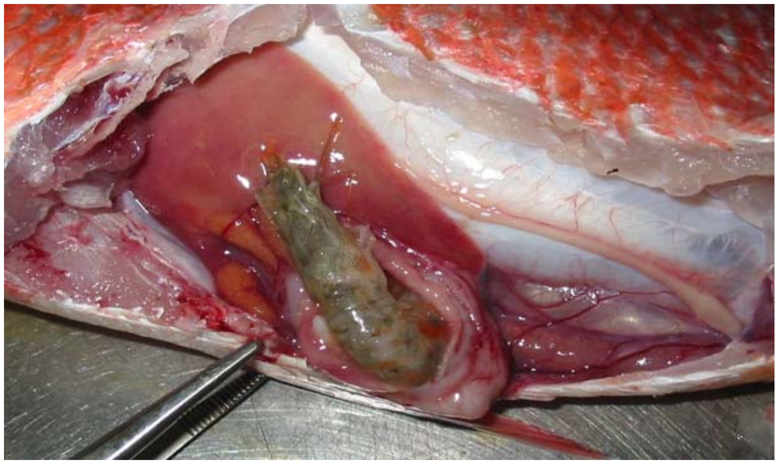

Figure 3-19. Red snapper stomach one hour after stomach prolapse. Stomach is back in place and fish can feed normally.

Figure 3-20. Overall view of red snapper 7 days after rapid decompression experiment in hyperbaric chamber 42 m depth simulation. Note good condition of tissues and organs and evidence (shrimp) of normal feeding.

*Fish Tag and Release*

Most releases and recaptures occurred during hook-and-line fishing aboard private recreational and recreational-for-hire vessels. Recapture data from headboats were highly under reported. Recaptured fish aboard all headboats fishing in the Gulf of Mexico were only reported if MML staff or student interns were aboard. Crew stated recaptures occurred during other trips but crews were too busy to report them.

Red grouper (n=8,765) were tagged and released from private recreational and recreational-for-hire vessels between October 9, 1990 and August 31, 2007 at depths ranging 6-81.7 m. Overall 5.5% (n= 484) of these fishes were reported recaptured, mostly between 2.1-45.7 m however a few fish (n= 4) were recaptured at depths 45.7-53.3 m.

Red snapper (n=8,303) were also tagged off private recreational and recreational-for-hire vessels during the same time period. Most were recaptured at depths ranging 12.5-30.5 m, the depths where most fish were initially tagged. Overall 8.1% (n=623) fish were reported recaptured. Recaptures decreased with depth (30.8 -36.6 m); however, a few fish (n=5) were recaptured at depths ranging 39.6-42.6 m.

Differences in Survival by Fish Length for Hook-and-Line Caught Fishes

Despite demonstrated differences in their ability to tolerate rapid decompression with respect to barotrauma, both species exhibited the same trend in survival from depth with respect to fish length. Analyses of combined recapture data from private recreational and recreational-for-hire vessels by fish length showed more larger fish of both species were recaptured. The proportion of recaptured small (< 38.1 cm FL) to larger red grouper ($\geq$381 mm FL) was compared using a log-likelihood G test. Sizes were chosen based on changes in swim bladder structure at around 38 cm in red grouper. Results were highly significant ($p$=9.7 x $10^{-19}$). Although red snapper never develop the secondary structure seen in red grouper, for consistency, the same size was used in analyses. Similar results were found when comparing recaptured small red snapper (< 38.1 cm FL) to larger red snapper ($\geq$38.1 cm FL) ($p$=9.5 x $10^{-6}$ ) (Table 3-4).

Table 3-4. Results of G tests comparing survival by fish length of small to large red grouper and red snapper using all recreational recaptures regardless of depth.

| **Test Group** | **No. Tagged** | **No. Recaptured** | **% Recaptured** | **G test result ($p$ value) ≤ 38.1cm vs. > 38.1 cm** |
|---|---|---|---|---|
| Red Grouper ≤38.1 cm | 3308 | 194 | 5.9 | 9.7 x $10^{-19}$ |
| > 38.1 cm | 1675 | 240 | 14.3 | df =1 |
| Red Snapper ≤38.1 cm | 3957 | 333 | 8.4 | 9.47 x $10^{-06}$ |
| > 38.1 cm | 1518 | 196 | 12.9 | df =1 |

When red grouper and red snapper recapture data were divided by sector (private recreational and recreational-for-hire) for analysis at a depth of 21.3 m, (depth of 100% survival from the chamber simulated studies) and size limit of 40.6 cm, results differed by sector. Analyses were conducted fish lengths < and > 40.6 because it was the red snapper size limit. The same size was used for red grouper for consistency. In the private recreational sector percent recaptures favored survival of small fish for both species. Survival favored larger fish in the recreational-for hire sector for both species (Table 3-5). Although in some studies this difference may be attributable to reporting rate, in this study, all headboat recaptures in the Gulf of Mexico were made by MML staff and student interns who recorded all recaptures regardless of size and many private recreational vessel owners were interested in the tagging program.

Table 3-5. Red grouper and red snapper recaptures by fish length and fishing sector for fishes tagged and recaptured at ≤ 21.3 m. Depth was chosen because chamber studies showed 100% survival for both species at this depth. Fish length was chosen because it was the legal size limit for Gulf of Mexico red snapper and for red grouper it provided both consistency and a larger sample size for analyses. Private Rec = private recreational vessels; Rec-for-Hire = recreational-for-hire vessels.

| Red Grouper | | | | | |
|---|---|---|---|---|---|
| Sector | Size (cm) | No. Tagged | No. Recaptured | % Recaptured | G crit & *p* value |
| Private Rec | ≤ 40.6 | 1029 | 127 | 12.3 | G =3.84 |
| | > 40.6 | 261 | 33 | 12.6 | $p$=0.922 |
| | | | | | |
| Rec-for-Hire | ≤ 40.6 | 6419 | 283 | 4.4 | G= 3.84 |
| | > 40.6 | 1083 | 116 | 10.7 | $p$=4.02x$10^{-13}$ |
| | | | | | |
| Red Snapper | | | | | |
| | | | | | |
| Private Rec | ≤ 40.6 | 270 | 34 | 12.6 | G=3.84 |
| | > 40.6 | 27 | 3 | 11.1 | $p$=0.845 |
| | | | | | |
| Rec-for-Hire | ≤ 40.6 | 1230 | 102 | 8.3 | G=3.84 |
| | > 40.6 | 296 | 50 | 16.9 | $p$=0.00021 |
| | | | | | |

*Tag and Release of Red Grouper Aboard Commercial Long-line Vessels*

Undersized (n=866) and legal (n=50) red grouper were tagged and released during long-line fishing trips aboard various commercial long-line fishing vessels in 2004 and 2005. Fish were tagged and released at 248 different sites in the eastern Gulf of Mexico. Capture depths ranged 37.8-99 m. No red snapper were captured during these fishing trips.

Of 916 released fish, 711 (78%) were observed to have immediately swum straight down post-release, 67 (7%) swam down slowly, and 175 (19%) floated at the surface. Red grouper caught at the same depth during the same long-line set varied in degree of outer signs of barotraumas from none to severe (Figures 3-21 and 3-22). Table 3-6 provides a breakdown of the immediate post-release fate of these fish by species, season, and depth.

Figure 3-21. Red grouper immediately following hook extraction after being brought up during a long-line set. Note lack of external signs of rapid decompression.

Eight released red grouper did not fall into these categories. One was eaten by a dolphin upon release; the rest (n=7) were not observed post-release; however, all suffered from trauma during capture. Three of the seven were covered with bite marks, one was gut hooked and two suffered some degree of

Figure 3-22. Red grouper caught on the same long-line set exhibiting various degrees of exophthalmia.

exophthalmia, although still alive. Thirteen (0.14%) of these fish were recaptured within approximately two years (64-715 days) of release. Growth ranged 25.4-241.3 mm depending on duration between original capture and recapture, a rate of .127-.635 mm.

Additional red grouper were tagged off commercial vessels using three different commercial gear types, rod and reel, electric rod and reel and long-line during normal fishing trips aboard commercial vessels at depths ranging 24.4-80.5 m. Recaptures (n=45) were at liberty between 3-2,172 days. Most (76%) recaptured fish were vented before release (Table 3-6).

Table 3-6. Immediate release fate of red grouper caught, vented, tagged, and released off long-line vessels on observer trips by species, tag depth (m), and season.

| | Winter (12/1 to 2/28) | | | | | Spring (3/1 to 5/31) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Depth (m)* | *0-37* | *38-53* | *54-68* | *69-83* | *84-99* | *0-37* | *38-53* | *54-68* | *69-83* | *84-99* |
| **Species** | | | | | | | | | | |
| **Red Grouper** | | | | | | | | | | |
| Straight Down | | 30 | 10 | 46 | | 4 | 224 | 68 | 133 | 10 |
| Down Slow | | 1 | 7 | 1 | | 2 | 11 | 11 | 24 | 4 |
| Floating | | 11 | 11 | 20 | | 3 | 27 | 13 | 38 | 6 |
| Other | | 0 | 1 | 0 | | 0 | 0 | 2 | 1 | 0 |

| | Summer (6/1 to 8/31) | | | | | Fall (9/1 to 11/30) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Depth (m)* | *0-37* | *38-53* | *54-68* | *69-83* | *84-99* | *0-37* | *38-53* | *54-68* | *69-83* | *84-99* |
| **Species** | | | | | | | | | | |
| **Red Grouper** | | | | | | | | | | |
| Straight Down | | 50 | | 0 | | | 86 | 46 | 2 | |
| Down Slow | | 0 | | 1 | | | 1 | 3 | 0 | |
| Floating | | 1 | | 3 | | | 9 | 30 | 1 | |
| Other | | 1 | | 0 | | | 1 | 1 | 1 | |

*Fish Venting*

Red grouper (n= 5,391 vented; n=1,932 not vented) and red snapper (n=5,694 vented; n=2,144 not vented) from the Fish Tagging Program that had data in all categories (tag depth, recapture depth, and treatment) were used to test survival of vented versus not vented red grouper and red snapper. For red grouper (n=322 vented; n=192 not vented) and red snapper (n=441vented; n=90 not vented) tagged and released from private recreational and recreational-for-hire vessels for fish of both species in the shallow water control group (fish caught on hook-and-line at 21 m) where barotrauma was not an issue, showed no significant difference in survival rates for vented and not vented red grouper ($p$=0.8671) or red snapper ($p$=0.8376) indicating venting in and of itself did not cause mortality (Table 3-7). Tables 3-8 and 3-9 show tag and recapture data for vented and not vented red grouper and red snapper by depth. Fish of both species showed significance at

Table 3-7. Red Grouper and red snapper tagged and released in the shallow water control group (fish caught at 21 m) where barotrauma was not an issue that were vented or not vented before release.

| **Species** | **No. Tagged & Vented** | **No. Recaps & Vented** | **% Recap** | **No. Tagged Not Vented** | **No. Recaps Not Vented** | **% Recap** | **G crit** | ***p* value** |
|---|---|---|---|---|---|---|---|---|
| Red Grouper | 322 | 27 | 8.4 | 192 | 17 | 8.9 | 3.8414 | 0.8671 |
| Red Snapper | 441 | 36 | 8.2 | 90 | 8 | 8.9 | 3.8414 | 0.8376 |

Table 3-8. Red grouper tagged and released by treatment (vented or not vented) by depth.

| Depth (m) | No. Tagged & Vented | No. Recaps & Vented | % Recap | No. Tagged Not Vented | No. Recaps Not Vented | % Recap | G crit | *p* value |
|---|---|---|---|---|---|---|---|---|
| ≥22, < 27 | 2,586 | 254 | 9.82 | 1,389 | 185 | 13.32 | 3.841 | 0.0031 |
| ≥27, < 43 | 1,423 | 117 | 8.22 | 448 | 42 | 9.38 | 3.841 | 0.4907 |
| ≥43,< 61 | 927 | 42 | 4.53 | 79 | 7 | 8.86 | 3.841 | 0.1490 |
| 61 | 455 | 6 | 1.32 | 16 | 1 | 6.25 | 3.841 | 0.3598 |
| Total | 5,391 | 419 | - | 1,932 | 235 | - | - | - |

Table 3-9. Red snapper tagged and released by treatment (vented or not vented) by depth.

| Depth (m) | No. Tagged & Vented | No. Recaps & Vented | % Recap | No. Tagged Not Vented | No. Recaps Not Vented | % Recap | G crit | *p* value |
|---|---|---|---|---|---|---|---|---|
| ≥22, < 27 | 2,088 | 206 | 9.87 | 1,403 | 194 | 13.83 | 3.841 | 0.0015 |
| ≥27, < 43 | 3,459 | 181 | 5.23 | 711 | 51 | 7.17 | 3.841 | 0.0614 |
| ≥43,< 61 | 135 | 3 | 2.2 | 28 | 1 | 3.57 | 3.8414 | 0.7279 |
| 61 | 12 | 0 | - | 2 | 0 | - | - | - |
| Total | 5,694 | 390 | - | 2,144 | 246 | - | - | - |

vented red grouper and red snapper by depth. Fish of both species showed significance at depths ≥ 22 and < 27 m with more not vented fish recaptured; however, at deeper depths there was no significant differences in survival. Field data differed from chamber study results as vented fish exhibited less trauma than not vented fish at 21 and 23 m for both species and for red snapper at deeper depths.

Table 3-10. Number of fish caught and percent survival rate by depth in commercial fish traps.

| Depth (m) | Species | Caught | Survived | % Survived |
|---|---|---|---|---|
| 52-64 | Vermilion | 39 | 36 | 92.3 |
| | Bank Sea Bass | 1 | 1 | 100 |
| | Red Grouper | 15 | 14 | 93.3 |
| | Porgy | 1 | 1 | 100 |
| 65-76 | Vermilion | 7 | 7 | 100 |
| | Bank Sea Bass | 1 | 0 | 0 |
| | Red Grouper | 0 | 0 | 0 |
| | Porgy | 0 | 0 | 0 |
| 77-82 | Vermilion | 13 | 0 | 0 |
| | Bank Sea Bass | 5 | 0 | 0 |
| | Red Grouper | 7 | 5 | 71.4 |
| | Porgy | 0 | 0 | 0 |
| 83-91 | Vermilion | 4 | 4 | 100 |
| | Bank Sea Bass | 0 | 0 | 0 |
| | Red Grouper | 1 | 1 | 100 |
| | Porgy | 0 | 0 | 0 |
| > 92 | Vermilion | 0 | 0 | 0 |
| | Bank Sea Bass | 0 | 0 | 0 |
| | Red Grouper | 0 | 0 | 0 |
| | Porgy | 0 | 0 | 0 |

Some (n=26) red grouper that were tagged and released off private recreational and recreational-for-hire vessels were recaptured 65-868 days later by commercial fishers. Tagging depth varied 3.7-80.5 m. Most (69%) recaptured fish had been vented before release. Red grouper recaptures (n=42) from tagging depths ranging 24.4-80.5 m, originally tagged in the commercial fishery by commercial long-line (n=27), electric reel (n=5) and rod and reel (n=12) showed 81% of recaptured fish had been vented before release.

*Fish Caught in Commercial Reef Fish Traps*

Only four fish species were caught in the traps including red grouper (*E. morio*), vermilion snapper (*Rhomboplites aurorubens*), bank sea bass (*Centropristis ocyurus*) and littlehead porgy (*Calamus proridens*). No red snapper were caught. The most abundant fish caught were vermilion snapper (Table 3-11).

Regardless of capture depth, most commercial trap caught fishes did not display outward signs of barotrauma. The few red grouper that did exhibit stomach prolapse appeared to otherwise be healthy. Although few (93) fish were caught, immediate survival was high over all depths fished and 92% were deemed to be in good condition and swam straight down following release. Unlike fishes caught at depth by other gear types, many trap caught released fishes did not require venting before release including red grouper. Twenty-two red grouper (6 legal, 16 undersized) caught in the traps were tagged and released, one fish was sacrificed.

One red grouper was recaptured after 315 days of freedom. Originally caught by commercial trap at 62.2 m (Site 1), it did not require venting before release. At release it was 48.3 cm FL and was recaptured at a depth of 34.7 m on rod and reel and reported to have grown to 58.4 cm.

Although most red grouper were tagged and released, a few were sacrificed under the auspices of a federal scientific permit to determine swim bladder condition and internal organs for abnormalities or damage caused by rapid decompression. Trap caught red grouper brought to the surface from 63 m showed no outward appearance of depth-induced trauma. Sacrificed red grouper showed that although some swim bladders ruptured, no internal hemorrhaging occurred. Internal organs appeared normal in some fish; however, a few had pinhole sized damage to their deflated swim bladders and/or torqued internal organs.

*Trap Fish Survival by Ascent Treatments*

Ascent rate for hand over hand trap retrieval averaged 0.45 m/sec, while winch retrieved traps ascended at an average rate of 1.22 m/sec. Although multiple experimental trials were originally scheduled for offshore trips off commercial fishing vessels during 2004 and 2005, only one set of experiments was possible during the time frame because offshore trips were continuously cancelled due to an inordinate number of hurricanes, tropical storms and weather fronts. Data were very limited and are shown as Table 3-11.

Table 3-11. Ascent rate of fish retrieved by hand and winch.

| | | | | SOAK | DEPTH | | RETRIEVAL | | RETRIEVAL | | | RELEASED |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SITE | LOCATION | DATE | TRAP# | TIME | M | Ft | TIMED | METHOD | RATE | | CATCH | CONDITION |
| | | | | | | | (mm:ss.oo) | | (m/sec) | (ft/sec) | | |
| 1 | 26.58/83.42 | 5/16/2006 | 1 | 4 HR | 63.1 | 207 | 00:26:34 | WINCH | 2.40 | 7.86 | RG & VS | 1 SAC, 3 FLT, 2SD |
| 1 | 26.58/83.42 | 5/16/2006 | 2 | 4 HR | 63.1 | 207 | 01:52:19 | BY HAND | 0.56 | 1.84 | RG & VS | 1 SAC, 1 SD |
| 1 | 26.57/83.41 | 5/16/2006 | 3 | 4 HR | 62.2 | 204 | 01:01:97 | WINCH | 1.00 | 3.30 | NO FISH | |
| 1 | 26.57/83.41 | 5/16/2006 | 4 | 4 HR | 62.2 | 204 | 02:23:37 | BY HAND | 0.43 | 1.42 | RG | 12 SD |
| 1 | 26.56/83.40 | 5/16/2006 | 5 | 4 HR | 61.0 | 200 | 01:14:31 | WINCH | 0.82 | 2.69 | VS | 9 SD |
| 1 | 26.56/83.40 | 5/16/2006 | 6 | 4 HR | 61.0 | 200 | 01:44:47 | BY HAND | 0.58 | 1.91 | NO FISH | |
| 3 | 26.05/83.45 | 5/17/2006 | 7 | 4 HR | 89.9 | 295 | 02:40:03 | BY HAND | 0.56 | 1.84 | NO FISH | |
| 3 | 26.05/83.45 | 5/17/2006 | 8 | 4 HR | 89.9 | 295 | 01:04:75 | WINCH | 1.39 | 4.56 | RG | 1 SD |
| 3 | 26.03/83.44 | 5/17/2006 | 9 | 4 HR | 88.7 | 291 | 02:56:50 | BY HAND | 0.50 | 1.65 | NO FISH | |
| 3 | 26.03/83.44 | 5/17/2006 | 10 | 4 HR | 88.7 | 291 | LOST TRAP | | | | | |
| 3 | 26.02/83.44 | 5/17/2006 | 11 | 4 HR | 90.8 | 298 | 02:28:97 | BY HAND | 0.61 | 2.00 | VS | 4 SD |
| 3 | 26.02/83.44 | 5/17/2006 | 12 | 4 HR | 90.8 | 298 | 01:23:65 | WINCH | 1.09 | 3.56 | NO FISH | |
| 4 | 25.37/83.42 | 5/18/2006 | 13 | 14 HR | 79.2 | 260 | 01:32:44 | WINCH | 0.86 | 2.81 | RG | 5 SD, 2 FLT |
| 4 | 25.56/83.42 | 5/18/2006 | 14 | 14 HR | 79.2 | 260 | 03:07:63 | BY HAND | 0.42 | 1.39 | NO FISH | |
| 4 | 25.56/83.42 | 5/18/2006 | 15 | 14 HR | 81.7 | 268 | 01:03:09 | WINCH | 1.29 | 4.25 | VS | 12 SD |
| 4 | 25.55/83.42 | 5/18/2006 | 16 | 14 HR | 79.9 | 262 | 02:52:09 | BY HAND | 0.46 | 1.52 | CRAB & BSB | 3 SD |
| 4 | 25.55/83.41 | 5/18/2006 | 17 | 14 HR | 80.8 | 265 | 02:30:97 | BY HAND | 0.54 | 1.76 | VS & BSB | 3 SD |
| 5 | 25.54/83.34 | 5/18/2006 | 18 | 4 HR | 71.3 | 234 | 01:15:59 | WINCH | 0.94 | 3.10 | VS & BSB | 4 SD |
| 5 | 25.54/83.34 | 5/18/2006 | 19 | 4 HR | 71.6 | 235 | 02:52:59 | BY HAND | 0.41 | 1.36 | VS | 4 SD |
| 5 | 25.55/83.34 | 5/18/2006 | 20 | 4 HR | 71.0 | 233 | 00:59:78 | WINCH | 1.19 | 3.90 | NO FISH | |
| 5 | 25.56/83.35 | 5/18/2006 | 21 | 4 HR | 72.2 | 237 | 03:09:65 | BY HAND | 0.38 | 1.25 | NO FISH | |
| 5 | 25.56/83.35 | 5/18/2006 | 22 | 4 HR | 71.9 | 236 | 03:36:16 | BY HAND | 0.33 | 1.09 | NO FISH | |
| 6 | 26.12/83.13 | 5/19/2006 | 23 | 4 HR | 51.8 | 170 | 01:00:56 | WINCH | 0.86 | 2.81 | VS | 4 SD |
| 6 | 26.12/83.13 | 5/19/2006 | 24 | 4 HR | 51.8 | 170 | 02:12:28 | BY HAND | 0.39 | 1.28 | VS & PORGY | 12 SD |
| 6 | 26.11/83.12 | 5/19/2006 | 25 | 4 HR | 51.8 | 170 | 00:53:31 | WINCH | 0.97 | 3.19 | NO FISH | |
| 6 | 26.10/83.12 | 5/19/2006 | 26 | 4 HR | 51.8 | 170 | 02:17:28 | BY HAND | 0.38 | 1.24 | VS | 4 SD |
| 6 | 26.10/83.12 | 5/19/2006 | 27 | 4 HR | 52.4 | 172 | 02:09:78 | BY HAND | 0.40 | 1.33 | NO FISH | |
| 2 | 26.25/83.55 | 5/20/2006 | 28 | 4 HR | 115.8 | 380 | 01:12:57 | WINCH | 1.60 | 5.23 | NO FISH | |
| 2 | 26.25/83.55 | 5/20/2006 | 29 | 4 HR | 115.8 | 380 | 04:10:31 | BY HAND | 0.46 | 1.52 | CRAB | 1 SD |
| 2 | 26.26/83.55 | 5/20/2006 | 30 | 4 HR | 115.8 | 380 | 01:18:91 | WINCH | 1.47 | 4.82 | NO FISH | |
| 2 | 26.26/83.55 | 5/20/2006 | 31 | 4 HR | 114.9 | 377 | 04:17:84 | BY HAND | 0.25 | 0.82 | NO FISH | |
| 2 | 26.27/83.55 | 5/20/2006 | 32 | 4 HR | 115.8 | 380 | 04:39:06 | BY HAND | 0.41 | 1.36 | NO FISH | |

| SPECIES | | CONDITION | |
|---|---|---|---|
| RG | RED GROUPER | SAC | SACRIFICED |
| VS | VERMILION SNAPPER | FLT | FLOATED |
| BSB | BANK SEA BASS | SD | STRAIGHT DOWN |

*Red Grouper Purchased from Commercial Fish Trappers*

None of the ten red grouper purchased from commercial fish trappers showed outward signs of depth-induced trauma (Figure 3-23), despite capture depths of 55-61 m. Many had intact gas filled swim bladders (Figure 3-24) and lacked any discernable internal trauma (Figure 3-25); however, a few had pinhole sized damage to their deflated swim bladders and/or torqued internal organs (Figures 3-26 through 3-28).

Figure 3-23. Commercial trap captured red groupers caught at 55-61 m not exhibiting the common external signs of barotraumas.

Figure 3-24. Intact inflated swim bladder excised from a 70.0 cm red grouper caught by commercial fish trap (55m).

Figure 3-25. Intact normally positioned stomach from a 58.0 cm red grouper caught in a commercial fish trap (55-61m).

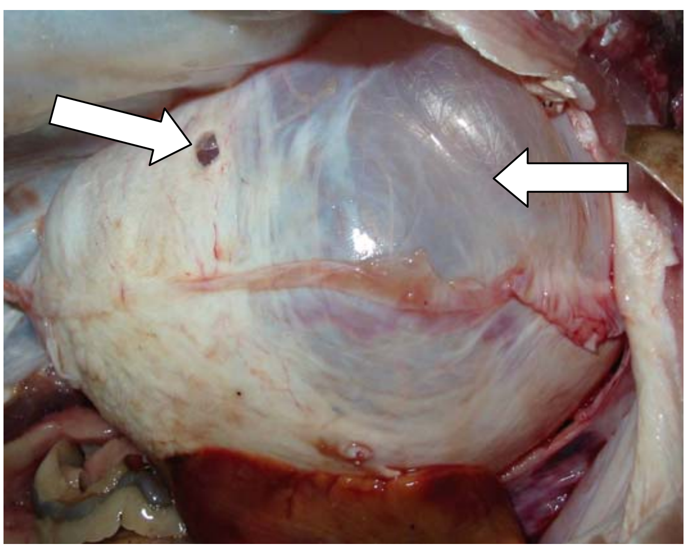

Figure 3-26. Swim bladder of a 70.0 cm red grouper caught in a commercial fish trap. Note pre-pinhole formation and semi-transparent stretched tissue of posterior portion of the swim bladder.

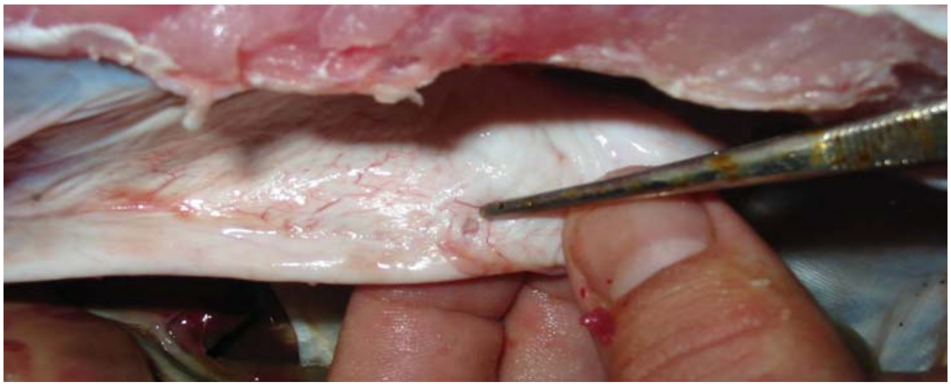

Figure 3-27. Swim bladder from a 67.5 cm commercial trap caught red grouper exhibiting pinhole trauma (55-61 m).

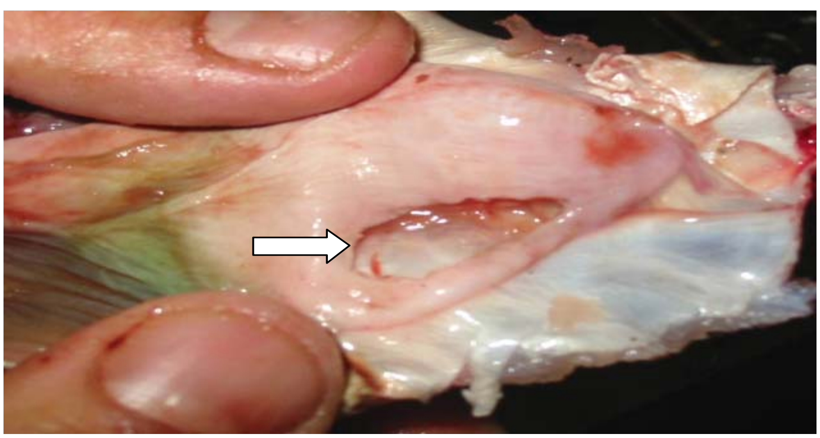

Figure 3-28. Swim bladder tear in a 57.7 cm commercial trap caught red grouper (55-61 m).

## Discussion

### *Acute Mortality*

Swim bladder rupture occurred in all red grouper and red snapper caught on hook-and-line at depths ranging ≥10 m. Although the degree of apparent bloating and other capture related symptoms increases with depth in physoclistic fishes, swim bladder ruptures are not necessarily lethal (Collins et al. 1999, Wilson 1993, Wilson and Burns 1996). Results from hyperbaric chamber experiments agreed with tag recapture data showing red snapper suffered less severe trauma than red grouper with respect to rapid decompression at least at depths ≤ 42.7 m, especially if swim bladder gases were released through venting or if the fish were rapidly recompressed. Direct observations using hyperbaric chambers showed red snapper rapidly decompressed at depths of 62 m can survive at surface depths (1 atm) if swim bladder gases were released. Red grouper could not survive at 1 atm from this depth if simply vented in the laboratory where they were unable to return to acclimated depth. They required rapid recompression to survive rapid decompression from this depth. Jarvis and Lowe (2008) also found degree of barotrauma injury and fish survival was species-specific for the various species of rockfishes tested and that rapid recompression of rockfish caught at 55-89 m enhanced survival.

### *Swim Bladder Differences*

Differences in anatomy and physiology between red grouper and red snapper influenced survival. Red grouper with their capacious thinner swim bladders have the capacity to hold greater quantities of swim bladder gases than the smaller thicker red snapper swim bladders resulting in much larger swim bladder tears during rapid decompression. Jarvis and Lowe (2008) also found disparities in swim bladder tissue thickness among various species of rockfishes and have postulated that swim bladder morphology may be responsible for differences in swim bladder tear incidence. They reported olive rockfish swim bladders with comparatively thin swim bladders had more severe swim bladder tears than other rockfish species with thicker swim bladder tissue and suffered higher mortality from barotraumas than other rockfish species such as vermilion, copper, and brown rockfishes that all have thicker swim bladders.

Tissue thickness is not the only morphological difference between red grouper and red snapper swim bladders. Brown-Peterson and Overstreet (Burns et al. 2008) showed blood vessels are more closely associated with rete in red grouper than in red snapper which probably contributes to the increased hemorrhaging in blood vessels associated with the swim bladders of red grouper, regardless of fish length. They reported red grouper swim bladders had less rete than those of red snapper possibly reducing gas exchange efficiency because fewer capillaries were available for gas absorption and resorption. Additionally, the close association and numerous connections between rete and other blood vessels with gas gland tissue in red grouper swim bladders reported by Brown-Peterson et al. (2006) probably promotes hemorrhaging during swim bladder rupture increasing internal trauma. These factors combined with a larger quantity of gas may be responsible for observed larger ruptures in the thin membrane of the red grouper swim bladder.

Reduced gas exchange resulting in increased internal pressure may have propelled escaped swim bladder gases to the eyes and crania resulting in the characteristic exophthalmia and cranial hemorrhaging commonly seen in red grouper caught in waters deeper than ≥ 27 m. Red grouper exhibited various degrees of exophthalmia, from all depths tested except 21.3 m. In all cases exophthalmia always occurred in both eyes simultaneously. Necropsies revealed the presence of gas behind both eyeballs when red grouper suffered from exophthalmia. The volume of gas present appeared to be too great to be accounted for simply by dissolved gas in tissues. It appeared swim bladder rupture also released gas into the ventral coelom and orbital regions, multiplying damage within the fish. This parallels results reported by Rogers et al. (2008) who reported an analogous response in rapidly decompressed rockfish, where escaped expanding gases following swim bladder rupture burst the peritoneum, entered the orbital regions, and increased pressure behind the eyes resulting in exophthalmia.

In contrast, the smaller red snapper swim bladder contains more retal area in the swim bladder than red grouper by fish length ($p<0.001$), which Brown-Peterson and Overstreet (Burns et al. 2008) postulated should increase gas exchange rates. Higher exchange efficiency of a smaller volume of gases combined with thicker tissue probably resulted in the smaller swim bladder tears observed in red snapper. Additionally, unlike the red grouper swim bladder, most rete in red snapper swim bladders were segregated from gas gland cells probably reducing the amount of hemorrhaging. This separation was especially apparent in smaller red snapper swim bladders (Brown-Peterson and Overstreet in Burns et al. 2008).

The intimate association of larger blood vessels, rete and gas gland tissue in red grouper probably leads to increased retal hemorrhaging with rapid decompression in all lengths of red grouper. Brown-Peterson and Overstreet (Burns et al. 2008) stated that "histological results show overall that red snapper survive rapid decompression better than red grouper, as evidenced by reduced mortality, smaller and less frequent tears in the swim bladder, and less of a tendency to hemorrhage, particularly in smaller fish. The higher percentage of rete area in the swim bladder of red snapper compared with red grouper suggests swim bladder gasses may be exchanged more rapidly in red snapper, allowing greater survival after rapid decompression." Although various authors have postulated that differences in intraspecific trauma of fishes caught at similar depths may be explained by relative swim bladder volume at capture (Arnold and Walker 1992, Rummer and Bennett 2005, Parker et al. 2006), for red grouper and red snapper differences in swim bladder structure documented by Brown-Peterson and Overstreet (Burns et al. 2008) are also important in determining the variations in trauma and survival from different depths for the two species.

*Laboratory Simulations of Depth Effects Using Fish Hyperbaric Chambers*

Although red grouper and red snapper swim bladder ruptures occurred at depths ≥ 10m, neither species suffered mortality during rapid decompression from depths ≤ 21.3 m. Tag and recapture data agreed showing higher recapture (survival) rates from shallow depths. Koenig (2001) reported rapid decompression from 20.0 m was not only non-lethal to red grouper and red snapper, but fishes caught, held and retrieved from cages at this depth for 13 days, were in excellent condition.

Differences between red grouper and red snapper survival occurred at simulated depths > 21.3 m. Overall, red grouper were much more susceptible to depth-related trauma than red snapper. Although 100% of the red grouper survived the 21.3 m experiments, only 50% of red grouper survived the 27.4 m depth simulations experiments and less (25%) of the red grouper survived during the 42.7 m chamber experiments. The 25% red grouper survival rate in the chambers was far less than the 85% survival rate reported by Wilson and Burns (1996) for potential survival from shipboard experimentation experiments. Red grouper were vented after removal from the hyperbaric chambers and placed into holding tanks at 1 atm to observe recovery. They were unable to return immediately to acclimated depth as were the fish returned in cages at sea.

Data from the depth simulation studies conducted in hyperbaric chambers showed although some red snapper suffered mortality or sub-lethal effects during rapid decompression from depths ≥ 42 m, others survived at 1 atm of pressure if vented. In contrast, red grouper never survived rapid decompression from these depths to 1 atm pressure in the laboratory, even when vented they must rapidly recompress at acclimation depth (Burns et al. 2004). Although rapid recompression could not be accomplished in laboratory holding tanks, when achieved through slow controlled incremental step-wise decompression experiments within hyperbaric chambers from the simulated depth of 42.7 m, all red grouper and red snapper survived, albeit there were differences in both the number of pressure increments required to acclimatize fish back to ambient surface atmospheric pressure and decompression times between the two species. Red grouper required five pressure increments (63, 50, 35, 20 and 5 *psi*) to acclimate to 1 atm of pressure, red snapper only needed four (63, 40, 25 and 15 *psi*). Despite requiring an additional stop, red grouper spent less cumulative time (76.5 hours) becoming acclimated to the various simulated ascent depths than red snapper (104 hours). In addition, red grouper depressurization occurred at increasing greater increments of pressure (20, 30, 43 and 75%) from the previous pressure whereas red snapper depressurization occurred in approximately equal increments of 39, 37 and 40% decreases from the previous pressure. Initial acclimation time to the simulated depth of 42.7 meters (63 *psi)* also differed. Red grouper took 71 hours to acclimate to depth while red snapper acclimated faster (52 hours). Finally, although red snapper needed more time to reacclimatize after each decrease in pressure, they were capable of handling larger pressure changes per increment than red grouper. At sea, Wilson (1993) reported a 95% survival rate for red grouper caught on hook-and-line and returned and held in cages at 43 m for up to eight days following the return of these fishes to *in situ* conditions.

Data were consistent with laboratory results from MARFIN Award NA97FF0349 of red grouper and red snapper subjected to depth simulations in fish hyperbaric chambers (Burns et al. 2004). Swim bladders of both species ruptured with a change from 1 to 2 atm of pressure (10-20 m); however, both species easily survived capture from these depths as well as rapid decompression from 21 m (100% survival). There are, however, marked differences in their ability to tolerate rapid decompression from deeper depths ($\geq$27 m). Data from depth simulations of 27.4 m in hyperbaric chambers have shown variable survival due to hemorrhaging in some red grouper, but results for red snapper show 100% survival with no complication. While some red snapper did suffer mortality or sub-lethal effects during rapid decompression from simulated depths ≤ 42 m, many survived when held at 1 atm pressure if vented. In contrast, red grouper never survived rapid decompression from simulated depths of ≤ 42 m to 1 atm pressure, even when vented (Burns et al. 2004). However, field data have shown that red grouper can survive rapid decompression from depths of 61 m or greater, if the fish were vented and immediately allowed to return to the prior habitat depth (Wilson and Burns 1996, Burns and Robbins 2006), criteria which could not be met in laboratory studies.

*Hyperbaric Chambers*

Red grouper in this study were vented after removal from the hyperbaric chambers and placed into holding tanks at 1 atm to observe recovery. They were unable to return immediately to acclimated depth. During necropsies the physical effects of rapid decompression on red grouper were obvious and showed they suffered more internal trauma than red snapper at the same depths. This was evident in the presence of massive visceral hemorrhaging and bilateral cranial clots unique to red grouper. Red grouper also exhibited various degrees of exophthalmia, from all depths tested except 21.3 m. In all cases exophthalmia always occurred in both eyes simultaneously and to the same extent. Necropsies revealed that gas was actually present behind the eyeball when red grouper suffered from exophthalmia. The volume of gas present appeared to be too great to be accounted for simply by dissolved gas in tissues. It appears that when the swim bladder bursts more gas is released into the ventral coelom, increasing the amount of damage to the fish. This parallels results reported for some species of rockfish (Rogers et al. 2008).

Venting these fishes was not successful in removing all swim bladder gases to prevent internal trauma caused by emboli formation within blood vessels and organs, especially the cranium and blood vessels leading to the eyes. The condition of the red grouper immediately removed from the chambers appeared viable. Fish were energetic and lively when first placed into the recovery tanks, repeatedly swimming down to the bottom of the tank trying to return to acclimatized depth. Rapidly fish began to exhibit more obvious and extreme external physical signs of depth induced trauma until death occurred within ½ hour after removal from the chamber. Rogers et al. (2008) reported a greater than 75% initial capture for rockfishes within the first 10 minutes of capture in spite of "species-specific differences in the types and degree of angling-induced barotrauma."

In the Wilson and Burns (1996) study, red grouper caught at 42 m and 43 m were immediately placed into the shipboard hyperbaric chambers for repressurization to determine survival rates when effects of rapid decompression were quickly countered. Survivorship was determined by the released fish's "ability to swim down rapidly and vigorously after release." This is the reason for the disparity in survival between the two studies. Unlike the red grouper in the laboratory experiments that were forced to remain at 1 atm of pressure, these fish were free to return to acclimatized pressure. On the other hand, results from the Wilson and Burns (1996) study are comparable to results from the controlled step-wise decompression portion of this study. Survival rate was 100% in this study versus the 85% reported by Wilson and Burns (1996); however, this disparity is probably due to initial fish condition. Fish in the controlled step-wise decompression experiments were in excellent condition. Fish in the Wilson and Burns (1996) study suffered the ill effects of rapid decompression and some had hook damage and more than likely represent an accurate estimate of red grouper survival under real world conditions.

In contrast to red grouper, red snapper did not suffer as massive internal trauma at the same simulated depths. The massive visceral hemorrhaging and bilateral cranial clots common in red grouper were never found in red snapper, even in those used in the 61.0 m chamber experiments. The survival rate for red snapper at 42.7 m was 60% and is comparable to the 56% red snapper survival at depths of 37-40 m reported by Gitschlag and Renaud (1994) and the 50% survival rate at 36 m reported by Koenig (2001). The 55% red snapper survival rate at 61.0 m found during this study supports previous findings of 60% survival at 50 m reported by Gitschlag and Renaud (1994).

Red snapper are much less prone to exophthalmia at shallower depths due to anatomical differences and a smaller volume of swim bladder gases within their bodies following swim bladder rupture. A few red snapper exhibited exophthalmia in one eye, a few in both eyes. In both scenarios the fish survived because the brain was undamaged. The fishes with exophthalmia in one eye were only blind in that eye and were capable of behaving normally and remained part of the school in the holding tanks. Fish which had succumbed to exophthalmia in both eyes, while completely blind, were able to use their sense of smell to locate food and fed and their lateral line sense to remain upright within the tanks. Although they mostly remained on the bottom of the tanks, they survived for months within the tanks until they had to be humanely euthanized at the end of the study as they could not be released or put in display tanks where they would starve because of competition by sighted individuals for food.

No effect of handling time were detected nor was handling time incorporated into the study to influence survival for either species; however, the average handling time (51.2 sec) during year two may have been too low to realize any effects. Koenig (2001) found surface interval (analogous to handling time) to be strongly related to mortality. Surface intervals in his study ranged from 3-18 min, far longer than the 9-103 sec range during year two. However, during year one, longer handling time (3-10 min) was probably responsible for the more variable survival observed at 42.7 m and 61.0 m and this does agree with Koenig's results. Holding time was also significant factor in rockfish survival (Jarvis and Lowe 2008).

*Swim Bladder Healing*

Parker et al. (2006) suggested that longer-term survival may be compromised by structural damage to the swim bladder and (or) other organs. Despite differences in severity of internal trauma from the hyperbaric chamber experiments, in all red grouper and red snapper that survived, regardless of simulated depth, swim bladder ruptures showed signs of healing within 24 hours. Within 24 hours, the tissue on both sides of the rupture was tenuously connected along the entire length of the rupture. All fish swim bladders were healed sufficiently so as to be functional within 2-4 days after chamber removal. The only visible sign of the rupture was a line of scar tissue. This line of scar tissue persisted over time and was used both in the laboratory and in the field as a physiognomic indicator of previous ruptures in captured and released fishes. Swim bladder rupture scars were also evident in fishes of both species that were caught on hook-and-line gear at depths > 10 m, not just experimental chamber fishes. These scars provide evidence that not only had the fishes been previously caught at depths > 10 m, but that they survived swim bladder rupture, healed and were then capable of resuming normal behavior. These data conflict with results reported by Rummer (2007) and Rummer and Bennett (2005) who stated that red snapper swim bladder tears required an average of 14 days for repair. Fish condition may have played a role in healing time. Live red snapper treatment upon arrival at each facility as well as differences in seawater treatment and sanitation during holding and experimentation differed. Rummer and Bennett (2005) prophylactically treated their red snapper with 50.00 mg/L nitrofurazone, dipped fish in 0.30 mg/L CuSo4 for 60 minutes and quarantined them for five days in mg/L Dylox and 2.50 mg/L Marex to eradicate bacterial, *Amylodinium* sp. and trematode infestation and then held fishes a minimum of 14 days in biologically filtered tanks before experimentation. Although fish in both studies had similar diets and were fed until sated, Rummer and Bennett (2005) did not feed fish for 24 hours before or during experimental trials. As seen in the methods section for this study, fish were only treated with a 5-minute freshwater dip with Formalin solution (2 drops 37% Formalin/3.8 liters of water) upon arrival but also dipped 7, 14, 21 and 28 days after the first dip treatment to kill any ectoparasites that hatched after the first dip based on the life cycles of the ectoparasites encountered in the sieved bath water. Fish were quarantined for one month to identify any health or parasite problems, to eliminate the possibility of complications from latent hook mortality, and to acclimate fish to handling and laboratory surroundings. Following quarantine, fish were divided into different experimental groups and well fed before being placed in the hyperbaric chambers. Another difference may be in the water quality used in the two studies. Raw seawater filtration was conducted through various types of filters was necessary to keep fish healthy.

Possible explanations for this disparity may be the result of different methodology both in chamber construction and experimental treatment. Data collected for this study were obtained from fish necropsy where trauma and healing could be directly observed and photographed. Although Rummer (2007) and Rummer and Bennett (2005) also necropsied their fish, they utilized two-dimensional X-ray images to determine simulated depth acclimation, decompression, swim bladder rupture after rapid decompression and organ displacement caused by expanding swim bladder gases following rupture and determining tissue boundaries and gas occupied areas may have been difficult. They also measured organ dimensions to estimate volumes; a method subject to error (Rogers et al. 2008).

*Stomach Prolapse and Feeding*

Although red grouper took more time to recover and begin normal feeding than red snapper following rapid decompressed from 42.7 m in both species the fish's stomach muscles pulled the stomach back into place and making normal feeding possible. Red grouper rapidly decompressed from 21.3 m and 27.4 m fed within two hours of removal from the chambers. Both species used in the step wise controlled acclimation study fed within 1-2 hours of removal from the chambers. To compare laboratory experimental fishes with those caught on hook-and-line, necropsies of red grouper and red snapper caught off headboats from depths > 10 m were conducted. These fishes showed evidence of recent stomach prolapse through the presence of the "esophageal ring." Externally, these fish appeared healthy and well fed. The presence of food in their stomachs indicated that they were feeding normally and supports findings reported for chamber experiment fishes.

In shallow waters, some fishers participating in the tag and release portion of this study reported multiple recaptures of undersized red grouper or red snapper that they had just tagged and released back into the water. Same day red grouper recaptures were much more common and were reported to occur anywhere from immediately to 30 minutes to one hour after the original capture and release. These "hook happy" fish were reported to be lively and did not appear to suffer from the catch and release experience.

*Fish Tag and Release*

Recaptures from the tagging portion of this study also support red grouper survival after rapid recompression at sea. Data showed vented red grouper can survive rapid decompression from depths of 61 m or greater, if fish are vented and can immediately return to habitat depth (Wilson and Burns 1996, Burns and Restrepo 2002, Burns and Robbins 2006), criteria that could not be accomplished in laboratory holding tanks that were only a few feet deep. The reason for the disparity in red grouper survival rates following release from the hyperbaric chambers and experiments at sea is that at sea red grouper could swim back to habitat depth. Fish are aware of the pressure at the depth to which they are acclimated and perceive pressure changes through sensory nerve endings in the swim bladder wall that stretch or slacken in response to changes in pressure. These nerve endings that signal the fish's brain to fire swim bladder neurons to initiate deflation or inflation of the swim bladder (Blaxter and Tyler 1972, Marshall 1970) must still function in fish with ruptured swim bladders. Thus, fish quickly removed from acclimation depth and then released strive to return to acclimation depth.

Returning to acclimation depth was possible for vented red grouper at sea, but although vented red grouper, removed from the chambers and placed into 900-liter holding tanks, attempted to swim back down to the depth at which they were acclimated within the chamber they could never achieve this depth. These fish kept swimming to the bottom of the tanks for half an hour, exhibiting more and more pronounced external signs of barotrauma infiltrating the cranial area as time passed until they died. However, some of these fishes would have been expected to survive if they could rapidly recompress as observed for red grouper released at sea, returned to depth in cages and the 100% survival during the controlled step-wise decompression.

Fish mortality due to barotrauma is not equivalent to nitrogen narcosis that causes “the bends” in divers. Trauma in fish is the result of damage caused by emboli within the fish’s blood and organs. The greater amount of retal area shared by gas gland cells in the red grouper swim bladder as well as the quantity of swim bladder gases within the more capacious red grouper swim bladder are probably responsible for the increased hemorrhaging that occurs in red grouper blood vessels associated with the swim bladder. The observed smaller extent of hemorrhaging that occurs in red snapper swim bladders probably results from the less intimate connection between rete and gas gland cells within the swim bladder and the lesser quantity of swim bladder gases housed within the smaller swim bladder.

*Differences in Survival by Size*

Survivorship by fish size appears to vary by species. Bartholomew and Bohnsack (2005) summarized findings on mortality with respect to fish length and mortality from thirteen studies with varying results. Two studies (Taylor and White 1992, Malchoff and MacNeill 1995) found lower mortality for smaller individuals for non-anadromous trout and striped bass. Studies on lake trout (Loftus 1986) and Chinook salmon (Bendock and Alexandersdottir 1993) reported higher mortality for larger fishes. Results from ten other studies on various species including cutthroat trout (Pauley and Thomas 1993), spotted seatrout (Murphy et al. 1995), rainbow trout (Schisler and Bergensen 1996), (striped bass (Bettoli and Osborne 1998, Nelson 1998), blue cod (Carbines 1999), black seabass and vermilion snapper (Collins et al. 1999) and common snook (Taylor et al. 2001) showed no difference in mortality rates by size. Fish length was also not a factor in red snapper survival according to Gitchlag and Renaud (1994); a finding at odds with results from this study.

Although small red grouper (< 38.1cm) appear to lack a secondary area located at the posterior ventral swim bladder when viewed under a dissecting microscope, Brown-Peterson and Overstreet (Burns et al. 2008) report that histological examination of this area revealed that even small red grouper (25.1 cm) have some vascularized tissue, as represented by blood vessels and capillaries but no organized gas resorption/secretion area at this length as smaller fish may not require as much gas for buoyancy. This difference may play a part in the disparity in fish survival by size and differences between species. Being a deeper bodied more robust fish than red snapper, it is not surprising it has a higher percentage of gas gland in the rete compared with red snapper at similar lengths. A benthic species, that remains in inshore nursery grounds until moving offshore with increased size, it probably requires additional assistance with gas exchange as it grows and begins its offshore migration.

Many fishers claim smaller fish of both species survived rapid decompression from depth better than larger fish (personal communication). Histological data by Brown-Peterson and Overstreet (Burns et al. 2008) appear to support this claim. They reported that although retal hemorrhaging was significantly higher in red grouper than in red snapper when adjusted for length, the percentage of both red grouper and red snapper with hemorrhaging in both rete and the swim bladder increased significantly by 50 mm fish length increments. Additionally, they reported hemorrhaging was rare in small red snapper compared with large red snapper; however, some hemorrhaging occurred in all red grouper regardless of fish length.

Koenig (2002) also found a positive trend for survival of smaller red grouper and red snapper over their larger counterparts during his analysis of the relationship between size and mortality for both species caught at 35 m and 40 m and maintained in his *in situ* cage experiments. These findings also agree with those of Wilson (1993) who reported that none of the large (> 737 mm) red grouper or scamp in his *in situ* cage experiments at 73 m survived. Only the smaller (< 584 mm) fish caught at every station survived. He found size at recapture to be important, with only fish < 584 mm surviving in his *in situ* cages at depths of 43-73 m for up to the eight-day project observation period.

A log-likelihood G test was run for private recreational and recreational-for-hire recaptures by size from this study. Results showed a significant difference in recapture rates for small (≤ 38.1 cm) and larger (> 38.1 cm) fish of both species (red grouper $p$=9.7x$10^{-19}$; red snapper $p$=9.47x$10^{-6}$). Results benefited survival of larger fish of both species. These results did not agree with those of swim bladder histology and field study results reported by Koenig (2001) and Wilson (1993) and Brown-Peterson and Overstreet (Burns et al 2008).

Released undersized red snapper caught off charter vessels and headboats in the waters off the Florida Panhandle face heavy predation from bottlenose dolphins (*Tursiops truncates*) (personal communication headboat and charter boat captains) (Figure 3-29).

Figure 3-29. Bottlenosed dolphin about to feed on an undersized red snapper just discarded from a headboat fishing off Panama City, Florida.

During two trips in April 2003, confirmed and probable takes by dolphins constituted a total of 28% and 23% of the day's catch. Some fish were removed directly from the hooks by dolphins before being landed (Burns et al. 2004). Similar predation has been reported for red grouper by recreational-for-hire captains (personal communication) who reported dolphins know their schedules and fishing locations and would meet vessels to prey on discarded fish.

Since predation would favor survival of larger fish, private recreational and recreational-for-hire data were analyzed separately. Private recreational recapture data at 21.3 m (no barotrauma effects) showed no difference in recapture rates for small and large fish of both species, but recreational-for-hire data showed survival favored larger fish.

*Recaptures Aboard Commercial Long-line Vessels*

Although only 13 of the 916 red grouper originally caught, tagged and released on long-line gear during this study were recaptured, it showed that red grouper can survive this fishing process and rapid decompression from depths ranging 38.4-80.5 m. Most fish (85%) were originally caught in less than 70 m. Wilson (1993) determined the potential survival of grouper to be no greater than 25% for fish caught at depths of 73 m. Conversely, he reported a potential survival of 95% at 43 m for red grouper under *in situ* conditions when protected in cages.

Seasonal mortality of fish caught at depth, based on thermal shock caused by large differences in water and air temperature during the summer has been reported for fish caught off charter and headboats off Texas (Sandra Diamond, personal communication) and off the Florida east coast (Roger DeBruler, personal communication). This summer phenomena was not readily apparent in the small sample of long-line caught reef fish off Southwest Florida as part of this study. More floaters were recorded during spring and fall. Most floaters suffered trauma resulting from depth-related injury as indicated by various degrees of exophthalmia, predation (some bite marks to covered with bite marks), or gear related wounds (gut hooked). Predation at some commercially fished sites was high and occurred both during ascent through the water column during capture as well as upon release.

*Fish Venting*

Data from laboratory hyperbaric chamber experiments from this study show venting can provide an edge for survival of some species when fish are not allowed to return to habitat depth. Collins et al. (1999) reported enhanced survival of vented black sea bass (*Centropristis striata*). Benthic species can return to habitat depth and survive the two to four day healing process. However, Collins et al. (1999) found that venting vermilion snapper (*Rhomboplites aurorubens)* did not provide as great a benefit for this small water column species. However, a pelagic species with a ruptured swim bladder cannot maintain itself in the water column for very long (Marshall 1973). A small vented water column species would be unable to maintain its position and hover for two days to accommodate swim bladder healing, instead it would sink to the bottom and become subject to bottom predators.

In addition to the physiological trauma that physoclistic fish species experience during rapid ascent from depth, it appears that other factors are involved that may modify the extent of damage experienced from rapid changes in pressure. Koenig (2001) who did not vent the fishes in his experiments found a significant “direct and strong relationship between depth-related mortality and surface interval.” The longer a fish remains at the surface filled with expanding swim bladder gasses within its body, the more internal trauma these gases will inflict. Venting removes escaped swim bladder gases from the fish’s body cavity following swim bladder rupture and reduced trauma in laboratory hyperbaric chamber studies. It can allow fish to regain control over buoyancy and return to habitat depth rather than floating at the surface where the fish is subject to the elements and predation from seabirds, marine mammals, sharks and other predatory fishes. Venting, however, has no effect on existing emboli. Returning to habitat depth enables fish recompression if fish can return rapidly to acclimation depth.

Venting in and of itself did not cause red grouper or red snapper mortality but it also did not provide long-term effects. Results from Restrepo’s two models developed to analyze short-term (within one month of tagging = Model 1) and long-term (1 year or longer = Model 2) red grouper recaptures were developed early in the study (Burns and Restrepo 2002). Model 1 supported the hypothesis that fish venting improved immediate survival for fish caught at depths greater than 21.3 m. Model 2 suggested that, long-term survival was influenced more by other factors such as year, depth of capture or location rather than venting, however; additional data collected showed that there appears to be little or no difference in fish survival in vented and not vented fish in the field and immediately returned to capture depth but there may an advantage when fish are caught at depth and held at the surface such as for laboratory studies, as brood stock, aquarium displays, live fishing tournaments, etc. . The short term Restrepo Model should be run with the new additional data.

*Fish Survival by Treatment*

Ascent rate for hand over hand trap retrieval averaged 0.45 m/s (1.6 ft/sec), while winch retrieved traps ascended at an average rate of 1.22 m/s (4 ft/sec). Trial sample size was too small to perform statistical analyses. Although Gitschlag and Renaud (1994) implied ascent rates play an important role in depth-induced mortality of red snapper, Koenig (2001) found no relationship between ascent rate and mortality in determining survival of reef fishes including red grouper and red snapper caught on electric reel from depths (18-55 m) and held in traps over time.

*Fish Traps*

Wilson and Burns (1996) found for fishes captured on rod and reel, depth-induced mortality of undersized reef fish increased with depth. Results from fish hyperbaric chambers studies support this finding. However, many fish caught in commercial fish traps were lively and did not exhibit external severe depth-induced trauma with rapid depressurization and did not require venting prior to release. Review of videotaped trap ascent showed these fish did not struggle during ascent. Those that struggled within the traps during ascent exhibited signs of barotrauma. Although few fish were caught during the study, survival was high over all depths fished based on observer determination of fish condition. Of 93 fish caught, six were rated to be in poor condition, two in fair condition, and the rest (92%) in good condition. With the exception of one red grouper (rated as good), which was sacrificed for internal examination, all fish in good and fair condition swam straight down after release. Only the six fish listed to be in poor condition floated. The low mortality seen in trap caught reef fishes, agrees with anecdotal information reported in a commercial trap sector study conducted in 1995 that showed high survivorship of trap caught fish (Alverson 1998). Researchers at the NOAA/NMFS Panama City and Pascagoula Laboratories have also noted differences in red grouper barotrauma captured in traps (Doug DeVries, personal communication) and observed high survivorship of trap caught fish at deep depths during NOAA fish surveys in the Gulf of Mexico (Kevin Rademacher, personal communication).

*Grouper from Commercial Fish Traps*

None of the purchased fish showed outward signs of depth-induced trauma, despite being captured at depths of 55-62 m. Many of the fish had intact gas filled swim bladders and lacked any discernable internal trauma; however, there were a few others that suffered from pinhole sized trauma to the swim bladder and were heavily torqued internally and it is unknown if these effects prove lethal over time. In their cage holding experiments, Rogers et al. (2008) found that in general, more (50%) fish with organ torsion died as opposed to those (28%) with no organ torsion; however, they found this difference was not significant.

Results suggest differences in depth-induced mortality in red grouper and red snapper are related to swim bladder morphology and fish anatomy and physiology. Swim bladder characteristics appear to be species- specific rather than family-specific and appear to contribute to the variation reported in survival from rapid decompression. Jarvis and Lowe (2008) concluded that the observable outward signs of barotrauma on the various rockfish species in their study “appear to be related to species differences in body morphology and also to the degree of vertical movement within the water column.” They reported that deep bodied more demersal rockfish species exhibited greater barotrauma than “elongate, laterally compressed bodied” more pelagic species. Results from this study support their findings. Red grouper, a robust, truly benthic species, has a capacious thin membraned swim bladder necessarily capable of holding a large volume of swim bladder gases that is subject to large ruptures and can cause fatal injuries during rapid decompression. The intimate association to rete, larger blood vessels and gas gland in the red grouper swim bladder results in increased hemorrhaging. Red snapper, a more streamlined pelagic schooling species, have smaller thicker swim bladders capable of holding less swim bladder gas and is prone to smaller tears. More rete in the red snapper swim bladder make gas exchange more efficient resulting in less hemorrhaging at all sizes(Brown-Peterson and Overstreet in Burns 2008). However, histological data, cage studies and data from private recreational tag recaptures support the minimum size rule as smaller red grouper and red snapper survive rapid decompression better than larger fish.

Ecomorphology and a fish’s physiology and behavior appear to be important factors in predicting survival during rapid decompression. Many pelagic species feed on elusive prey such as other fishes and squid while truly demersal species tend to be benthic ambush predators or feed on invertebrates. Pelagic species, more likely to travel through various depths on a regular basis than truly benthic species, may have evolved thicker swim bladders to more easily deal with pressure changes. Additionally, pelagic species are more streamlined than demersal species and may require less swim bladder gas for buoyancy. Another factor may be due to physiological changes related to the amount of physical activity (how much the fish struggles) during ascent from depth that occur during fishing activities (Lee and Bergersen 1996, Wilde et al. 2000).

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# Chapter Four: Red Grouper (*Epinephelus morio*) Movement Patterns in the Eastern Gulf of Mexico and South Atlantic off the State of Florida

## Abstract

Although data analyzed for this chapter came from studies originally designed to determine undersized bycatch survival in the reef fish recreational-for-hire, private recreational and commercial long-line fisheries in the eastern Gulf of Mexico and South Atlantic off the Florida east coast, some general movement trends for red grouper were discernable. Data were analyzed by plotting original capture and recaptures within a GIS and by calculating the distance between points. Coordinates of locations (to the nearest minute, to protect exact fishing sites) where fish were caught were exported to a Geographical Information System (GIS) developed using ArcGIS® 9.x (ESRI, 2004) to perform spatial analyses. Since fishers reported tagging and recapture locations to the nearest minute of latitude and longitude, and based on Florida's proximity to the equator, the definition of movement used in this study was travel of at least 1 minute or 3 km from the original tagging site. This spatial resolution of reporting imposed restrictions on analysis, therefore only moves greater than 3 km were credited as actual movement. Fish movement patterns were analyzed with regard to size, bathymetry and hurricane occurrence. A chi square test was used to determine if fish size was related to movement. Separate tests were run for the Gulf of Mexico and Atlantic. Most red grouper were site faithful and fish tended to be larger with distance from shore. However for fishes that did exhibit long distance movements a stepwise, forward logistic regression red grouper

movement model was developed to determine if long distance movements were the result of hurricanes and tropical storms. Fish movements in the eastern Gulf of Mexico (n=1,011), Florida Keys (n=29) and the South Atlantic off the Florida east coast (n=49) were analyzed. The model indicated two types of movement: 1) individual fish movements by depth (changes of depth of 5m, 10 m, and 20m) and 2) movement by multiple (48) groups of similar sized small to medium (25.4-49.5 cm) sized red grouper (cohort movement). Most movement involved red grouper ≥ 38.1 cm; the length at which tissue in the posterior portion of the ventral wall of the red grouper swim bladder became vascularized and additional gas gland cells developed to provide additional buoyancy. While hurricanes have been documented to influence red grouper movements (Franks 2003), model results showed that although some fish moved during periods when tropical storms or hurricanes were present, other red grouper moved in their absence. Movement due to named tropical storms or hurricanes was not significant. The two significant variables identified by the model were number of days at large between tag and recapture and length at recapture ($p<0.001$). A second model was developed to examine red grouper movement in relation to depth based on groups of fish that changed depth by a minimum of 5 m, 10 m, 20 m and fish that did not change depth or exhibited zero movement. At the ≥ 5m depth difference level, recapture length and growth were significantly different; but tagging length was not. At ≥ 10m and ≥ 20 m differences of both tagging and recapture lengths and growth were significantly different. In all cases, fish that moved into deeper water exhibited greater growth than those that did not move.

## Introduction

Discerning fish movement and migration patterns is of critical importance in understanding the life history of fishes (Cushing 1981). Fishery management depends upon knowledge of the all habitats required by different fish life stages as fish progress from egg to adult. This information has become increasing important as agencies transform management strategies from single species management to ecosystem management (Witherell 2004, U.S. Commission on Ocean Policy 2004). Just as the minimum size limit has been the cornerstone of traditional fisheries management, marine protected areas (MPAs) have become the foundation of ecosystem management (Bohnsack 1993, Bohnsack and Ault 1996, Pew 2003, Ault et al. 2006). Inherent in this concept of fisheries management is the tenant that MPAs provide prime habitat for fish breeding stock that will provide future recruits to depleted areas through spillover (Bohnsack 1994). Knowledge of fish movements as related to habitats, seasons and function for each life stage is necessary for creating better reserves (Crosby et al. 2000, Meester et al. 2001, Meester et al. 2004, Humston et al. 2004, Nowlis and Friedlander 2004).

Many fishes move to utilize different habitats, from feeding grounds to spawning grounds, where the larvae are transported by currents to nursery grounds, and from nursery grounds to grow until they are large enough to join adults on the feeding grounds completing the cycle. Red grouper follow this strategy, spawning offshore and utilizing currents to transport larvae to inshore nursery grounds. Thus current speed, direction and transport play important roles in transporting fish from one habitat to another (Helfman

2007). Red grouper utilize shallow inshore habitats as nursery grounds and move to deeper offshore habitats as they mature. Like many reef fish species, red grouper exhibit site fidelity over long periods of time although extensive movements by some "vagrants" have been documented (Moe 1966, Bullock and Smith 1991, Koenig and Coleman 2006). Current knowledge of fish life history appears to profit fish that do not exhibit movement over vagrants (Bohnsack 1996) but there must be a biological advantage to vagrants, whether it is colonization of new territory or maintaining genetic homogeneity; thus it important to investigate their movements and contributions to the species.

The tag/release study provided useful red grouper movement data. Although most fish did not move, analyses were conducted on those that did in an attempt to determine the purpose of the movements detected. Hurricanes have been documented to influence red grouper movement (Franks 2003). A forward logistic regression red grouper movement model was developed to determine if long distance movements detected in the database were influenced by hurricanes and tropical storms.

## Methods

### *Fish Tag and Release*

#### Fish Tagging

Undersized red grouper were tagged by Mote Marine Laboratory (MML) staff, student interns and volunteers, as well as by charter boat and headboat captains and crew, private recreational and commercial fishers throughout the eastern Gulf of Mexico and off the southeastern Florida coast (Figure 4-1) as components of a variety of funded studies to determine undersized reef fish bycatch survival.

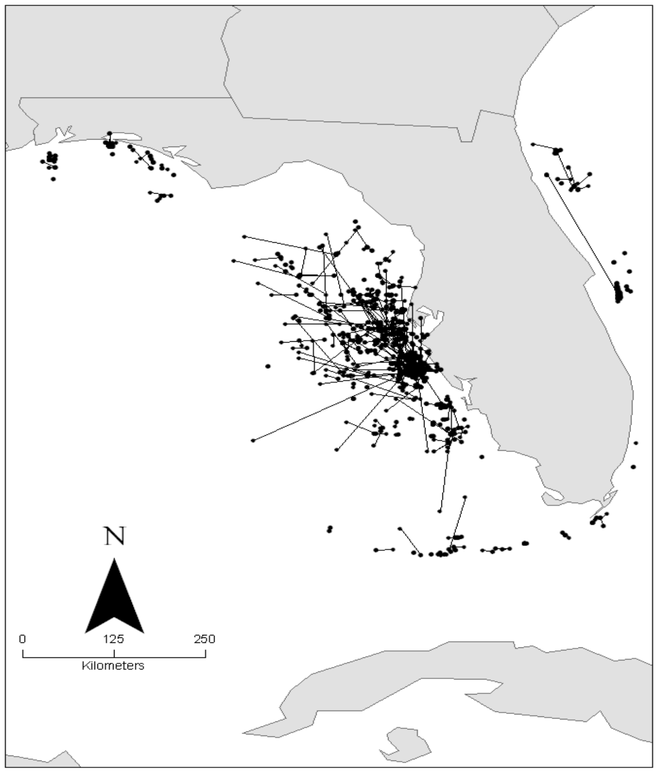


Figure 4-1. Study area including long distance movements of tagged and recaptured red grouper.

All red grouper were tagged using single-barbed Hallprint® plastic dart tags inserted at an angle next to the anterior portion of the dorsal fin. These tags have already been used successfully in MML's Reef Fish Tagging Program. Data collected included tagging date, gear type, tag number, time of day, bait used, water depth, fork length in inches, fish condition upon release, amount of time the fish was out of the water, whether or not the fish was vented and the capture location to the nearest one degree of latitude and longitude. Tag information included tag number and the 1-800 toll-free dedicated telephone number at Mote. The telephone was answered personally during work hours and calls regarding tag return information were recorded on weekends, holidays and evenings by an answering machine.

Return data including tag number, date of capture, gear type, bait type, water depth, fork length in inches, capture location, overall condition of the fish and of the area around the tag insertion site and whether the fish was kept or released, were recorded. Data were entered on a PC computer using Paradox® software into a temporary file. A second individual proofed the entered data against the original data sheet. If no errors were detected or after errors were corrected, data were then transferred electronically into the permanent reef fish database. Since fishers reported tagging and recapture locations to the nearest minute of latitude and longitude, and based on Florida's proximity to the equator, the definition of movement used in this study was travel of at least 1 minute or 3 km from the original tagging site.

Publicity Campaign and Tag Lottery

To increase recapture reporting, a publicity campaign including MML press releases presentations at scientific conferences and fishing club meetings and publication of information in various issues of a MARFIN funded Reef Fish Survival Study (RFSS) newsletter, were used to disseminate project objectives and results. Copies of the newsletter were sent to all study participants as well as to fisheries scientists, fishery management agencies, industry representatives, and newspaper "Outdoor" writers and fishing magazine writers, who requested them. In addition, a tag lottery was held at the end of each year. The winning tag was chosen from all tags returned during that year. Both the tagger and the person returning the tag each received $100.

Data Analyses

Length/frequency data for red grouper were utilized to examine fish length (cm) with distance (km) from shore at time of tagging in the South Atlantic off Florida and in the eastern Gulf of Mexico. A length/frequency histogram of fish lengths (cm) at original capture was constructed by placing fish lengths in 5 cm wide bins. Regressions of mean fish lengths (representing counts of 10 or more fishes) versus original capture distance from shore (km) were superimposed upon the length/frequency histogram. Regressions of the $r^2$ of the means and the $r^2$ of each individual fish were drawn. No means were calculated for categories with less than 10 fishes. A line of best fit for the regressions was calculated using the equation $y = m*x + b$, where $y$ = distance from shore (km), $m$ = slope, $x$ = fish length (FL in cm) and $b$ = y intercept. A linear regression was then run on the regression using all fish lengths to determine if results were significant, i.e. the relationship between the two variables (fish length and distance from shore) were significantly correlated.

Data were analyzed for general distributional trends and size-depth relationships. Red grouper movement was mapped by plotting capture and recaptures within a Geographical Information System (GIS) and by calculating distance between points. The spatial resolution of reporting (one minute of latitude and longitude) imposed restrictions on this analysis, therefore only moves greater than 3 km were used in analyses. Coordinates of locations (to the nearest minute, to protect exact fishing sites) where fish were caught were exported to a GIS developed using ArcGIS® 9.x (ESRI, 2004) to perform spatial analyses. Fish movement patterns were analyzed with regard to movement with size, bathymetry and hurricane occurrence.

Ancillary data, such as bathymetry were acquired from the state of Florida's Geographic Data Library (2004). These data were used to produce geo-referenced maps of locations where red grouper and red snapper were tagged and recaptured by projecting movement data in local UTM NAD 83 coordinate systems (16N and 17N in the Gulf and 18N in the Atlantic). Sigmaplot, Oriana, and GEODISTN (Syrjala 1996) were used to perform statistical analyses. A chi square test was used to determine if fish size was related to movement. Tests were run for both the eastern Gulf of Mexico and South Atlantic.

Red Grouper Movement Model

Possible fish movement induced by hurricanes and tropical storms was examined by a stepwise, forward logistic regression model. The model tested for relationships between movement and environmental or demographic factors. The dependent variable, a binary categorical variable, was whether a fish moved or not (movement defined as $\geq$ one minute of latitude or longitude). Independent variables included whether or not a hurricane or named tropical storm occurred in the study area during each individual fish's time at large, length at tagging, length at recapture, depth at tagging (extrapolated from the National Geophysical Data Center's Coastal Relief Model, Divins and Metzger 2007), depth at recapture (also from the Coastal Relief Model), days at large, growth during time at large, and geographic region (eastern Gulf of Mexico, Florida Keys, or South Atlantic off the Florida east coast.

Red Grouper Movement in Relation to Depth

Differences in fishes that moved within depth and those that moved between depths were examined by first sampling the depth at tag and recapture from the National Geophysical Data Center's Coastal Relief Model (Divins and Metzger 2007). At locations where fish were very close to land, model accuracy can result in fish appearing to be in very shallow water or on land (depths of > 1m or positive elevations). These fish were removed from the analysis leaving 1,090 fishes included in analyses. The difference between tag and recapture depth for each fish was calculated. Fishes were classified into four groups: those that changed depth by at least 5 m, at least 10 m, and at least 20 m. Length at tagging, length at recapture, and growth were compared for fishes by depth group using a Mann-Whitney U test.

Red Grouper "Cohort Movement"

Data were examined for occurrences of multiple similar sized fishes moving from one location to another. The criteria for group movement were that all fishes needed to be tagged at the same location, on the same date, and recaptured together at a second identical location, on the same date. Groups were mapped and data summarized in a table.

## Results

### *Red Grouper*

At total of 16,753 red grouper tag and release events (includes some recaptured fish re-released) occurred between October 1990 and July 2007. Total number of fish tagged and released was 15,724. Recapture coordinates were reported for 96.2% of recaptured fish.

Of these 1,204 (7.7%) fish were recaptured at least once; an additional 151 fish were recaptured multiple times (Table 4-1). Most red grouper (98%) were tagged and

Table 4-1. Number of single and multiple red grouper recaptures from October 1, 1990-July 31, 2007.

| Number of Recaptures | Number of Times Recaptured |
|---|---|
| 1,053 | 1 |
| 124 | 2 |
| 18 | 3 |
| 5 | 4 |
| 2 | 5 |
| 1 | 6 |
| 1 | 7 |

recaptured in the Gulf of Mexico as opposed to 2% from the South Atlantic. Fish were tagged and released by private recreational (13.9%), recreational-for-hire (69.0%) and commercial (12.4%) fishers. The remainder included 0.2% tagged and released during research cruises and 4.5% with insufficient data to determine fishing sector. Gear types included rod and reel, electric rod and reel and commercial bottom long-line.

Most recaptures were reported caught off headboats (42.3%), followed by those caught by recreational fishers (22.2%) and charter vessels (13.6%) sector. Fish caught ranged in size from 14.6-114.3 cm at original capture and from 20.3- 81.3 cm at recapture. Days of freedom ranged 0-4, 677 days. Fish tagged inshore off headboats but recaptured by commercial long-line gear ranged from 37.5-58.4 cm when tagged and 45.7-90.8 cm when recaptured. Days of freedom for these fish ranged 43-1,309 days. These recaptures illustrate the offshore movement of red grouper and their transfer from inclusion in the inshore recreational-for-hire fishery to the offshore commercial long-line fishery. Red grouper tagged off commercial long-line (n=1,238) and bandit (electric reel) (n=328) vessels and recaptured (long-line: n=52; bandit: n=16) included fish which ranged in size from 30.5-62.2 cm at release and 33.0-68.6 cm at recapture. Fish were at liberty for anywhere from 3-2,172 days after release.

Of 1,204 red grouper recaptures, 42.9% exhibited zero movement and 15.4% were recaptured within 3 km of the release site. None of these fish (58.3%) was used in the analyses because movement was defined as a fish having been recaptured > 3 km from the original tagging site. However, some fish (6.1%) did exhibit long distance movements of 50 km or greater (Figure 4-1). The greatest distance traveled was for a fish that had traveled 360.3 km from the release site. Four red grouper were reported to have traveled from the Gulf to the South Atlantic but these recaptures could not be verified.

Red Grouper Movement Model

A complete summary of the variables used in the stepwise, forward logistic regression model applied to test for significant relationships between movement and environmental or demographic factors is found in Table 4-2. The model was based on the following parameters: 1) time frame for red grouper tagged and recaptured (October 1, 1999-July 31, 2007), 2) total number of fish tagged (n=16,753 [includes some recaptures]), 3) total number of unique fish (tagged and released only once) (n=15,724), and 4) total recaptures (n=1,204) of fish recaptured at least once.

Table 4-2. Summary of variables and results of logistic regression movement model. Significant variables (p<0.05) were Length at recapture (TL cm) and Days at Large.

| Variable | Mean | St Dev | Min | Max | Exp (B) | 95% CI for exp (B) | *p*-value |
|---|---|---|---|---|---|---|---|
| Move | 0.376 | 0.485 | 0 | 1 | | | |
| Hurricane (Y=1,N=0) | 0.275 | 0.447 | 0 | 1 | | | 0.669 |
| Length at tag (TL cm) | 39.311 | 6.789 | 20.32 | 76.2 | | | 0.592 |
| Depth at tag (Meters) | -21.992 | 15.836 | -231 | 0 | | | 0.191 |
| Length at recap (TL cm) | 42.525 | 8.43 | 20.32 | 81.28 | 1.112 | 1.063-1.163 | 0.000 |
| Depth at recap (Meters) | -22.911 | 21.628 | -511 | 0 | | | 0.059 |
| Days at large | 141.102 | 197.104 | 2 | 1801 | 1.002 | 1.001-1.003 | 0.000 |
| Growth (cm) | 3.2131 | 4.747 | 0 | 27.94 | | | 0.592 |
| Atlantic (Y=1,N=0) | 0.044 | 0.204 | 0 | 1 | | | 0.324 |
| Keys (Y=1,N=0) | 0.025 | 0.157 | 0 | 1 | | | 0.737 |
| Gulf (Y=1,N=0) | 0.931 | 0.253 | 0 | 1 | | | 0.450 |

Not all recaptures were used in the model. Those that occurred on the same day they were tagged or recaptured multiple times in one day were deleted from the file. After data "clean up," 1,090 recaptures were examined for relationships between movement and environmental and/ or demographic factors. From these, moves from 408 recaptures were used because they fit the criteria.

The stepwise logistic regression identified two variables as significant: number of days at large between tag and recapture, and length at recapture ($p<0.001$, Table 4-2). The model indicates a moderately good fit (-2LL, Cox and Snell $R^2=0.088$ and Nagelkerke $R^2=0.120$). Exp(B) for days at large was 1.003, indicating for every additional day an animal is at large, the odds of moving increase by 0.3%, when length at recapture is held constant. Exp(B) for length at recapture was 1.112, indicating that for every 2.5 cm increase in length of a fish at recapture, the odds of moving increase by 1.12%, when days at large are held constant.

The model indicated two types of movement. The first type was individual fish movements across depth contours with changes in depth of at least 5 m, 10 m, and 20 m associated with growth (movement with ontogeny). The second type was movement by multiple groups of similar sized small to medium (25.4-49.5 cm) sized red grouper, both immature (44%) and mature (56%) often but not exclusively within depth contours.

Red Grouper Movement in Relation to Depth

In both the South Atlantic off Florida and eastern Gulf of Mexico the trend was for smaller red grouper to be found inshore and progressively larger fish to occur with increasing mean distance from shore (Figure 4-2). Linear regression calculations showed an $r^2$ value of 0.926 for mean fish lengths and an $r^2$ of 0.043 for all fish lengths in the Atlantic and an $r^2$ value of 0.741 for mean fish lengths and an $r^2$ of 0.163 for all fish lengths in the Gulf of Mexico. Regression coefficients are shown as Table 4-3. The linear regressions run on the regression using all fish lengths (off both Florida coasts) to determine if results were significant, i.e., the relationship between the two variables (fish lengths and distance from shore) were significantly correlated was significant for both the Atlantic and eastern Gulf of Mexico ($p < 0.001$).

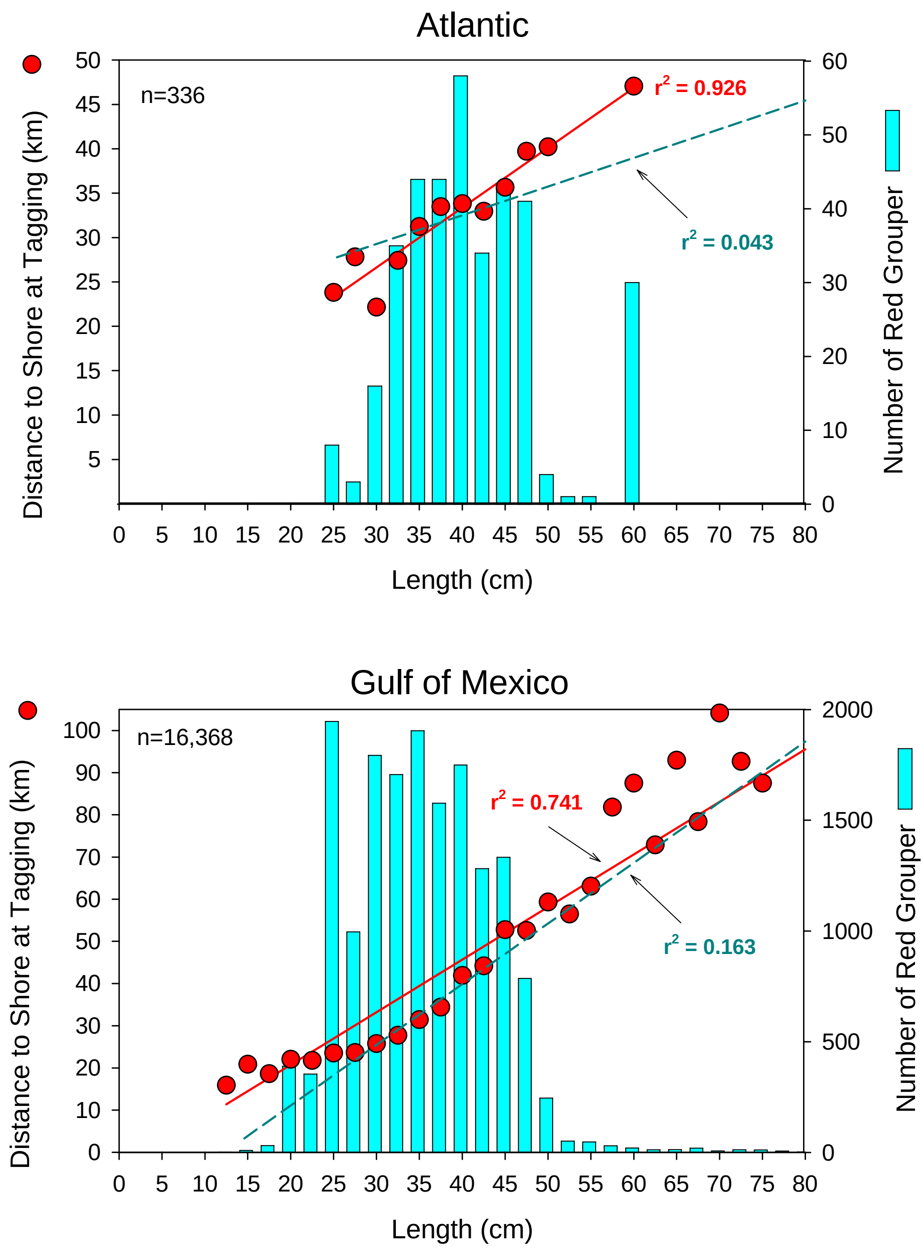


Figure 4-2. Graph of a first order linear regression (red line) through the means (red circles) of red grouper lengths (cm) ≥ 10 per size class and a first order regression through all fish lengths (cyan dotted line) of fish size by distance from shore superimposed over a length/frequency graph of red grouper captured in the South Atlantic off the Florida east coast and eastern Gulf of Mexico.

Table 4-3. Results of linear regression on regression using all fish to test the relationship between fish length and distance from shore for significance for red grouper caught and measured in the South Atlantic off the Florida east coast.

**RED GROUPER ATLANTIC**
**Linear Regression**

Column 1 = distance to shore. Column 2 = fish length
Col 1 = 19.585 + (0.323 * Col 2)
N = 332
R = 0.208Rsqr = 0.0434 Adj Rsqr = 0.0405
Standard Error of Estimate = 11.194

| | Coefficient | Std. Error | t | P |
|---|---|---|---|---|
| Constant | 19.585 | 3.469 | 5.645 | < 0.001 |
| Col 2 | 0.323 | 0.0835 | 3.868 | < 0.001 |

Analysis of Variance:

| | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Regression | 1 | 1874.935 | 1874.935 | 14.963 | < 0.001 |
| Residual | 330 | 41351.601 | 125.308 | | |
| Total | 331 | 43226.536 | 130.594 | | |

**RED GROUPER GULF**
**Linear Regression**

Column 1 = distance to shore. Column 2 = fish length
Col 1 = -18.275 + (1.457 * Col 2)
N = 15985
R = 0.407Rsqr = 0.165 Adj Rsqr = 0.165
Standard Error of Estimate = 25.890

| | Coefficient | Std. Error | t | P |
|---|---|---|---|---|
| Constant | -18.275 | 0.966 | -18.925 | < 0.001 |
| Col 2 | 1.457 | 0.0259 | 56.270 | < 0.001 |

Analysis of Variance:

| | DF | SS | MS | F | P |
|---|---|---|---|---|---|
| Regression | 1 | 2122324.057 | 2122324.057 | 3166.297 | < 0.001 |
| Residual | 15983 | 10713177.005 | 670.286 | | |
| Total | 15984 | 12835501.063 | 803.022 | | |

Movement offshore with ontogeny was clearly visible as small undersized red grouper tagged off recreational-for-hire and private recreational vessels near shore were recaptured offshore in deeper waters by commercial reef fish long-line and bandit fishers (Figure 4-3). Fish that moved across contour depths could also be distinguished from those that did not by differences in size and growth rates (Table 4-4).

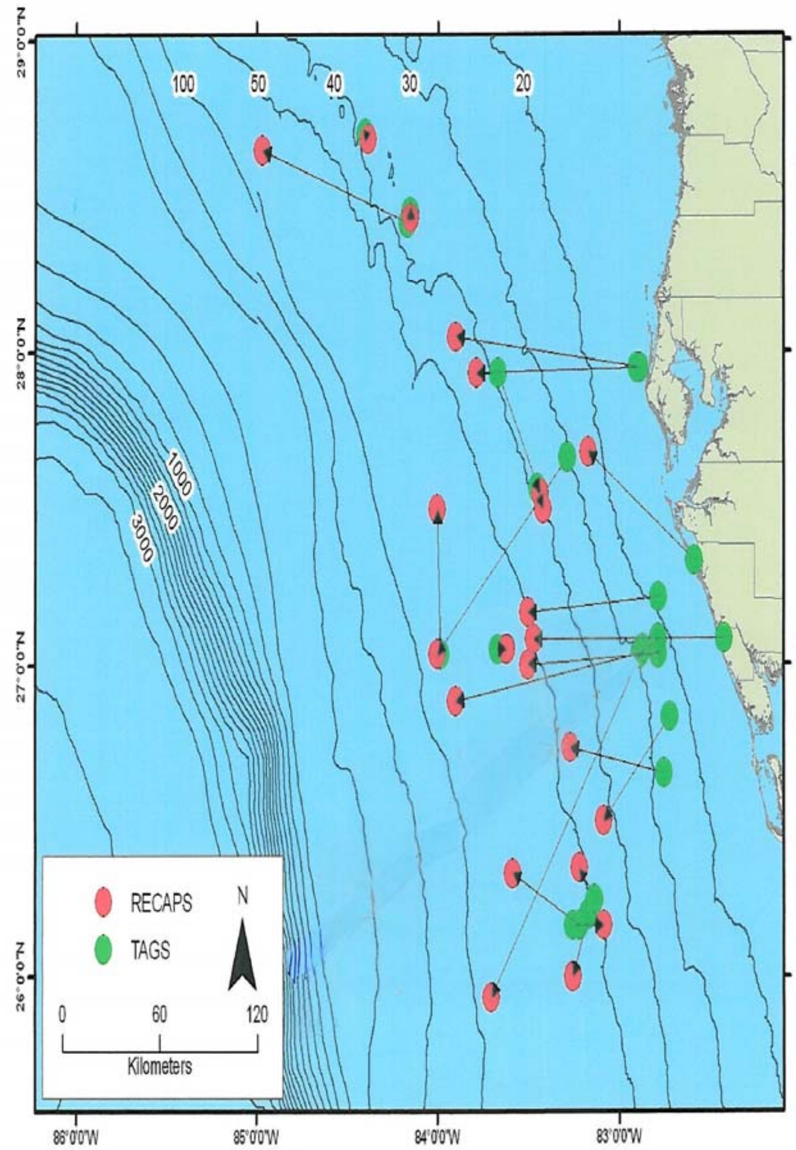


Figure 4-3. Red grouper movements plotted from recaptures. Because latitude and longitude were recorded to the nearest minute, not second, to protect exact fishing spots, red grouper tagged and released just offshore, appear as if on land. Most recaptures show ontogenic movement offshore.

Table 4-4: Summary statistics for fish movement in relation to changes in depth during movement. Fish were classified into two groups; 1) (labeled as change) those whose movements resulted in a change in depth of 5 m, 10m, and 20m and 2) (labeled as no change) those that either did not move or whose movement did not result in a change of the specified magnitude. The fish that did not

| | | | tag length cm | recap length cm | Growth cm |
|---|---|---|---|---|---|
| 5 meters of depth | no change | mean | 39.294 | 42.113 | 2.819 |
| | | st dev | 6.756 | 8.128 | 4.318 |
| | | n | 890 | 890 | 890 |
| | change | mean | 39.980 | 45.187 | 5.207 |
| | | st dev | 6.985 | 9.271 | 5.994 |
| | | n | 199 | 199 | 199 |
| 10 meters of depth | no change | mean | 39.319 | 42.266 | 2.946 |
| | | st dev | 6.756 | 8.204 | 4.420 |
| | | n | 1025 | 1025 | 1025 |
| | change | mean | 41.123 | 49.291 | 8.168 |
| | | st dev | 7.308 | 9.211 | 6.897 |
| | | n | 64 | 64 | 64 |
| 20 meters of depth | no change | mean | 39.345 | 42.443 | 3.124 |
| | | st dev | 6.779 | 8.295 | 4.637 |
| | | n | 1057 | 1057 | 1057 |
| | change | mean | 42.228 | 50.129 | 7.902 |
| | | st dev | 7.051 | 9.156 | 6.109 |
| | | n | 32 | 32 | 32 |

At the 5 m depth difference level, recapture length and growth were significantly different; but tagging length was not. Fish that changed depth by 5 m had a greater recapture length and exhibited more growth than those that did not change depth. At the 10 m depth difference level, all factors (tagging length, recapture length, and growth) were significantly different. Fish that changed depth by 10 m had greater tagging and recapture lengths and grew more than those that did not. Like those that changed depth by 10 m, at the 20 m difference, all factors (tagging length, recapture length, and growth) were different. Fish that changed depth by 20 m had greater tagging and recapture lengths and growth than those that did not. It should be noted that in all cases, the proportion of fish that changed depths compared to those that did not move or did not change depth was very small; which may skew statistical results in some cases.

**Red Grouper "Cohort Movement"**

Individuals (n=126) within forty- eight red grouper groups, ranging in size from 25.4-49.5 cm appeared to have moved together (Table 4-5). Movement distances ranged from 3.2 km to 120.3 km (mean = 13.55, sd =23.62) and group size ranged from 2 fish to 6 fish (mean = 2.63, sd =1.00). Group movement occurred in both the Gulf of Mexico near the Florida Panhandle (Figure 4-4) and in the eastern Gulf of Mexico (Figure 4-5). Movement was documented to occur during all months of the year with the exception of April and within 13 of the 16 years of the study. Fish length (at tagging and recapture) in movement groups did not differ from those not in movement groups (U=62675.5, $p$=0.651 and U=61871.0, $p$=0.495, respectively), nor did growth that occurred between captures (U=64160.5, $p$=0.977); however, for the most part fish lengths within each group were similar.

Table 4-5. Groups of red grouper that appeared to move together. Fish were tagged on the same date at the same location and were recaptured on a different data at a different location. In some cases, groups moved similarly but at different dates; see notes. Depth is expressed as elevation so depth readings are expressed negative.

| TAG # | TAG DATE | RECAP DATE | GROUP # | DIST MOVED (km) | TAG LENGTH (cm) | TAG DEPTH (m) | RECAP LENGTH (cm) | RECAP DEPTH (m) | DAYS OUT | GROWTH (cm) | NOTES |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1008 | 1/24/1991 | 4/30/1992 | 1 | 120.31 | 25.40 | -11.23 | 30.48 | -35.43 | 462 | 4.54 | |
| 1009 | 1/24/1991 | 4/30/1992 | 1 | 120.31 | 30.48 | -11.23 | 35.56 | -35.43 | 462 | 4.54 | |
| 1270 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 35.56 | -8.87 | 35.81 | -13.98 | 18 | 2.64 | |
| 1277 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 41.91 | -8.87 | 43.18 | -13.98 | 18 | 3.04 | |
| 1281 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 30.48 | -8.87 | 30.48 | -13.98 | 18 | 2.54 | |
| 1284 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 35.56 | -8.87 | 35.56 | -13.98 | 18 | 2.54 | |
| 8512 | 9/7/1991 | 6/18/1992 | 3 | 63.81 | 33.02 | -26.49 | 35.56 | -22.97 | 285 | 3.54 | |
| 8523 | 9/7/1991 | 6/18/1992 | 3 | 63.81 | 36.83 | -26.49 | 40.64 | -22.97 | 285 | 4.04 | |
| 8533 | 9/7/1991 | 6/18/1992 | 3 | 63.81 | 39.04 | -26.49 | 40.64 | -22.97 | 285 | 3.17 | |
| 4287 | 12/7/1991 | 8/3/1992 | 4 | 4.89 | 48.26 | -24.57 | 55.88 | -21.99 | 240 | 5.54 | SAME MOVEMENT AS GROUP 5 |
| 4289 | 12/7/1991 | 8/3/1992 | 4 | 4.89 | 33.02 | -24.57 | 55.88 | -21.99 | 240 | 11.54 | |
| 4299 | 12/7/1991 | 8/3/1992 | 4 | 4.89 | 35.56 | -24.57 | 46.99 | -21.99 | 240 | 7.04 | |
| 4251 | 12/24/1991 | 8/3/1992 | 5 | 4.89 | 40.64 | -24.57 | 43.18 | -21.99 | 223 | 3.54 | SAME MOVEMENT AS GROUP 4 |
| 4252 | 12/24/1991 | 8/3/1992 | 5 | 4.89 | 41.91 | -24.57 | 46.99 | -21.99 | 223 | 4.54 | |
| 4288 | 12/24/1991 | 8/3/1992 | 5 | 4.89 | 35.56 | -24.57 | 40.64 | -21.99 | 223 | 4.54 | |
| 8608 | 12/27/1991 | 6/7/1992 | 6 | 17.99 | 33.02 | -17.90 | 40.64 | -10.90 | 163 | 5.54 | |
| 8609 | 12/27/1991 | 6/7/1992 | 6 | 17.99 | 44.45 | -17.90 | 49.53 | -10.90 | 163 | 4.54 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10549 | 6/10/1992 | 6/17/1992 | 7 | 3.69 | 32.39 | 4.75 | 33.02 | -2.34 | 7 | 2.79 | |
| 10550 | 6/10/1992 | 6/17/1992 | 7 | 3.69 | 39.37 | 4.75 | 40.64 | -2.34 | 7 | 3.04 | |
| 10159 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 36.83 | -17.90 | 36.83 | 4.35 | 52 | 2.54 | |
| 10166 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 45.72 | -17.90 | 45.72 | 4.35 | 52 | 2.54 | |
| 10168 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 45.72 | -17.90 | 45.72 | 4.35 | 52 | 2.54 | |
| 10174 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 44.45 | -17.90 | 44.45 | 4.35 | 52 | 2.54 | |
| 10074 | 8/19/1992 | 9/4/1992 | 9 | 5.11 | 46.99 | -22.97 | 46.99 | -22.97 | 16 | 2.54 | |
| 10080 | 8/19/1992 | 9/4/1992 | 9 | 5.11 | 44.45 | -22.97 | 44.45 | -22.97 | 16 | 2.54 | |
| 10083 | 8/19/1992 | 10/28/1992 | 10 | 6.35 | 43.18 | -22.97 | 43.18 | -22.97 | 70 | 2.54 | |
| 10091 | 8/19/1992 | 10/28/1992 | 10 | 6.35 | 38.10 | -22.97 | 38.10 | -22.97 | 70 | 2.54 | |
| 10131 | 8/20/1992 | 5/21/1993 | 11 | 4.02 | 34.29 | -26.41 | 38.10 | -36.19 | 274 | 4.04 | |
| 10138 | 8/20/1992 | 5/21/1993 | 11 | 4.02 | 48.26 | -26.41 | 53.34 | -36.19 | 274 | 4.54 | |
| 10142 | 8/20/1992 | 7/31/1993 | 12 | 8.44 | 44.45 | -26.41 | 50.80 | -30.93 | 345 | 5.04 | |
| 10144 | 8/20/1992 | 7/31/1993 | 12 | 8.44 | 43.18 | -26.41 | 48.26 | -30.93 | 345 | 4.54 | |
| 10115 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 45.72 | -32.81 | 55.88 | -32.81 | 765 | 6.54 | |
| 10116 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 43.18 | -32.81 | 55.88 | -32.81 | 765 | 7.54 | |
| 10117 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 43.18 | -32.81 | 55.88 | -32.81 | 765 | 7.54 | |
| 10119 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 44.45 | -32.81 | 58.42 | -32.81 | 765 | 8.04 | |
| 10186 | 9/4/1992 | 2/21/1995 | 14 | 6.06 | 45.72 | -10.90 | 63.50 | 4.35 | 900 | 9.54 | |
| 10191 | 9/4/1992 | 2/21/1995 | 14 | 6.06 | 49.53 | -10.90 | 63.25 | 4.35 | 900 | 7.94 | |
| 2428 | 3/10/1993 | 6/20/1993 | 15 | 4.03 | 53.34 | -24.99 | 55.88 | -24.99 | 102 | 3.54 | |
| 2430 | 3/10/1993 | 6/20/1993 | 15 | 4.03 | 53.34 | -24.99 | 55.88 | -24.99 | 102 | 3.54 | |
| 13242 | 7/10/1997 | 7/31/1997 | 16 | 4.03 | 30.48 | -17.90 | 30.48 | -17.90 | 21 | 2.54 | |
| 13249 | 7/10/1997 | 7/31/1997 | 16 | 4.03 | 50.80 | -17.90 | 50.80 | -17.90 | 21 | 2.54 | |
| 15694 | 7/24/1997 | 8/29/1997 | 17 | 4.02 | 37.47 | -18.51 | 38.10 | -18.51 | 36 | 2.79 | SAME MOVEMENT AS GROUP 18 |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 15695 | 7/24/1997 | 8/29/1997 | 17 | 4.02 | 34.93 | -18.51 | 35.56 | -18.51 | 36 | 2.79 | |
| 17250 | 7/24/1997 | 8/29/1997 | 17 | 4.02 | 38.10 | -18.51 | 38.10 | -18.51 | 36 | 2.54 | |
| 16413 | 8/5/1997 | 8/29/1997 | 18 | 4.02 | 31.75 | -18.51 | 34.93 | -18.51 | 24 | 3.79 | |
| 16415 | 8/5/1997 | 8/29/1997 | 18 | 4.02 | 38.74 | -18.51 | 38.74 | -18.51 | 24 | 2.54 | |
| 16480 | 8/27/1997 | 10/1/1997 | 19 | 3.69 | 34.29 | -24.99 | 35.56 | -24.99 | 35 | 3.04 | |
| 16485 | 8/27/1997 | 10/1/1997 | 19 | 3.69 | 33.02 | -24.99 | 33.02 | -24.99 | 35 | 2.54 | |
| 16503 | 8/27/1997 | 10/1/1997 | 19 | 3.69 | 40.64 | -24.99 | 40.64 | -24.99 | 35 | 2.54 | |
| 18862 | 10/10/1997 | 4/28/1998 | 20 | 6.65 | 27.94 | -12.21 | 27.94 | -18.51 | 200 | 2.54 | |
| 18863 | 10/10/1997 | 4/28/1998 | 20 | 6.65 | 27.94 | -12.21 | 27.94 | -18.51 | 200 | 2.54 | |
| 15954 | 1/20/1998 | 5/27/1998 | 21 | 7.56 | 35.56 | -12.21 | 35.56 | -12.21 | 127 | 2.54 | |
| 15964 | 1/20/1998 | 5/27/1998 | 21 | 7.56 | 40.64 | -12.21 | 40.64 | -12.21 | 127 | 2.54 | |
| 16051 | 1/29/1998 | 3/15/1998 | 22 | 12.16 | 33.02 | -25.45 | 38.10 | -25.45 | 45 | 4.54 | |
| 16052 | 1/29/1998 | 3/15/1998 | 22 | 12.16 | 48.26 | -25.45 | 48.26 | -25.45 | 45 | 2.54 | |
| 16033 | 2/19/1998 | 6/2/1998 | 23 | 110.82 | 35.56 | -26.41 | 38.10 | -14.08 | 103 | 3.54 | |
| 16038 | 2/19/1998 | 6/2/1998 | 23 | 110.82 | 38.10 | -26.41 | 43.18 | -14.08 | 103 | 4.54 | |
| 18171 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 45.72 | -25.45 | 45.72 | -25.45 | 62 | 2.54 | |
| 18175 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 48.26 | -25.45 | 48.26 | -25.45 | 62 | 2.54 | |
| 18176 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 45.72 | -25.45 | 45.72 | -25.45 | 62 | 2.54 | |
| 18177 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 40.64 | -25.45 | 40.64 | -25.45 | 62 | 2.54 | |
| 20302 | 6/9/1998 | 6/30/1998 | 25 | 3.69 | 38.10 | -12.21 | 38.10 | -17.90 | 21 | 2.54 | |
| 23683 | 6/9/1998 | 6/30/1998 | 25 | 3.69 | 26.67 | -12.21 | 26.67 | -17.90 | 21 | 2.54 | |
| 23687. | 6/9/1998 | 6/30/1998 | 25 | 3.69 | 26.67 | -12.21 | 27.94 | -17.90 | 21 | 3.04 | |
| 23004 | 8/14/1998 | 11/21/1998 | 26 | 5.17 | 30.48 | -14.12 | 35.56 | -21.28 | 99 | 4.54 | |
| 23007 | 8/14/1998 | 11/21/1998 | 26 | 5.17 | 43.18 | -14.12 | 43.18 | -21.28 | 99 | 2.54 | |
| 23421 | 3/18/1999 | 6/16/1999 | 27 | 9.73 | 33.02 | -17.90 | 34.93 | -17.90 | 90 | 3.29 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 23428 | 3/18/1999 | 6/16/1999 | 27 | 9.73 | 35.56 | -17.90 | 36.83 | -17.90 | 90 | 3.04 | |
| 30149 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 45.72 | -17.90 | 45.72 | -24.99 | 112 | 2.54 | |
| 30152 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 37.47 | -17.90 | 37.47 | -24.99 | 112 | 2.54 | |
| 30153 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 44.45 | -17.90 | 44.45 | -24.99 | 112 | 2.54 | |
| 30160 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 43.18 | -17.90 | 43.18 | -24.99 | 112 | 2.54 | |
| 34368 | 2/26/2001 | 3/15/2001 | 29 | 6.05 | 29.21 | -12.21 | 29.21 | -12.21 | 17 | 2.54 | |
| 34369 | 2/26/2001 | 3/15/2001 | 29 | 6.05 | 35.56 | -12.21 | 35.56 | -12.21 | 17 | 2.54 | |
| 33348 | 3/14/2001 | 7/11/2001 | 30 | 7.37 | 33.02 | -21.37 | 36.20 | -18.51 | 119 | 3.79 | |
| 33349 | 3/14/2001 | 7/11/2001 | 30 | 7.37 | 43.18 | -21.37 | 45.72 | -18.51 | 119 | 3.54 | |
| 36919 | 3/28/2001 | 5/21/2001 | 31 | 3.70 | 30.48 | -17.90 | 40.64 | -17.90 | 54 | 6.54 | |
| 36920 | 3/28/2001 | 5/21/2001 | 31 | 3.70 | 39.37 | -17.90 | 40.64 | -17.90 | 54 | 3.04 | |
| 36786 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 46.36 | -25.54 | 46.36 | -25.54 | 56 | 2.54 | |
| 36797 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 40.01 | -25.54 | 41.91 | -25.54 | 56 | 3.29 | |
| 36799 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 30.48 | -25.54 | 31.75 | -25.54 | 56 | 3.04 | |
| 37403 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 43.18 | -25.54 | 43.79 | -25.54 | 56 | 2.78 | |
| 40627 | 7/25/2001 | 3/20/2002 | 33 | 6.39 | 33.66 | -18.51 | 41.91 | -25.54 | 238 | 5.79 | |
| 40632 | 7/25/2001 | 3/20/2002 | 33 | 6.39 | 33.66 | -18.51 | 34.29 | -25.54 | 238 | 2.79 | |
| 37660 | 11/10/2001 | 11/24/2001 | 34 | 3.71 | 45.72 | -14.12 | 45.72 | -7.66 | 14 | 2.54 | |
| 37666 | 11/10/2001 | 11/24/2001 | 34 | 3.71 | 30.48 | -14.12 | 30.48 | -7.66 | 14 | 2.54 | |
| 39945 | 6/26/2002 | 7/3/2002 | 35 | 12.50 | 38.10 | -24.99 | 38.10 | -17.90 | 7 | 2.54 | |
| 39950 | 6/26/2002 | 7/3/2002 | 35 | 12.50 | 35.56 | -24.99 | 35.56 | -17.90 | 7 | 2.54 | |
| 45306 | 6/27/2003 | 7/10/2003 | 36 | 3.20 | 34.29 | -17.90 | 34.29 | -24.99 | 13 | 2.54 | SAME MOVEMENT AS GROUPS 37 AND 38 |
| 45307 | 6/27/2003 | 7/10/2003 | 36 | 3.20 | 33.02 | -17.90 | 33.66 | -24.99 | 13 | 2.79 | |
| 44999 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 33.02 | -17.90 | 33.02 | -24.99 | 19 | 2.54 | SAME MOVEMENT AS GROUPS 36 AND 38 |
| 45304 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 41.91 | -17.90 | 43.18 | -24.99 | 19 | 3.04 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 45335 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 33.02 | -17.90 | 33.66 | -24.99 | 19 | 2.79 | |
| 45339 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 34.29 | -17.90 | 36.20 | -24.99 | 19 | 3.29 | |
| 45341 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 32.39 | -17.90 | 33.02 | -24.99 | 19 | 2.79 | |
| 45342 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 38.74 | -17.90 | 38.74 | -24.99 | 19 | 2.54 | |
| | | | | | | | | | | | |
| 45315 | 6/27/2003 | 10/4/2003 | 38 | 3.20 | 30.48 | -17.90 | 31.75 | -24.99 | 99 | 3.04 | SAME MOVEMENT AS GROUPS 36 AND 37 |
| 45362 | 6/27/2003 | 10/4/2003 | 38 | 3.20 | 47.63 | -17.90 | 48.90 | -24.99 | 99 | 3.04 | |
| 45626 | 7/2/2003 | 7/9/2003 | 39 | 7.39 | 31.12 | -24.99 | 31.12 | -24.99 | 7 | 2.54 | |
| 45630 | 7/2/2003 | 7/9/2003 | 39 | 7.39 | 43.18 | -24.99 | 43.18 | -24.99 | 7 | 2.54 | |
| 45657 | 7/7/2003 | 7/23/2003 | 40 | 6.06 | 40.01 | -24.99 | 40.64 | -24.99 | 16 | 2.79 | |
| 45658 | 7/7/2003 | 7/23/2003 | 40 | 6.06 | 31.75 | -24.99 | 31.75 | -24.99 | 16 | 2.54 | |
| 46120 | 7/23/2003 | 4/24/2004 | 41 | 9.78 | 33.02 | -24.99 | 35.56 | -17.90 | 276 | 3.54 | |
| 46124 | 7/23/2003 | 4/24/2004 | 41 | 9.78 | 33.02 | -24.99 | 38.10 | -17.90 | 276 | 4.54 | |
| 45260 | 9/8/2003 | 10/24/2003 | 42 | 10.67 | 40.64 | -30.58 | 43.18 | -21.23 | 46 | 3.54 | |
| 45262 | 9/8/2003 | 10/24/2003 | 42 | 10.67 | 45.72 | -30.58 | 48.26 | -21.23 | 46 | 3.54 | |
| 45263 | 9/8/2003 | 10/24/2003 | 42 | 10.67 | 43.18 | -30.58 | 50.80 | -21.23 | 46 | 5.54 | |
| 45272 | 10/24/2003 | 6/8/2004 | 43 | 4.62 | 45.72 | -21.23 | 53.34 | -30.58 | 228 | 5.54 | |
| 45273 | 10/24/2003 | 6/8/2004 | 43 | 4.62 | 48.26 | -21.23 | 53.34 | -30.58 | 228 | 4.54 | |
| 45276 | 10/24/2003 | 6/8/2004 | 43 | 4.62 | 35.56 | -21.23 | 51.44 | -30.58 | 228 | 8.79 | |
| 45269 | 10/24/2003 | 6/28/2004 | 44 | 4.97 | 48.26 | -21.23 | 50.80 | -30.58 | 248 | 3.54 | |
| 45275 | 10/24/2003 | 6/28/2004 | 44 | 4.97 | 45.72 | -21.23 | 50.80 | -30.58 | 248 | 4.54 | |
| 45278 | 10/24/2003 | 6/28/2004 | 44 | 4.97 | 43.18 | -21.23 | 52.07 | -30.58 | 248 | 6.04 | |
| 45260 | 10/24/2003 | 8/27/2004 | 45 | 5.54 | 43.18 | -21.23 | 49.53 | -21.23 | 308 | 5.04 | |
| 45270 | 10/24/2003 | 8/27/2004 | 45 | 5.54 | 35.56 | -21.23 | 40.64 | -21.23 | 308 | 4.54 | |
| 45277 | 10/24/2003 | 8/27/2004 | 45 | 5.54 | 49.53 | -21.23 | 53.34 | -21.23 | 308 | 4.04 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 45859 | 1/22/2004 | 4/17/2004 | 46 | 23.59 | 41.91 | -50.10 | 44.45 | -57.94 | 86 | 3.54 | |
| 45864 | 1/22/2004 | 4/17/2004 | 46 | 23.59 | 46.99 | -50.10 | 46.99 | -57.94 | 86 | 2.54 | |
| 54565 | 3/29/2005 | 4/21/2005 | 47 | 7.71 | 40.64 | -38.50 | 45.72 | -31.38 | 23 | 4.54 | |
| 54565 | 3/29/2005 | 4/21/2005 | 47 | 7.71 | 45.72 | -38.50 | 45.72 | -31.38 | 23 | 2.54 | |
| 57523 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 40.64 | -24.99 | 40.64 | -24.99 | 40 | 2.54 | |
| 57525 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 38.10 | -24.99 | 40.01 | -24.99 | 40 | 3.29 | |
| 57526 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 48.26 | -24.99 | 50.80 | -24.99 | 40 | 3.54 | |
| 57527 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 30.48 | -24.99 | 35.56 | -24.99 | 40 | 4.54 | |
| 57529 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 36.83 | -24.99 | 44.45 | -24.99 | 40 | 5.54 | |
| 57531 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 34.29 | -24.99 | 35.56 | -24.99 | 40 | 3.04 | |
| 1008 | 1/24/1991 | 4/30/1992 | 1 | 120.31 | 25.40 | -11.23 | 30.48 | -35.43 | 462 | 4.54 | |
| 1009 | 1/24/1991 | 4/30/1992 | 1 | 120.31 | 30.48 | -11.23 | 35.56 | -35.43 | 462 | 4.54 | |
| 1270 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 35.56 | -8.87 | 35.81 | -13.98 | 18 | 2.64 | |
| 1277 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 41.91 | -8.87 | 43.18 | -13.98 | 18 | 3.04 | |
| 1281 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 30.48 | -8.87 | 30.48 | -13.98 | 18 | 2.54 | |
| 1284 | 1/26/1991 | 2/13/1991 | 2 | 9.70 | 35.56 | -8.87 | 35.56 | -13.98 | 18 | 2.54 | |
| 8512 | 9/7/1991 | 6/18/1992 | 3 | 63.81 | 33.02 | -26.49 | 35.56 | -22.97 | 285 | 3.54 | |
| 8523 | 9/7/1991 | 6/18/1992 | 3 | 63.81 | 36.83 | -26.49 | 40.64 | -22.97 | 285 | 4.04 | |
| 8533 | 9/7/1991 | 6/18/1992 | 3 | 63.81 | 39.04 | -26.49 | 40.64 | -22.97 | 285 | 3.17 | |
| 4287 | 12/7/1991 | 8/3/1992 | 4 | 4.89 | 48.26 | -24.57 | 55.88 | -21.99 | 240 | 5.54 | SAME MOVEMENT AS GROUP 5 |
| 4289 | 12/7/1991 | 8/3/1992 | 4 | 4.89 | 33.02 | -24.57 | 55.88 | -21.99 | 240 | 11.54 | |
| 4299 | 12/7/1991 | 8/3/1992 | 4 | 4.89 | 35.56 | -24.57 | 46.99 | -21.99 | 240 | 7.04 | |
| 4251 | 12/24/1991 | 8/3/1992 | 5 | 4.89 | 40.64 | -24.57 | 43.18 | -21.99 | 223 | 3.54 | SAME MOVEMENT AS GROUP 4 |
| 4252 | 12/24/1991 | 8/3/1992 | 5 | 4.89 | 41.91 | -24.57 | 46.99 | -21.99 | 223 | 4.54 | |
| 4288 | 12/24/1991 | 8/3/1992 | 5 | 4.89 | 35.56 | -24.57 | 40.64 | -21.99 | 223 | 4.54 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 8608 | 12/27/1991 | 6/7/1992 | 6 | 17.99 | 33.02 | -17.90 | 40.64 | -10.90 | 163 | 5.54 | |
| 8609 | 12/27/1991 | 6/7/1992 | 6 | 17.99 | 44.45 | -17.90 | 49.53 | -10.90 | 163 | 4.54 | |
| 10549 | 6/10/1992 | 6/17/1992 | 7 | 3.69 | 32.39 | 4.75 | 33.02 | -2.34 | 7 | 2.79 | |
| 10550 | 6/10/1992 | 6/17/1992 | 7 | 3.69 | 39.37 | 4.75 | 40.64 | -2.34 | 7 | 3.04 | |
| 10159 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 36.83 | -17.90 | 36.83 | 4.35 | 52 | 2.54 | |
| 10166 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 45.72 | -17.90 | 45.72 | 4.35 | 52 | 2.54 | |
| 10168 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 45.72 | -17.90 | 45.72 | 4.35 | 52 | 2.54 | |
| 10174 | 7/14/1992 | 9/4/1992 | 8 | 29.34 | 44.45 | -17.90 | 44.45 | 4.35 | 52 | 2.54 | |
| 10074 | 8/19/1992 | 9/4/1992 | 9 | 5.11 | 46.99 | -22.97 | 46.99 | -22.97 | 16 | 2.54 | |
| 10080 | 8/19/1992 | 9/4/1992 | 9 | 5.11 | 44.45 | -22.97 | 44.45 | -22.97 | 16 | 2.54 | |
| 10091 | 8/19/1992 | 10/28/1992 | 10 | 6.35 | 38.10 | -22.97 | 38.10 | -22.97 | 70 | 2.54 | |
| 10131 | 8/20/1992 | 5/21/1993 | 11 | 4.02 | 34.29 | -26.41 | 38.10 | -36.19 | 274 | 4.04 | |
| 10138 | 8/20/1992 | 5/21/1993 | 11 | 4.02 | 48.26 | -26.41 | 53.34 | -36.19 | 274 | 4.54 | |
| 10142 | 8/20/1992 | 7/31/1993 | 12 | 8.44 | 44.45 | -26.41 | 50.80 | -30.93 | 345 | 5.04 | |
| 10144 | 8/20/1992 | 7/31/1993 | 12 | 8.44 | 43.18 | -26.41 | 48.26 | -30.93 | 345 | 4.54 | |
| 10115 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 45.72 | -32.81 | 55.88 | -32.81 | 765 | 6.54 | |
| 10116 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 43.18 | -32.81 | 55.88 | -32.81 | 765 | 7.54 | |
| 10117 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 43.18 | -32.81 | 55.88 | -32.81 | 765 | 7.54 | |
| 10119 | 8/20/1992 | 9/24/1994 | 13 | 12.87 | 44.45 | -32.81 | 58.42 | -32.81 | 765 | 8.04 | |
| 10186 | 9/4/1992 | 2/21/1995 | 14 | 6.06 | 45.72 | -10.90 | 63.50 | 4.35 | 900 | 9.54 | |
| 10191 | 9/4/1992 | 2/21/1995 | 14 | 6.06 | 49.53 | -10.90 | 63.25 | 4.35 | 900 | 7.94 | |
| 2428 | 3/10/1993 | 6/20/1993 | 15 | 4.03 | 53.34 | -24.99 | 55.88 | -24.99 | 102 | 3.54 | |
| 2430 | 3/10/1993 | 6/20/1993 | 15 | 4.03 | 53.34 | -24.99 | 55.88 | -24.99 | 102 | 3.54 | |
| 13242 | 7/10/1997 | 7/31/1997 | 16 | 4.03 | 30.48 | -17.90 | 30.48 | -17.90 | 21 | 2.54 | |
| 13249 | 7/10/1997 | 7/31/1997 | 16 | 4.03 | 50.80 | -17.90 | 50.80 | -17.90 | 21 | 2.54 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 15694 | 7/24/1997 | 8/29/1997 | 17 | 4.02 | 37.47 | -18.51 | 38.10 | -18.51 | 36 | 2.79 | SAME MOVEMENT AS GROUP 18 |
| 15695 | 7/24/1997 | 8/29/1997 | 17 | 4.02 | 34.93 | -18.51 | 35.56 | -18.51 | 36 | 2.79 | |
| 17250 | 7/24/1997 | 8/29/1997 | 17 | 4.02 | 38.10 | -18.51 | 38.10 | -18.51 | 36 | 2.54 | |
| 16413 | 8/5/1997 | 8/29/1997 | 18 | 4.02 | 31.75 | -18.51 | 34.93 | -18.51 | 24 | 3.79 | SAME MOVEMENT AS GROUP 17 |
| 16415 | 8/5/1997 | 8/29/1997 | 18 | 4.02 | 38.74 | -18.51 | 38.74 | -18.51 | 24 | 2.54 | |
| 16480 | 8/27/1997 | 10/1/1997 | 19 | 3.69 | 34.29 | -24.99 | 35.56 | -24.99 | 35 | 3.04 | |
| 16485 | 8/27/1997 | 10/1/1997 | 19 | 3.69 | 33.02 | -24.99 | 33.02 | -24.99 | 35 | 2.54 | |
| 16503 | 8/27/1997 | 10/1/1997 | 19 | 3.69 | 40.64 | -24.99 | 40.64 | -24.99 | 35 | 2.54 | |
| 18862 | 10/10/1997 | 4/28/1998 | 20 | 6.65 | 27.94 | -12.21 | 27.94 | -18.51 | 200 | 2.54 | |
| 18863 | 10/10/1997 | 4/28/1998 | 20 | 6.65 | 27.94 | -12.21 | 27.94 | -18.51 | 200 | 2.54 | |
| 15954 | 1/20/1998 | 5/27/1998 | 21 | 7.56 | 35.56 | -12.21 | 35.56 | -12.21 | 127 | 2.54 | |
| 15964 | 1/20/1998 | 5/27/1998 | 21 | 7.56 | 40.64 | -12.21 | 40.64 | -12.21 | 127 | 2.54 | |
| 16051 | 1/29/1998 | 3/15/1998 | 22 | 12.16 | 33.02 | -25.45 | 38.10 | -25.45 | 45 | 4.54 | |
| 16052 | 1/29/1998 | 3/15/1998 | 22 | 12.16 | 48.26 | -25.45 | 48.26 | -25.45 | 45 | 2.54 | |
| 16033 | 2/19/1998 | 6/2/1998 | 23 | 110.82 | 35.56 | -26.41 | 38.10 | -14.08 | 103 | 3.54 | |
| 16038 | 2/19/1998 | 6/2/1998 | 23 | 110.82 | 38.10 | -26.41 | 43.18 | -14.08 | 103 | 4.54 | |
| 18171 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 45.72 | -25.45 | 45.72 | -25.45 | 62 | 2.54 | |
| 18175 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 48.26 | -25.45 | 48.26 | -25.45 | 62 | 2.54 | |
| 18176 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 45.72 | -25.45 | 45.72 | -25.45 | 62 | 2.54 | |
| 18177 | 3/15/1998 | 5/16/1998 | 24 | 9.76 | 40.64 | -25.45 | 40.64 | -25.45 | 62 | 2.54 | |
| 20302 | 6/9/1998 | 6/30/1998 | 25 | 3.69 | 38.10 | -12.21 | 38.10 | -17.90 | 21 | 2.54 | |
| 23683 | 6/9/1998 | 6/30/1998 | 25 | 3.69 | 26.67 | -12.21 | 26.67 | -17.90 | 21 | 2.54 | |
| 23687. | 6/9/1998 | 6/30/1998 | 25 | 3.69 | 26.67 | -12.21 | 27.94 | -17.90 | 21 | 3.04 | |
| 23004 | 8/14/1998 | 11/21/1998 | 26 | 5.17 | 30.48 | -14.12 | 35.56 | -21.28 | 99 | 4.54 | |
| 23007 | 8/14/1998 | 11/21/1998 | 26 | 5.17 | 43.18 | -14.12 | 43.18 | -21.28 | 99 | 2.54 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 23421 | 3/18/1999 | 6/16/1999 | 27 | 9.73 | 33.02 | -17.90 | 34.93 | -17.90 | 90 | 3.29 | |
| 23428 | 3/18/1999 | 6/16/1999 | 27 | 9.73 | 35.56 | -17.90 | 36.83 | -17.90 | 90 | 3.04 | |
| 30149 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 45.72 | -17.90 | 45.72 | -24.99 | 112 | 2.54 | |
| 30152 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 37.47 | -17.90 | 37.47 | -24.99 | 112 | 2.54 | |
| 30153 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 44.45 | -17.90 | 44.45 | -24.99 | 112 | 2.54 | |
| 30160 | 3/22/2000 | 7/12/2000 | 28 | 21.78 | 43.18 | -17.90 | 43.18 | -24.99 | 112 | 2.54 | |
| 34368 | 2/26/2001 | 3/15/2001 | 29 | 6.05 | 29.21 | -12.21 | 29.21 | -12.21 | 17 | 2.54 | |
| 34369 | 2/26/2001 | 3/15/2001 | 29 | 6.05 | 35.56 | -12.21 | 35.56 | -12.21 | 17 | 2.54 | |
| 33348 | 3/14/2001 | 7/11/2001 | 30 | 7.37 | 33.02 | -21.37 | 36.20 | -18.51 | 119 | 3.79 | |
| 33349 | 3/14/2001 | 7/11/2001 | 30 | 7.37 | 43.18 | -21.37 | 45.72 | -18.51 | 119 | 3.54 | |
| 36919 | 3/28/2001 | 5/21/2001 | 31 | 3.70 | 30.48 | -17.90 | 40.64 | -17.90 | 54 | 6.54 | |
| 36920 | 3/28/2001 | 5/21/2001 | 31 | 3.70 | 39.37 | -17.90 | 40.64 | -17.90 | 54 | 3.04 | |
| 36786 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 46.36 | -25.54 | 46.36 | -25.54 | 56 | 2.54 | |
| 36797 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 40.01 | -25.54 | 41.91 | -25.54 | 56 | 3.29 | |
| 36799 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 30.48 | -25.54 | 31.75 | -25.54 | 56 | 3.04 | |
| 37403 | 5/30/2001 | 7/25/2001 | 32 | 5.14 | 43.18 | -25.54 | 43.79 | -25.54 | 56 | 2.78 | |
| 40627 | 7/25/2001 | 3/20/2002 | 33 | 6.39 | 33.66 | -18.51 | 41.91 | -25.54 | 238 | 5.79 | |
| 40632 | 7/25/2001 | 3/20/2002 | 33 | 6.39 | 33.66 | -18.51 | 34.29 | -25.54 | 238 | 2.79 | |
| 37660 | 11/10/2001 | 11/24/2001 | 34 | 3.71 | 45.72 | -14.12 | 45.72 | -7.66 | 14 | 2.54 | |
| 37666 | 11/10/2001 | 11/24/2001 | 34 | 3.71 | 30.48 | -14.12 | 30.48 | -7.66 | 14 | 2.54 | |
| 39945 | 6/26/2002 | 7/3/2002 | 35 | 12.50 | 38.10 | -24.99 | 38.10 | -17.90 | 7 | 2.54 | |
| 39950 | 6/26/2002 | 7/3/2002 | 35 | 12.50 | 35.56 | -24.99 | 35.56 | -17.90 | 7 | 2.54 | |
| 45306 | 6/27/2003 | 7/10/2003 | 36 | 3.20 | 34.29 | -17.90 | 34.29 | -24.99 | 13 | 2.54 | SAME MOVEMENT AS GROUPS 37 AND 38 |
| 45307 | 6/27/2003 | 7/10/2003 | 36 | 3.20 | 33.02 | -17.90 | 33.66 | -24.99 | 13 | 2.79 | |
| 44999 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 33.02 | -17.90 | 33.02 | -24.99 | 19 | 2.54 | SAME MOVEMENT AS GROUPS 36 AND 38 |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 45304 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 41.91 | -17.90 | 43.18 | -24.99 | 19 | 3.04 | |
| 45335 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 33.02 | -17.90 | 33.66 | -24.99 | 19 | 2.79 | |
| 45339 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 34.29 | -17.90 | 36.20 | -24.99 | 19 | 3.29 | |
| 45341 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 32.39 | -17.90 | 33.02 | -24.99 | 19 | 2.79 | |
| 45342 | 6/27/2003 | 7/16/2003 | 37 | 3.20 | 38.74 | -17.90 | 38.74 | -24.99 | 19 | 2.54 | |
| 45315 | 6/27/2003 | 10/4/2003 | 38 | 3.20 | 30.48 | -17.90 | 31.75 | -24.99 | 99 | 3.04 | SAME MOVEMENT AS GROUPS 36 AND 37 |
| 45362 | 6/27/2003 | 10/4/2003 | 38 | 3.20 | 47.63 | -17.90 | 48.90 | -24.99 | 99 | 3.04 | |
| 45626 | 7/2/2003 | 7/9/2003 | 39 | 7.39 | 31.12 | -24.99 | 31.12 | -24.99 | 7 | 2.54 | |
| 45630 | 7/2/2003 | 7/9/2003 | 39 | 7.39 | 43.18 | -24.99 | 43.18 | -24.99 | 7 | 2.54 | 45630 |
| 45657 | 7/7/2003 | 7/23/2003 | 40 | 6.06 | 40.01 | -24.99 | 40.64 | -24.99 | 16 | 2.79 | 45657 |
| 45658 | 7/7/2003 | 7/23/2003 | 40 | 6.06 | 31.75 | -24.99 | 31.75 | -24.99 | 16 | 2.54 | 45658 |
| 46120 | 7/23/2003 | 4/24/2004 | 41 | 9.78 | 33.02 | -24.99 | 35.56 | -17.90 | 276 | 3.54 | |
| 46124 | 7/23/2003 | 4/24/2004 | 41 | 9.78 | 33.02 | -24.99 | 38.10 | -17.90 | 276 | 4.54 | 46124 |
| 45260 | 9/8/2003 | 10/24/2003 | 42 | 10.67 | 40.64 | -30.58 | 43.18 | -21.23 | 46 | 3.54 | 45260 |
| 45262 | 9/8/2003 | 10/24/2003 | 42 | 10.67 | 45.72 | -30.58 | 48.26 | -21.23 | 46 | 3.54 | 45262 |
| 45263 | 9/8/2003 | 10/24/2003 | 42 | 10.67 | 43.18 | -30.58 | 50.80 | -21.23 | 46 | 5.54 | 45263 |
| 45272 | 10/24/2003 | 6/8/2004 | 43 | 4.62 | 45.72 | -21.23 | 53.34 | -30.58 | 228 | 5.54 | |
| 45273 | 10/24/2003 | 6/8/2004 | 43 | 4.62 | 48.26 | -21.23 | 53.34 | -30.58 | 228 | 4.54 | |
| 45276 | 10/24/2003 | 6/8/2004 | 43 | 4.62 | 35.56 | -21.23 | 51.44 | -30.58 | 228 | 8.79 | |
| 45269 | 10/24/2003 | 6/28/2004 | 44 | 4.97 | 48.26 | -21.23 | 50.80 | -30.58 | 248 | 3.54 | |
| 45275 | 10/24/2003 | 6/28/2004 | 44 | 4.97 | 45.72 | -21.23 | 50.80 | -30.58 | 248 | 4.54 | |
| 45278 | 10/24/2003 | 6/28/2004 | 44 | 4.97 | 43.18 | -21.23 | 52.07 | -30.58 | 248 | 6.04 | |
| 45260 | 10/24/2003 | 8/27/2004 | 45 | 5.54 | 43.18 | -21.23 | 49.53 | -21.23 | 308 | 5.04 | |
| 45270 | 10/24/2003 | 8/27/2004 | 45 | 5.54 | 35.56 | -21.23 | 40.64 | -21.23 | 308 | 4.54 | |
| 45277 | 10/24/2003 | 8/27/2004 | 45 | 5.54 | 49.53 | -21.23 | 53.34 | -21.23 | 308 | 4.04 | |

Table 4-5. (Continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 45859 | 1/22/2004 | 4/17/2004 | 46 | 23.59 | 41.91 | -50.10 | 44.45 | -57.94 | 86 | 3.54 | |
| 45864 | 1/22/2004 | 4/17/2004 | 46 | 23.59 | 46.99 | -50.10 | 46.99 | -57.94 | 86 | 2.54 | |
| 54565 | 3/29/2005 | 4/21/2005 | 47 | 7.71 | 40.64 | -38.50 | 45.72 | -31.38 | 23 | 4.54 | |
| 54569 | 3/29/2005 | 4/21/2005 | 47 | 7.71 | 45.72 | -38.50 | 45.72 | -31.38 | 23 | 2.54 | |
| 57523 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 40.64 | -24.99 | 40.64 | -24.99 | 40 | 2.54 | |
| 57525 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 38.10 | -24.99 | 40.01 | -24.99 | 40 | 3.29 | |
| 57526 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 48.26 | -24.99 | 50.80 | -24.99 | 40 | 3.54 | |
| 57527 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 30.48 | -24.99 | 35.56 | -24.99 | 40 | 4.54 | |
| 57529 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 36.83 | -24.99 | 44.45 | -24.99 | 40 | 5.54 | |
| 57531 | 7/26/2007 | 9/4/2007 | 48 | 11.08 | 34.29 | -24.99 | 35.56 | -24.99 | 40 | 3.04 | |

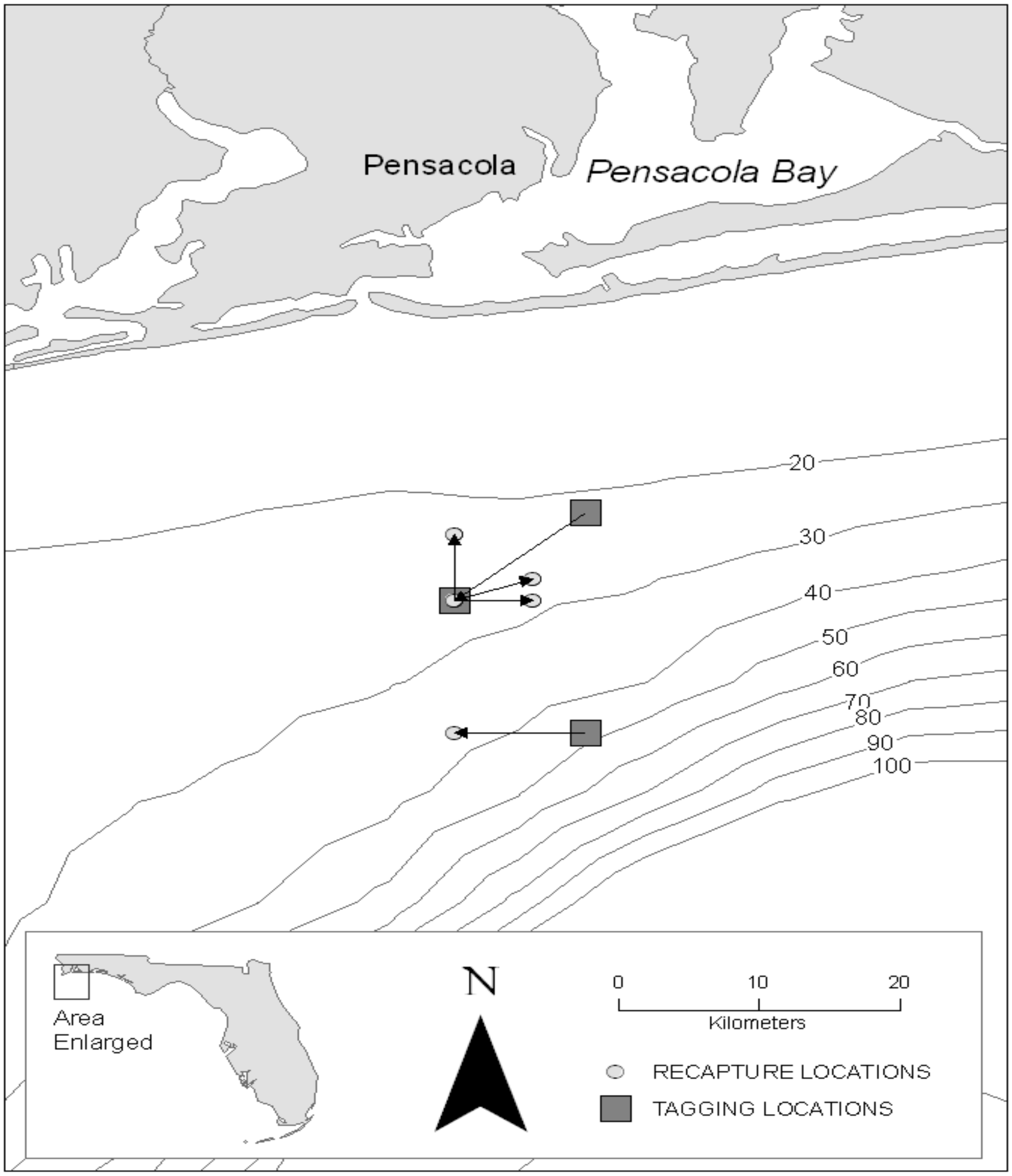


Figure 4-4. Group movement by red grouper near the panhandle of Florida. Grey squares represent locations were fish were tagged, white circles represent locations were fish were recaptured.

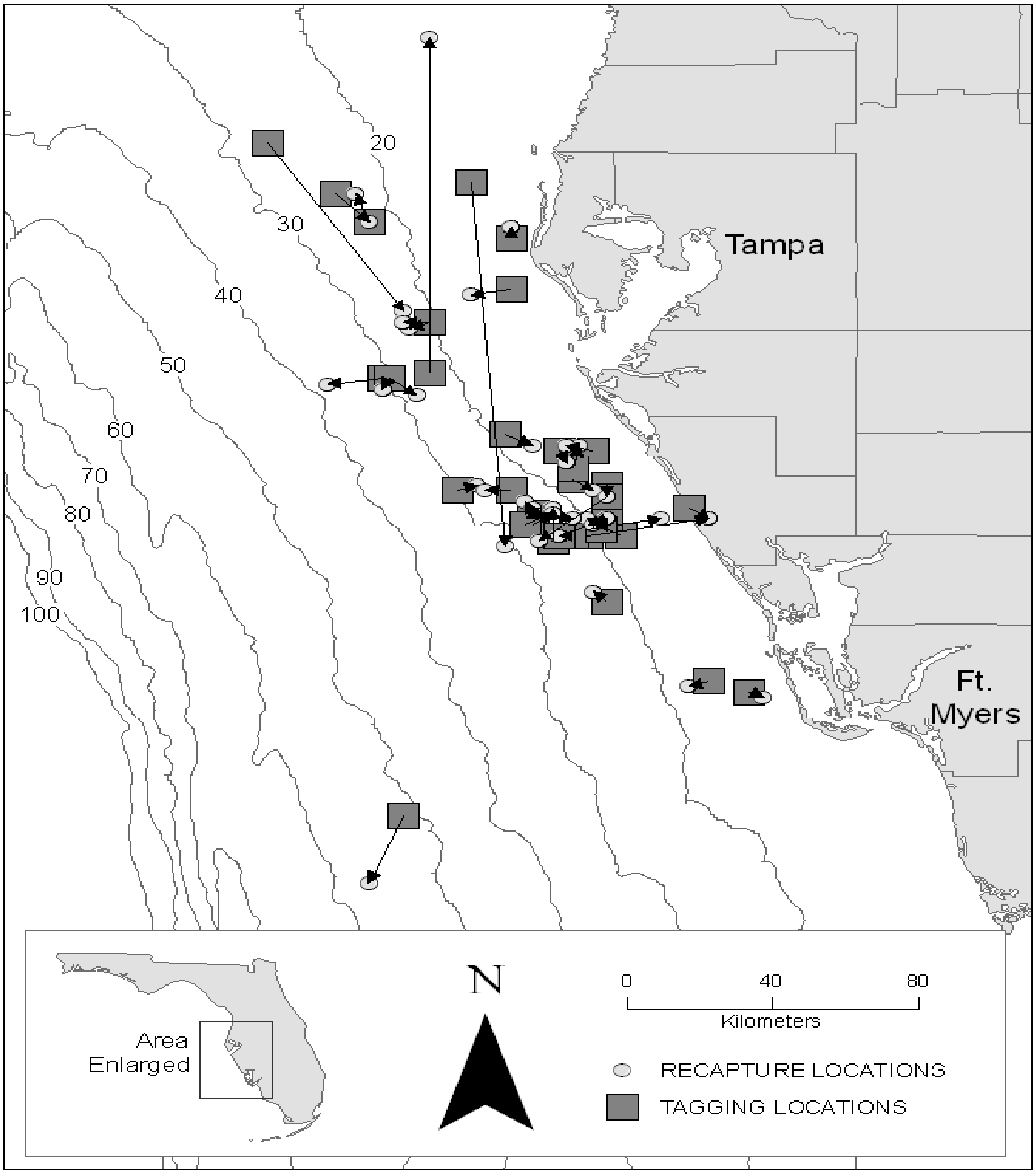


Figure 4-5. Group movement by red grouper in the far eastern Gulf of Mexico. Grey squares represent locations were fish were tagged, white circles represent locations were fish were recaptured.

## Discussion

### *Distance from Shore and Size Distribution*

Fish length increased with distance from shore in both the South Atlantic off Florida and the eastern Gulf of Mexico. When the regression for all fish was tested for significance, the two variables (fish length and distance from shore) were significantly correlated (for both the Atlantic and the eastern Gulf of Mexico. These data agree with life history accounts (Moe 1966, Bullock and Smith 1991, Koenig and Coleman 2006) of juvenile red grouper occupying shallow coastal locations and moving offshore with ontogeny to inhabit offshore waters on the shelf.

*Movement*

The majority (62.8%) of red grouper in this study exhibited little or no movement within the limitations of spatial resolution. Fishes originally captured and tagged off commercial long-line vessels were recovered either at the original capture site or a few kilometers away. Although most of these fish were not legal sized, they were larger than those tagged inshore. Results are consistent with those reported by Koenig and Coleman (2006) who stated that older red grouper on the mid-to outer west Florida shelf displayed high site fidelity, moving no more than 1.2 nautical miles from their original tagging site. They ascribed this observed high site fidelity to the species' excavation behavior (pit excavation in soft bottom sediments) and mating behavior. Unlike other grouper, red grouper do not spawn in large pelagic spawning aggregations. Instead, they practice lek mating behavior where males defend defined territories, in this case excavated large pits (Scanlon et al. 2005, Koenig and Coleman 2006).

For fish that moved two types of movement were found. The first type was individual fish movements with changes in depth associated with growth. Whereas few large red grouper moved long distances, ontogenetic movements by smaller red grouper were substantial (69.2-212.4 km). Spatial analysis of fish tagged off recreational-for-hire boats and recaptured by commercial vessels demonstrates the ontogenetic offshore movement from inshore waters toward deep shelf waters with increasing size described in Moe (1966) and Koenig and Coleman (2006). Data are also in agreement with life history information published by Bullock and Smith (1991) who reported ontogenetic movement of small red grouper off Southwest Florida moving from shallow water (3-18 m) to depths greater than 36 m as fish increased size and where these fish became part of the commercial catch. In addition to the association of offshore movement into deeper depth contours with fish length, most movement occurred in fish ≥ 38.1 cm; the length when tissue in the red grouper swim bladder posterior ventral wall became vascularized and additional gas gland cells developed providing additional buoyancy (Chapter 3).

Red Grouper "Cohort Movement"

Movement by multiple groups of similar sized small to medium (25.4-49.5 cm) sized red grouper, both immature (44%) and mature (56%) often but not exclusively within depth contours. Tagging data from this study reveal that groups of similar sized fishes caught together on the same date at the identical location were then recaptured together on a different matching date at some other same site. These groups consisting of 2-6 fishes of identical or similar lengths appear to move together and movement originates from the same site on the same date. Although fish lengths (at tagging and recapture) in movement groups did not differ from those not in movement groups (U=62675.5, $p$=0.651 and U=61871.0, $p$=0.495, respectively), nor did growth that occurred between captures (U=64160.5, $p$=0.977), for the most part fish lengths within the groups was similar. These similar sized fish that travel together may have either been spawned in the same area or may “know” each other from living in the same inshore area as juveniles (Jones et al. 2005).

Personal observations of capture-held fish, revealed some behaviors that may explain group movements. Red grouper captured from the same areas may “know” each other and exist in a localized social hierarchy. Hierarchies have been described for other fish species (Nakano 1994, Sloman et al. 2000, Chase et al. 2002, Whiteman and Cőté 2004, Grosenick et al. 2007).

An established hierarchy was observed in the behavior and associated coloration of captive red grouper maintained in large experimental tanks (personal observation) that were captured from the same location. The alpha fish (pale beige) was the most aggressive not only to conspecifics but also to human caretakers. It was the first to feed and investigate new situations. The omega fish (deep maroon) was the last to feed and could be freely attacked by all other fish within the tank. No separations within the tank were required in tanks where fish were caught at the same location. However when fishes caught at different disparate locations were kept in the same tank no underwater barriers within the tank could prevent constant fighting. Two alpha (beige) fishes were observed to burrow under, jump over, push aside or bite through protective plastic mesh netting to reach each other. Fights between alpha fishes ended when one of the combatants was removed from the tank or was killed (personal observation). In addition to behavior, fish rank within the tank was clearly defined by coloration. Alpha fishes were always beige in what was described as “Phase 4 of six” in Grace et al. (1994). As fishes decreased in rank, their coloration darkened to shades of light to darker red. Omega fish were deep maroon with white spots similar to “Phase 1 of six” described in Grace et al. (1994).

While it is unknown how common or widespread cohort movement of red grouper might be due to the nature of fishery-dependent recaptures, forty-eight of these groups have been identified and individuals within groups appeared to have moved together. Group size ranged from 2 to 6 fishes (mean = 2.63, sd =1.00). Fishes within each group were of similar size and fish group lengths ranged from 25.4-49.5 cm. These groups moved distances ranging 3.2 km to 120.3 km (mean = 13.55, sd =23.62) and occurred during all months of the year with the exception of April. Documented within 13 of the 16 continuous years of the study, group movement was noted in both the Gulf of Mexico near the Florida Panhandle and in the eastern Gulf of Mexico. No significant long distance group movement was observed in the South Atlantic. This lack of observed long distance movement may be the result of substantially less data from the South Atlantic coupled with the narrow east coast shelf.

Hurricanes

In addition to ontogenetic movements of small red grouper, long distance movements for larger red grouper have been documented. Some of these movements have been attributed to hurricanes. Franks (2003) reported the appearance of red grouper off Mississippi following hurricane events. After Hurricane Lili in 2002, juvenile and adult red grouper were commonly caught on artificial reefs and petroleum platforms off Mississippi where they had not previously been reported. Although no longer as common in these areas, red grouper are periodically still caught by anglers (Jim Franks, University of Southern Mississippi, Gulf Coast Marine Laboratory campus, personal communication, January 2008). However, while hurricanes have been documented to influence red grouper movements, results of the logistic regression indicated movement due to tropical storms or hurricanes was not significant. Although some fish moved during periods when tropical storms or hurricanes were present, other red grouper moved in their absence. Data from this model may not have identified hurricanes as significant because data used covered a very long time period (17 years) and an extensive geographical area. It may also be that the criteria for movement (> 3 km) may have affected the analyses that the criteria for a hurricane was too broad as it included tropical storms.

Reports of red grouper onshore/offshore movements that appear unrelated to ontogeny or hurricanes have been explained by commercial fishers as inshore summer feeding migrations (SEDAR 2006). Bullock and Smith (1991) included a comment by Bannerot mentioning seasonal offshore (27-91 m) movements of adult red grouper in the Florida Keys. Moe (1972) reported 22 tagged red grouper traveled 16 miles within 50 days.

McGovern et al. (2005) found that 23% of recaptured gag (n=435) they tagged (n=3,878) off South Carolina had moved over 185 km southward to be recaptured off Florida at St. Augustine, Cape Canaveral, the Florida Keys and in the Gulf of Mexico. Gag that traveled the greatest distances were primarily medium sized fishes ranging 68.6-81.3 cm. They suggested that this southerly movement might have been related to spawning migrations however they were unable to show seasonal movement trends. Similar to red grouper movement, the largest fish demonstrated strong site fidelity exhibiting zero movement from original tagging sites.

Genetic analyses of red grouper population structure found little genetic difference in red grouper from the U.S. South Atlantic, U.S. Gulf of Mexico and the Mexican Gulf. Both larval dispersal and possible contact during the Pleistocene combined with the time scale of $N_e$ generations for genetic mutations to occur have been postulated to explain the genetic homogeneity (Richardson and Gold 1997, Zatcoff *et al.* 2004). Cohort movement may provide an additional mechanism in preventing significant heterozygote deficiencies and prevent local and large-scale population differentiation. Of the 126 fish comprising the 48 cohort groups detected in this study, 56% were of sufficient size to reproduce. Since red grouper do not aggregate to spawn and males and females co-habitate all year (Coleman et al. 1996), these small groups moving distances of 3.2 km to 120.3 km (mean = 13.55, sd =23.62) in various directions, may contribute to maintaining genetic homogeneity as a small number of individuals with high reproductive potential can populate an area if conditions are favorable (Hedgecock 1994).

While it is clear that ontogenetic movements enable red grouper to utilize various habitats during different life stages, the advantage of "cohort movements" is less apparent. These fishes may be vagrants following ocean currents or influenced by environmental carrying capacity or forced by conspecific territoriality to move to new areas but there must be some biological advantage or this pattern of red grouper movement would not persist over the years. Additional investigation of this movement is necessary in understanding red grouper life history.

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# Chapter Five: Evaluation of the Efficacy of the Minimum Size Rule in the Red Grouper and Red Snapper Fisheries With Respect to J and Circle Hook Mortality and Barotrauma and the Consequences for Survival and Movement: Concluding Remarks

The addition of Standard 9 to the Manguson-Stevens Act, prompted by national concerns regarding fisheries' bycatch, required revision of regional Fishery Management Plans to limit bycatch. It states "Conservation and management measures shall, to the extent practicable: (A) minimize bycatch and (B) to the extent bycatch cannot be avoided, minimize the mortality of such bycatch" (Tagart 2004). Various strategies have been employed by fishery managers to reduce bycatch such as technological advances in fishing gear, catch quotas, seasonal and/or area closures and IFQs and buyouts designed to limit fishing thus reducing bycatch. Although these strategies may result in bycatch reduction, zero bycatch is unattainable and necessitates that bycatch data be included in stock assessments and in comprehending ecosystem effects (Tagart 2004).

Chapter One presents a brief overview of some of the issues facing undersized red grouper and red snapper fishery management off Florida. It also outlines the subject of the studies conducted to address some of these issues and to use experimental results as a means to evaluate the efficacy of the minimum size rule as a tool in red grouper and red snapper management. As such, it serves as an introduction to the chapters that followed.

In Chapter Two, experiments designed to gain an understanding of how J and circle hooks affected red grouper and red snapper mortality were discussed. The first hypothesis was there was no difference in hook release mortality for red grouper and red snapper was rejected. Necropsy results from headboat client caught fish showed red snapper suffered the greatest acute hook trauma with 49.1% mortality resulting from hooking, almost equaling all other sources (50.9%) of red snapper mortality combined. Only 20% of red grouper acute mortalities were attributed to hook injuries. Similar to acute hook mortality rates, red snapper deaths from latent hook mortality (29%) were much higher relative to red grouper (7%). The second and third null hypotheses tested using data from a tag/release study that there would be no difference in recapture rates for red grouper caught on circle and J hooks and second, that there would be no difference in recapture rates of red snapper caught on circle versus J hooks were rejected. Circle hooks reduced red grouper but not red snapper hook mortality. Red snappers originally caught on J hooks had a slightly better recapture rate that those initially caught on circle hooks.

The final hypothesis that hook mortality dissimilarity resulted as a consequence of differences in ecomorphology and feeding behavior was accepted. Results showed dentition, jaw lever ratios, and feeding type and feeding behavior, including prey residence time in the mouth before swallowing differed between the two species. Although there was a difference in survival by hook type there was no relationship with fish size. Both species have a large gape at small sizes allowing small fish of both species to swallow hooks. Circle hooks are not a panacea and do not enhance survival of red snapper with regard to the minimum size rule; however, they do benefit red grouper and anglers should be encouraged to use circle hooks when targeting red grouper.

Depth-induced mortality caused by trauma during rapid decompression acutely impacts survival of undersized reef fish discarded in compliance with minimum size regulations (Render and Wilson 1994, Gitschlag and Renaud 1994, Render and Wilson 1996, Collins et al. 1999). Although many reef fish species suffer mortality from injuries caused by rapid decompression, mortality varies among species based on their anatomy, physiology, and behavior. If not allowed to return to an appropriate depth immediately, red grouper (*Epinephelus morio*) die from rapid decompression at shallower depths than red snapper (*Lutjanus campechanus*). Although Wilson and Burns (1996) have shown that red grouper, gag, and scamp can potentially survive decompression in sufficient numbers to justify a minimum size rule if fish are rapidly allowed to return to the corresponding habitat depth, differences in morphology influence survival.

Red grouper had larger (in relation to body size), thinner swim bladders containing more gas than red snapper leading to larger swim bladder ruptures than those of red snapper. Red grouper > 38.1 cm FL developed a star shaped area on the posterior swim bladder ventral wall, absent in red snapper that incorporated some rete and a greater number of gas gland cells that would aid in gas production and increase buoyancy but would increase trauma during rapid decompression. Overall, red snapper survived rapid decompression better than red grouper because of a smaller quantity of gas in the swim bladder and less tendency to hemorrhage, especially in smaller fish. Swim bladders of both red groupers and red snappers rupture with rapid change of pressure of 1 atm of pressure (10 m). Data from hyperbaric chamber studies showed that while both red grouper and red snapper can easily survive rapid decompression from 21 m, some red grouper suffered trauma at 27 m but red snapper did not. There were even greater differences in their ability to tolerate rapid decompression from deeper depths (≥ 42 m). Some red snapper did suffer mortality or sub-lethal effects during rapid decompression from depths ≥ 40 m., however, many (60%) survived at 1 atm pressure when vented. In contrast, only 25% of red grouper survived rapid decompression from 42 m in the laboratory and never survived rapid decompression from depths of 61m or greater to 1 atm pressure, even when vented (Burns et al. 2004). Results of these investigations were compared with data from red grouper and red snapper fish tagging studies. However, at sea red grouper survival from this depth and deeper occurred when red groupers were vented and immediately allowed to return to habitat depth. This species specific difference in survival demonstrates that morphological and physiological differences between the two species determine the ability to adjust to rapid depressurization. Although the effects of barotraumas affect both red grouper and red snapper, red grouper begin to experience difficulties at 27.4 m whereas red snapper trauma occurs closer to 42 m. Although both species benefited from venting during laboratory studies, benefits varied by species, depth simulation and extent of trauma. Some red groupers caught on commercial long-line gear, tagged, vented and released were recaptured up to 2,172 days of freedom. Many red grouper caught in commercial fish traps at depths of 61 m were less likely to suffer severely ruptured swim bladders. Their swim bladders were intact and inflated or if ruptured, the swim bladders had a much smaller linear or pinhole wound than red grouper caught on hooks at any depth. These fishes did not show the common external symptoms of rapid depressurization. However, necropsies revealed fishes with damaged swim bladders did have gases escape into the body cavity and some of these fishes had torqued internal organs.

Although red snapper survive rapid changes in depth better than red grouper, overall, swim bladder histology and cage studies and recapture data all indicate that smaller fish of both species survive rapid decompression from depth better than larger fish. These data support the minimum size rule; however, heavy predation can reverse this advantage. Additional research on predation especially by dolphins should be conducted.

Analyses of data presented in Chapter Four, were used to develop movement models for red grouper and elucidate general movement trends for red grouper in the eastern Gulf of Mexico. Although most red grouper were site faithful and fish tended to be larger with distance from shore, for fishes that did exhibit long distance movements a stepwise, forward logistic regression red grouper movement model was developed to determine if long distance movements were the result of hurricanes and tropical storms. The model indicated two types of movement: the first was individual fish movements across depth contours with changes of depth of at least 5 m, 10 m and 20 m associated with growth (ontogeny) and the second was movement of individuals within multiple (48) groups of similar sized small to medium (25.4-49.5 cm) sized fish ("cohort movement"), both immature (44%) and mature (56%) often but not exclusively within depth contours. While hurricanes have been documented to influence red grouper movements (Franks

2003), model results showed that although some fish moved during periods when tropical storms or hurricanes were present, other red groupers moved in their absence. Movement due to named tropical storms or hurricanes was not found to be significant, possibly because of the large geographical area covered by the study and analysis covering 16 years. The two significant variables identified by the model were number of days at large between tag and recapture and length at recapture ($p<0.001$). Red grouper movement in relation to depth based on groups of fish that changed depth by a minimum of 5 m, 10 m, 20 m and fish that did not change depth or exhibited zero movement showed at the ≥ 5 m depth difference level, recapture length and growth were significantly different, but tagging length was not. At ≥ 10m differences of both tagging and recapture lengths and growth were significantly different. Fish that changed depth ≥20m showed the same results as those that changed depth by ≥ 10 m. In all cases, fish that moved across contour depths into deeper water exhibited greater growth than those that did not cross contour depths or did not move.

The minimum size rule can be an efficacious tool in red grouper and red snapper fishery management; however, factors such as regional predation can reduce its effectiveness. Combining this rule with the NMFS model of ecosystem–based management of marine fisheries would enhance survival. Mitsuyasu and Fluharty (2004) stated the NMFS Ecosystem Principles Panel defined ecosystem-based management as: "A comprehensive … management approach would require managers to consider all interactions that a target fish stock has with predators, competitors, and prey species; the effects of weather and climate on fisheries biology and ecology; the complex interactions between fishes and their habitat; and the effects of fishing on fish stocks and their habitat."

Additionally, traditional fishery management practices in the Gulf of Mexico and South Atlantic have placed reef fish species into specific management groups such as the grouper/snapper complex. Problems arise when these species are treated as a single management unit and identical regulations are imposed on all species within the complex. Taxonomic features used to group individual species into genera and families should not be used to manage a species because individual species that evolved from a common progenitor over time adapted to fill particular niches. These adaptations have been encoded within the bio-mechanical functions of a species and are responsible for behavioral responses. These behavior responses influence a species interaction with habitat, conspecifics, predators and prey. Results from this research demonstrate these responses also influence a species' response to fishing practices and gear.

It should be expected that survival of different species with regard to fishing gear and practices will be variable dependent on the ecological role the species plays within the ecosystem it inhabits. Although much thought has been given to the effects of outside interactions, little consideration has been given to understanding the bio-mechanical functions of a species that govern physical and behavioral responses to fishing gear and practices that affect fish mortality and should be included in the ecosystem paradigm.

Although this study provides insights regarding red grouper and red snapper mortality from hooks and barotrauma, there are no simple answers regarding the minimum size rule. Hook mortality can affect small red grouper and red snapper as well as larger legal sized fish because of their large gape. Although circle hooks are beneficial for red grouper, they do not show the same favorable results for red snapper. This is unfortunate as red snapper suffer higher hook mortality than red grouper. Survival from rapid decompression from depth favors smaller fish of both species because of less hemorrhaging of rete and gas gland cells in the swim bladders of smaller fish. However, this advantage can be lost if significant predation occurs, especially dolphin depredation. Future research should focus on investigating and quantifying predation by region as predation would favor survival of larger fish. Fish venting, a controversial issue, does not appear to kill red grouper or red snapper from the injection of pathogens or from injury by anglers during venting as evidenced by similar recapture rates for vented and not vented fish in shallow water where barotrauma does not cause mortality. Venting proved useful in the laboratory in quickly removing escaped swim bladder gases from the fish's body cavity allowing the stomach muscles to pull the stomach back into place quicker than waiting for diffusion so fish were able to feed normally within a few hours. At sea, any benefits would favor benthic species that would return to normal habitat whereas a pelagic species would need to sit on the bottom for two days until the swim bladder submucosal layer healed leaving them vulnerable to increased predation. However, venting is not a panacea and has no effect on emboli. Depth mortality is higher for red grouper than red snapper at comparable depths and perhaps commercial red grouper regulation should be by tonnage. However, the reef fish recreational and recreational-for-hire fisheries tag/recapture data from off Southwest Florida show high fishing pressure for red grouper based on single and multiple recaptures at shallow inshore areas. In addition to bag limits, the minimum size rule would prevent removal of small fish from inshore nursery areas where they have a greater chance of survival.

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