J and Circle Hook Mortality and Barotrauma and the Consequences for Red Snapper Survival

By
Karen Mary Burns, Ph.D.

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 a minimum size rule.

To evaluate some aspects of the efficacy of the minimum size rule in the red snapper fishery off South Atlantic and Gulf of Mexico off Florida traditional fisheries data were collected and analyzed in light of fish physiology, eco-morphology and behavior. Study objectives included 1) determination of the causes of hook mortality in 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 related to feeding behavior, 2) examination of the effects of rapid depression from depth on fish survival by inspection of red snapper swim bladders in both healthy and swim bladder ruptured fish from various water depths, comparison of tag and recapture data, and laboratory simulations using fish hyperbaric chambers to determine healing and survival from rapid depression trauma, and 3) evaluation of some of the consequences imposed by the minimum size limit based on study results.

To evaluate the role hook mortality plays in species survival moribund red snapper caught aboard headboats were necropsied. 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. Red snapper latent hook mortality (29%) was also high. Tag recaptures were used to test the null hypothesis that there would be no difference in recapture rates of red snapper caught on circle versus J hooks. The null hypothesis was rejected. 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 resulted from eco-morphology and feeding behavior. Dentition, jaw lever ratios, and feeding type and feeding behavior, including prey residence time in the mouth before swallowing were determined. Red

1

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 long. 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. Prey residence time in the mouth before swallowing was short ($\bar{x}$ = red snapper: 3.74 second) Red snapper demonstrate eco-morphological propensities in feeding morphology that translate into specific feeding behaviors that help clarify differences in J and circle hook mortality and may prove useful in designing predictive models for determining J and circle hook mortalities for other species.

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) 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, and a fish tagging study using tag returns as a proxy for survival. Red grouper had larger (in relation to body size) and thinner swim bladders than red snapper. Red snapper swim bladder ruptures were smaller with thicker tissue 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) however; some survived at sea (Burns and Robbins 2006). 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 determine the ability to adjust to rapid depressurization. Some red grouper caught on commercial long-line gear, tagged, released and vented were recaptured after 2,172 days of freedom.

Introduction

Red snapper, *Lutjanus campechanus*, support important recreational, recreational-for-hire, and commercial fisheries, comprising significant portions of the reef fish catch in the South Atlantic and Gulf of Mexico. 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 were landed in Florida by these fisheries (NOAA Fisheries MRFSS, 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, red snapper are highly regulated in both the South Atlantic and Gulf of Mexico. Although there are recreational bag limits and closed seasons for 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 red snapper 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 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).

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. 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. Unless survival of bycatch by gear type is determined it will be difficult to enact regulations to control bycatch levels.

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.

5

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.

It was unknown if these techniques such as venting 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

6

(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 mirable. This close association between gas gland cells and rete (Figure1) is essential for swim bladder gas production
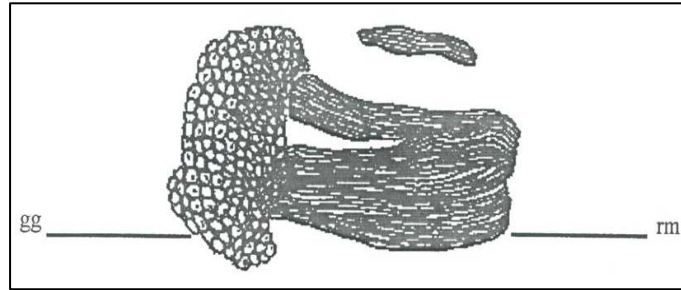

Figure 1. Illustration of the close association of the gas glands (gg) and the rete mirable (rm) in the red grouper swim bladder ventral wall.

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.

Materials and Methods

Acute Mortality

Monitoring for acute mortality occurred in 1999 and 2003. Moribund 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.

9

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 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 snapper were caught using hook and line and tagged (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). 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. Both large and small tags were used; tag size was determined by fish length.
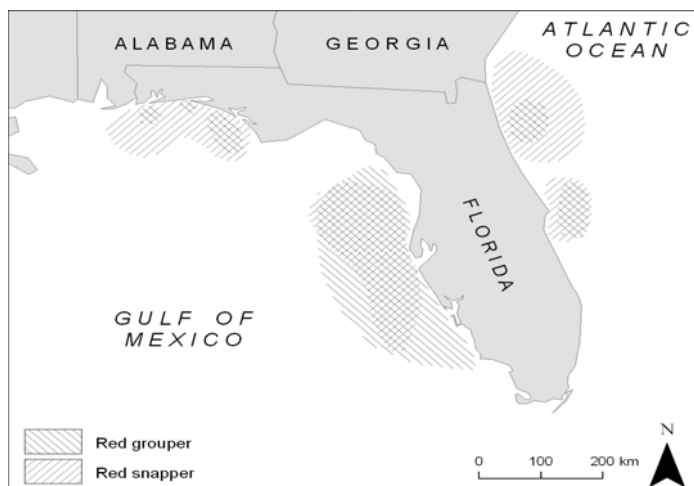
Figure 2. Study area where red grouper and red snapper were tagged.

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.

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.

Publicity Campaign

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 he hypothesis that there would be no difference in recapture rates for red snapper caught on circle and J hooks. 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 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) 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 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 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 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 56 red snapper feeding sequences filmed only 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.

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, Fort 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 regardless of fish density and fish care. When tested in the hyperbaric chambers fish not maintained under very strict sanitation protocols sustained more severe 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), were used to produce laboratory simulations of pressure changes red grouper and red snapper 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. 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), 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.

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

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.

Results

*Acute Mortality*During 1999 and 2003 when acute mortalities were noted and classified, 171 mortalities were recorded during tagging trips. The 171 fish included 13.6% of all red snapper caught 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. Depth-related effects (barotraumas) accounted for 13.5% of red snapper mortality. Mortality in the "other" category claimed 37.4% of red snapper. 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 4); if oriented downward it typically punctured or destroyed the liver (Figure 5). Depth-related injuries were easily distinguished from hook injuries 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 6).
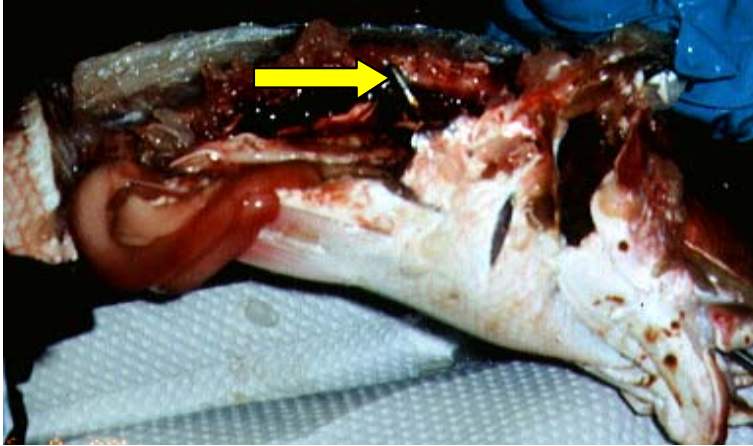
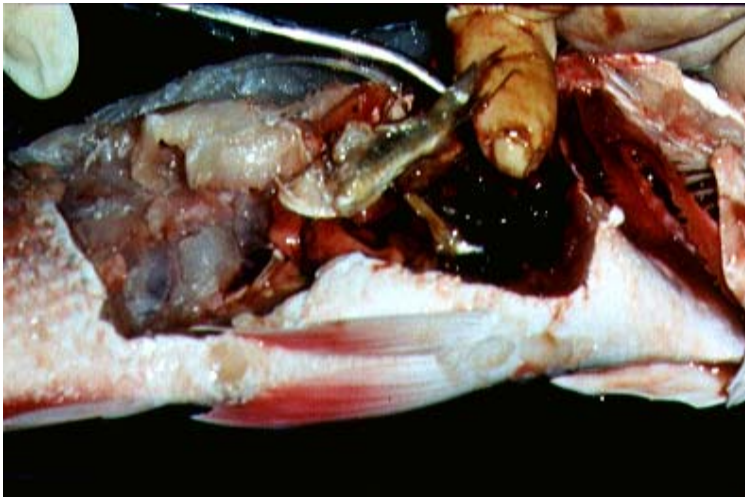Figure 4. Red snapper killed by J hook trauma.

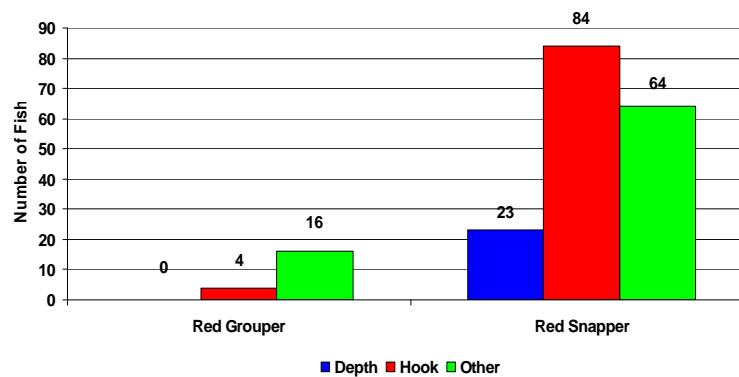Figure 5. Red snapper killed by a J hook macerating the liver

Figure 6. Number of red grouper and red snapper acute shipboard mortalities partitioned by cause of death
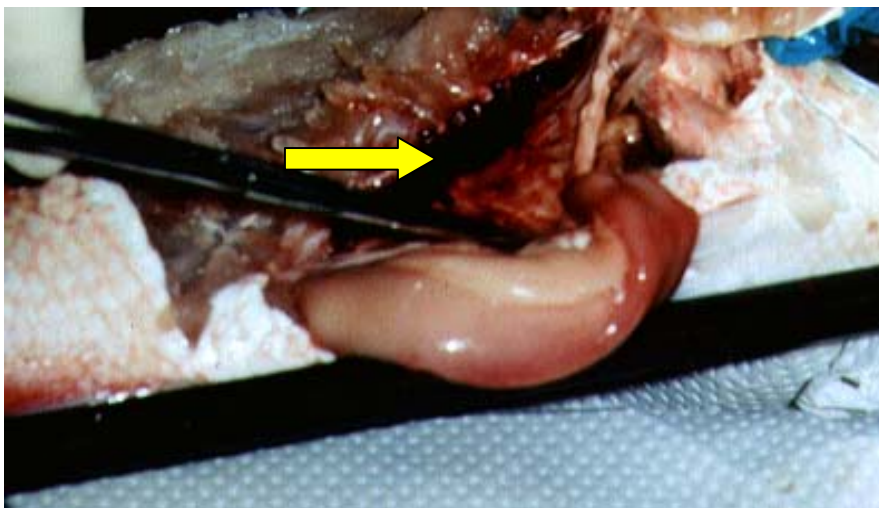
Latent Mortality

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

Similar to acute mortality rates, red snapper deaths from latent hook mortality (29%) were high. 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 7). The remainder of fish in the absence of hook damage (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 snapper (n=5,317) were tagged and released at depths ranging $\leq$ .5 m to $\geq$ 99 m. Red snapper captures were spread over a 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. 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.

For comparison, red snapper hook data were compared with data from red grouper to test the hypothesis that there was no difference in red grouper and red snapper recaptures by hook type.   Some fish were originally caught on J hooks; others on circle hooks (Table 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 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). 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). 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.

Table 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	4.49×10^{-8}
Red Snapper	2145	269	12.5	3172	258	8.1	2.3×10^{-6}

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 (> 27.4 m), twice as many red snapper originally caught on J hooks were recaptured (Table 2).

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

Water	Depth	$\leq$	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 snapper top canine, top fused and depressible tooth length was long (Figures 8 and 9). There were a reduced number of teeth in the red snapper bottom jaw and a greater space between bottom teeth (Figure 10). Red snapper jaw lever ratios were high (0.32 closing/0.22 opening). Mandibular shape was not greatly extended and the ascending process was short and somewhat narrow (Figure 11).

Figure 8. Red snapper upper canine teeth

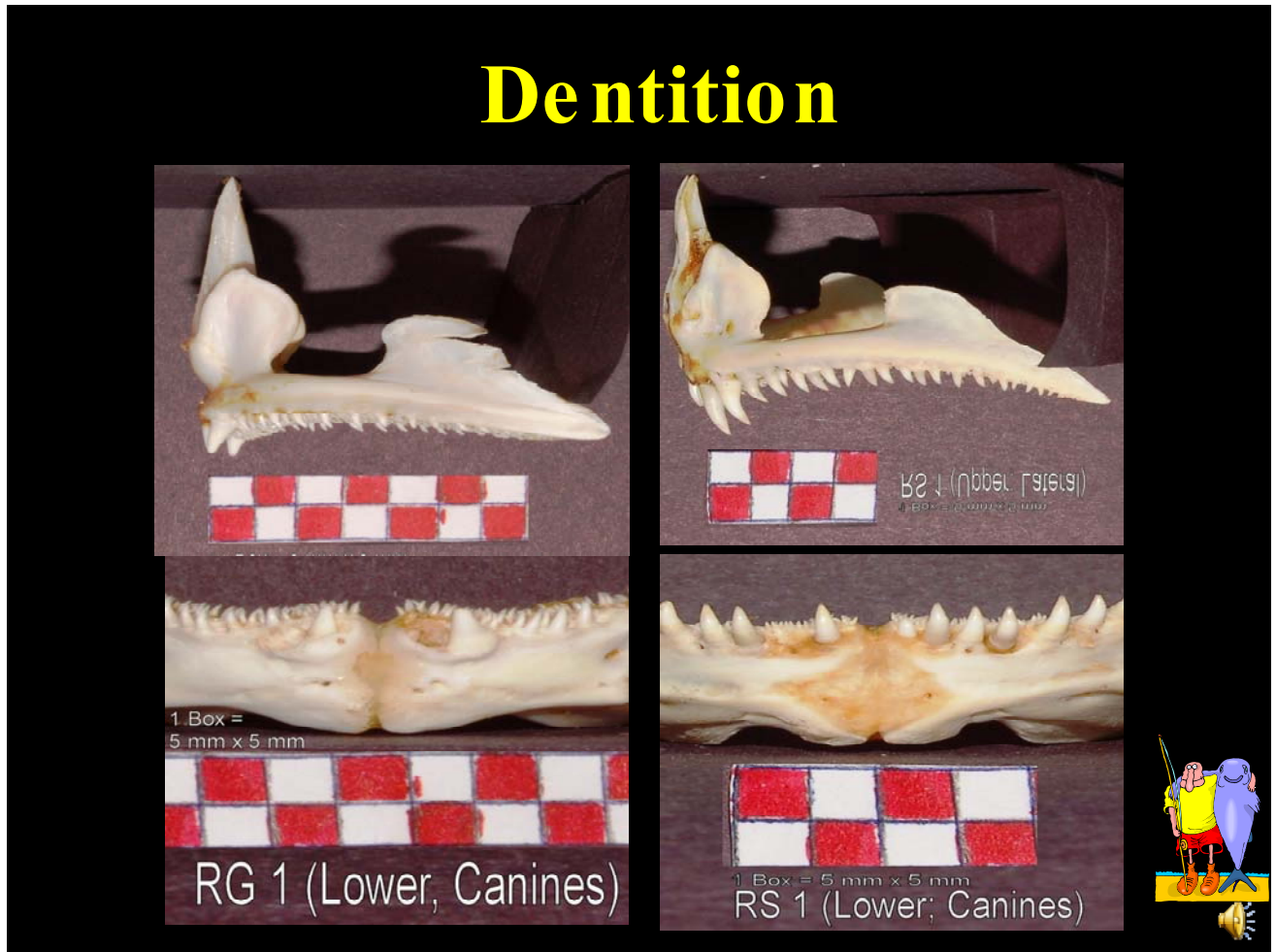Figure 9. Rows of conical teeth in both red snapper upper and lower jaws.

Figure 10. Comparison of red grouper (left) and red snapper (right) dentition showing difference in tooth size and reduction in the number of teeth in the bottom jaw.

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

Figure 11. Lateral view of red snapper lower jaw including the location of the ascending process.

Feeding Videos

Red snapper video was compared with those of red grouper. 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.

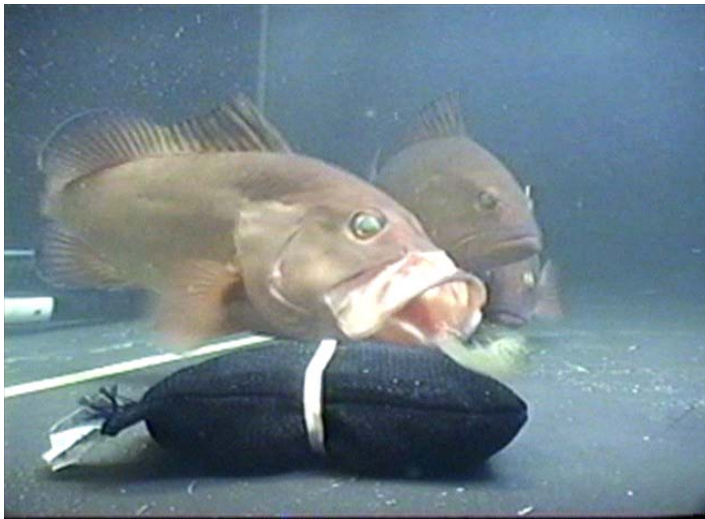Video analyses revealed red grouper were ambush suction feeders. They approached prey, examined it and then enveloped it by expanding their large buccal cavity (Figure 12). Prey was orally manipulated (mouthed) and swallowed whole. Unlike red snapper, which immediately swam away from the prey capture 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 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 12. Red grouper exhibiting suction feeding showing full buccal extension as entire shrimp is drawn into the fish's mouth.

Figure 13. 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 13). 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 $\bar{x}$=6.62 seco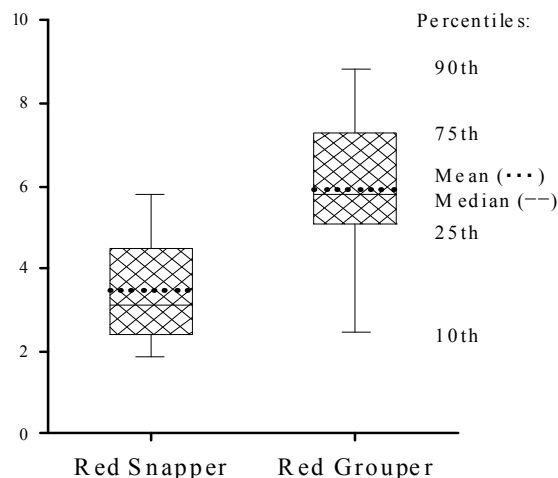nds) (Figure 14). The null hypothesis that there was no difference between the two species in prey residence time within the mouth before swallowing was rejected (*p<0.001*). Data passed the normality test (*p=0.157*) and the equal variance test (*p=0.489*). The difference was -2.373 and t = -4.339 with 37 degrees of freedom (*p=< 0.001*) with a 95% confidence interval for difference of means: -3.481 to -1.265.

Figure 14. Difference in prey residence time in the fish's mouth before swallowing between species.

Swim Bladder Differences
Acute Mortality

None of the 56 moribund red grouper caught off headboats died from barotrauma, however most were caught in shallow depths ranging 21-28 m. Necropsy results for 171
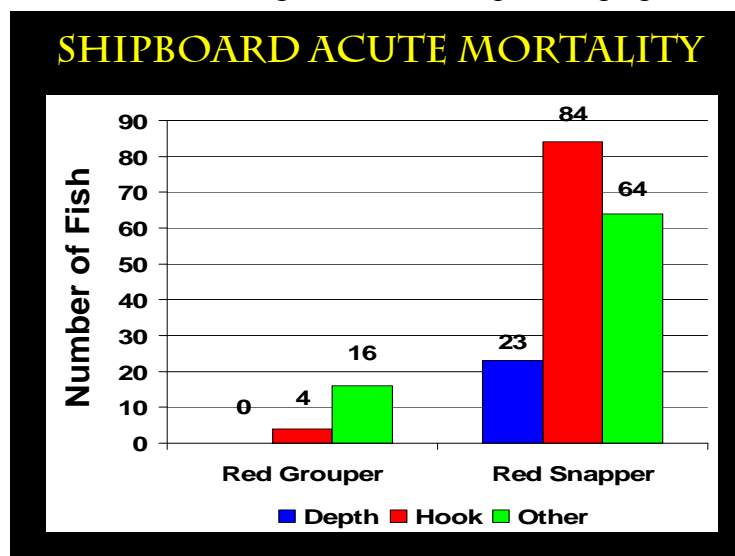

moribund red snapper caught at depths ranging 11-43 m showed depth-related effects accounted for only 13.5% of red snapper mortality while 49.1% succumbed to hook injuries; nearly the same percentage (50.9%) as all other sources of mortality combined (Figure 15). Red snapper mortality was highest (59.1% of all red snapper mortalities) at depths between 27.7 - 42.7 m; the depths at which most red snapper were

Figure 15. Acute shipboard mortality partitioned by cause of death.

caught; however hook trauma not barotraumas accounted for more mortality even at these depths (60.4% of all mortalities in this depth category).

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 16). 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 (Figure 17). Ruptures in red grouper swim bladders were always larger in red grouper swim bladders than those of red snapper for hook and line caught fish (Figures 18 and 19).
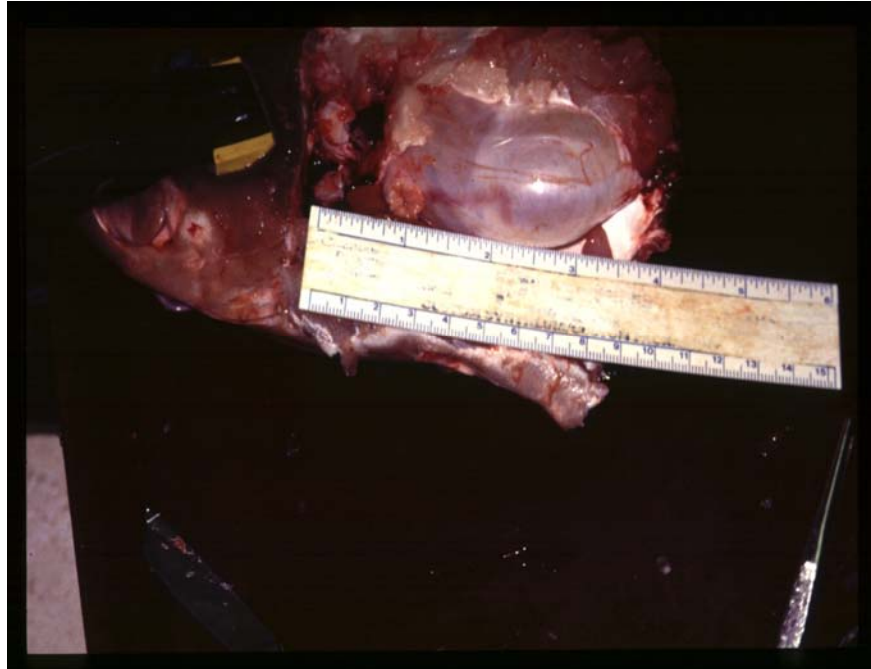
Figure 16. Inflated red grouper swim bladder showing swim bladder size in proportion to total body size.

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 20). 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 normal brain function. These fishes survived for months and had to be humanely euthanized at the end of the study.
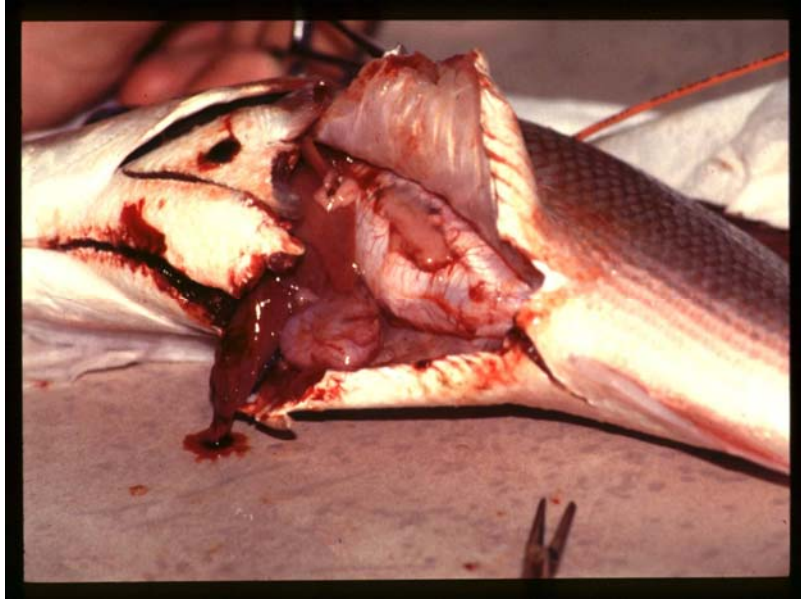
29

Figure 17. Inflated red snapper swim bladder showing size in proportion to total body size.
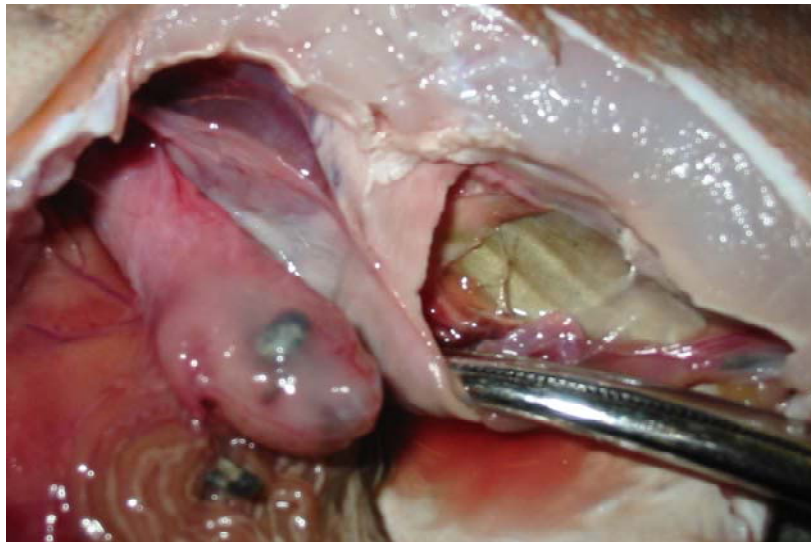

Figure 18. Initial rupture in a red grouper swim bladder.
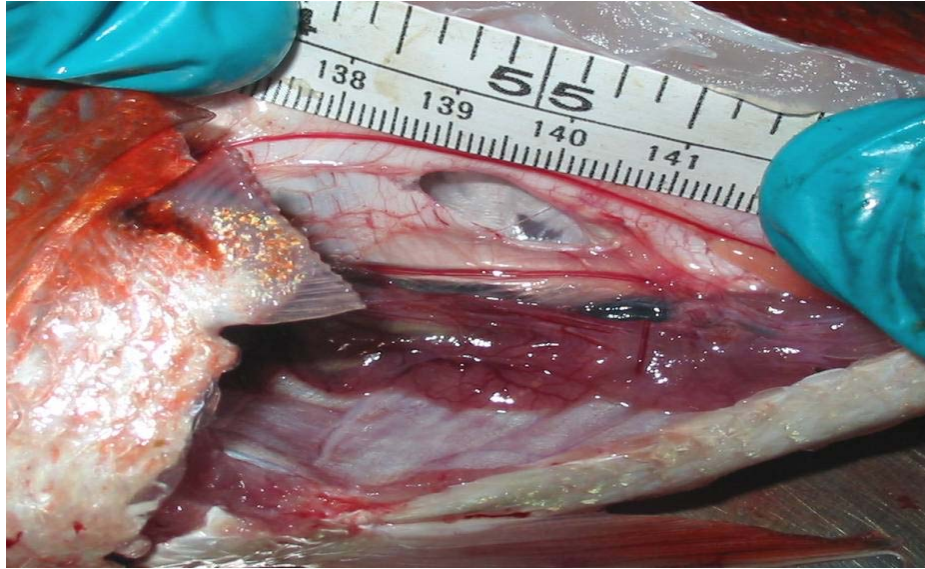
30

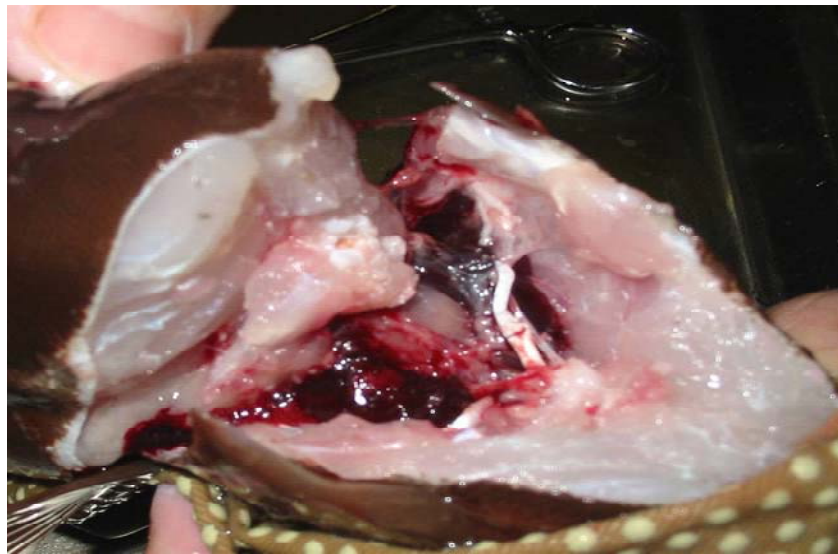Figure 19. Initial rupture in a red snapper swim bladder.

Figure 20. Bilateral postcranial hemorrhages in red grouper rapidly decompressed from 21.3 m.

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 21). Under a dissecting microscope, this posterior area also appeared absent in small (< 30.5 cm FL) red grouper. Beginning vascularization was visible under a dissecting microscope, at 30.5 cm FL; however tissue changes in this posterior area were detectable in histological tissue samples of smaller (25.1 cm FL) red groupers. This secondary structure is absent in red snappers of any size. This structure composed of mostly gas gland cells appears to function to increase buoyancy and appears to be fully functional at 38 cm – the size at which red grouper leave inshore nursery grounds and begin to move offshore with ontogeny (Figure 22).
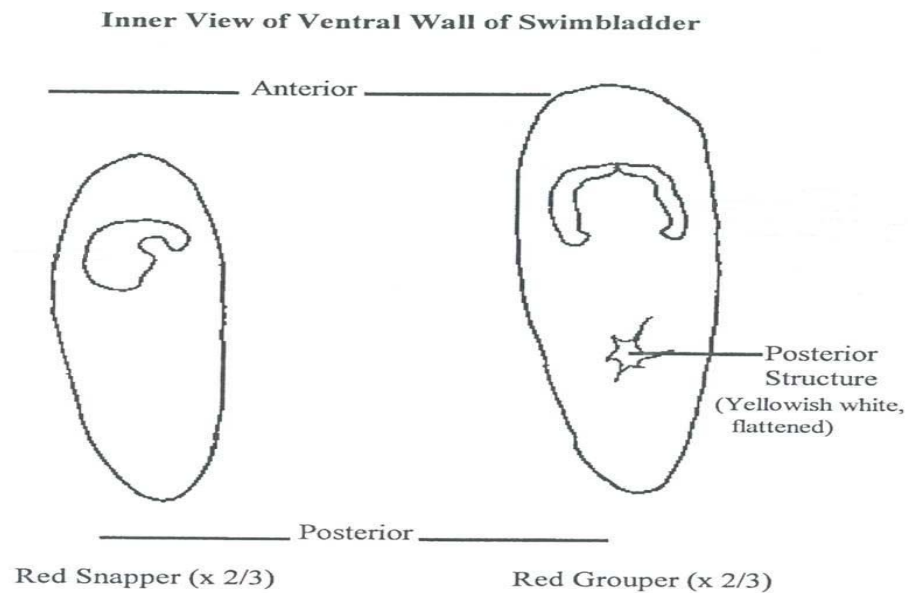

Figure 21. Inner view of the ventral wall of a red snapper and red grouper swim bladder showing the differences in areas of gas absorption and resorption and the secondary structure in the red grouper posterior portion of the swim bladder.
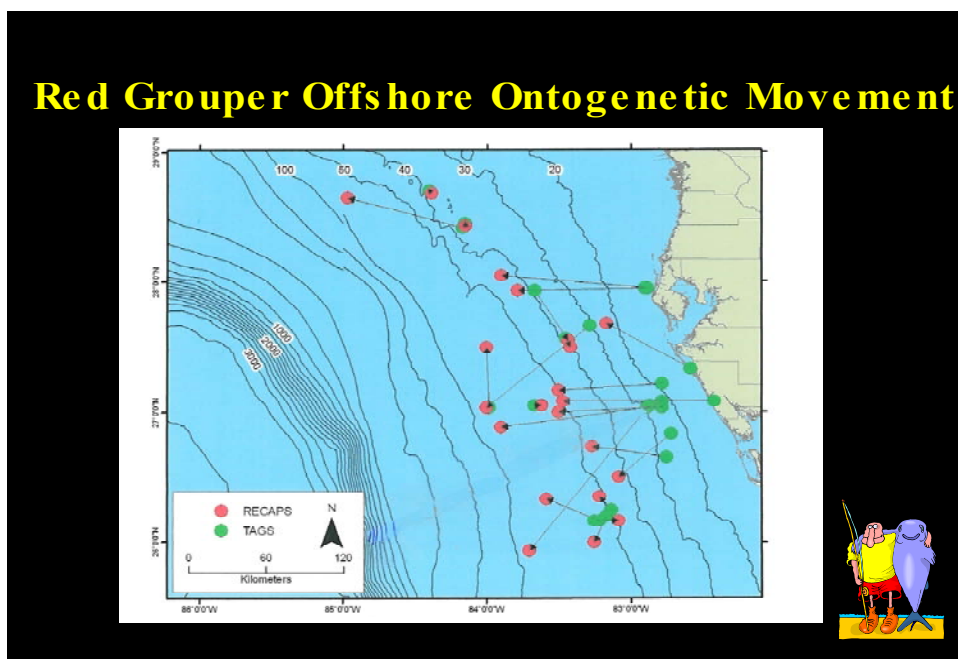
Figure 22. Red grouper movement offshore with ontogeny determined from tagging data.

Histological work by Brown-Peterson (Burns et al 2008) has shown differences in swim bladder tissue between the two species that affect rates of hemorrhaging. Figure 23 is a comparison of swim bladder sections containing hemorrhaged tissue (the darker purple color areas) from both species showing these differences. In the red grouper swim bladder, the close association and large number of connections between gas gland cells and rete and larger blood vessels is apparent. This close association and additional connections between gas gland cells and rete in red grouper in swim bladder wall showed more hemorrhaging in blood vessels associated with the swim bladder than did red snapper.

The connections in the red snapper swim bladder are different. There were more rete and they were grouped together and not as intimately associated with gas gland cells as in red grouper. This separation leads to less hemorrhaging in the red snapper swim bladder than in red grouper. Although retal area increased significantly with body length for both species, red snapper had a significantly higher percentage of retal area within the swim bladder when adjusted for length (p<0.001) (Figure 24). Red grouper had a significantly higher percentage of retal area occupied by gas gland than red snapper when adjusted for fish length (Figure 25).
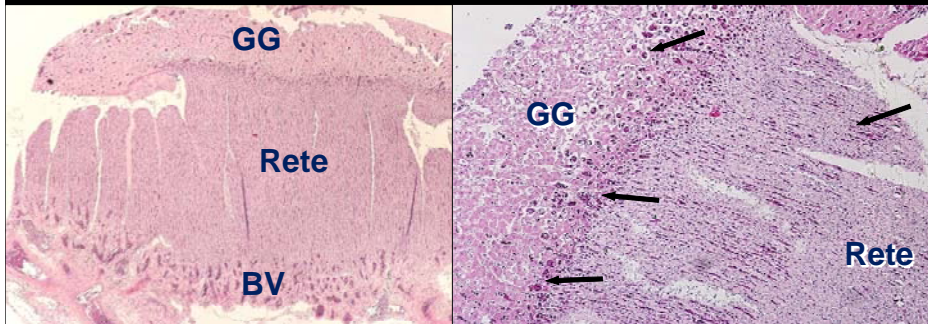
Figure 23. Comparison of red grouper hemorrhaged swim bladder tissue (left) and red snapper hemorrhaged swim bladder tissue (right) showing the closer association of gas gland cells, rete and large blood vessels in the red grouper swim bladder.
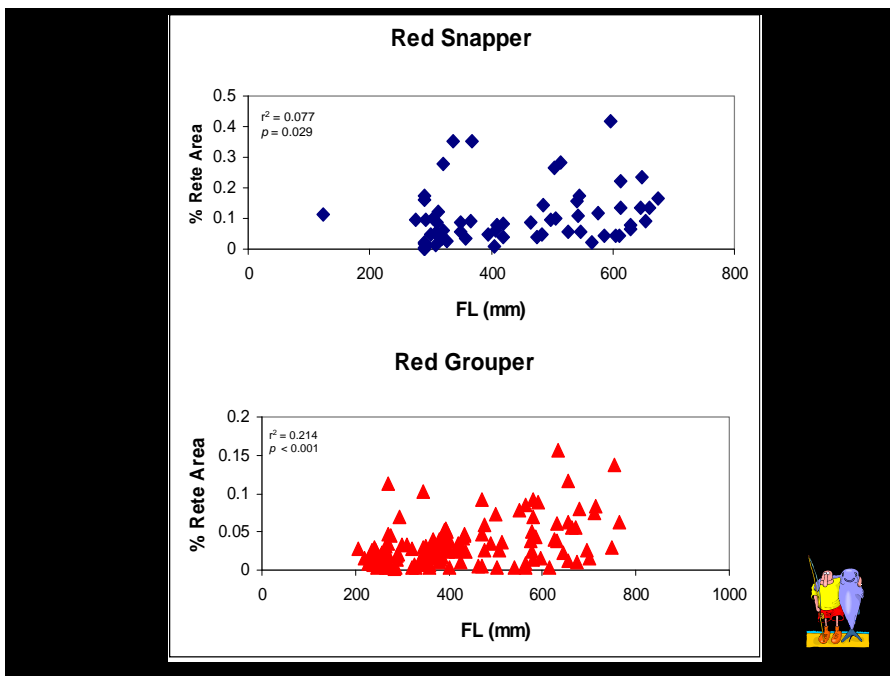
Figure 24. Comparison of percent of retal area found within the tissue of red snapper and red grouper swim bladder wall.

34
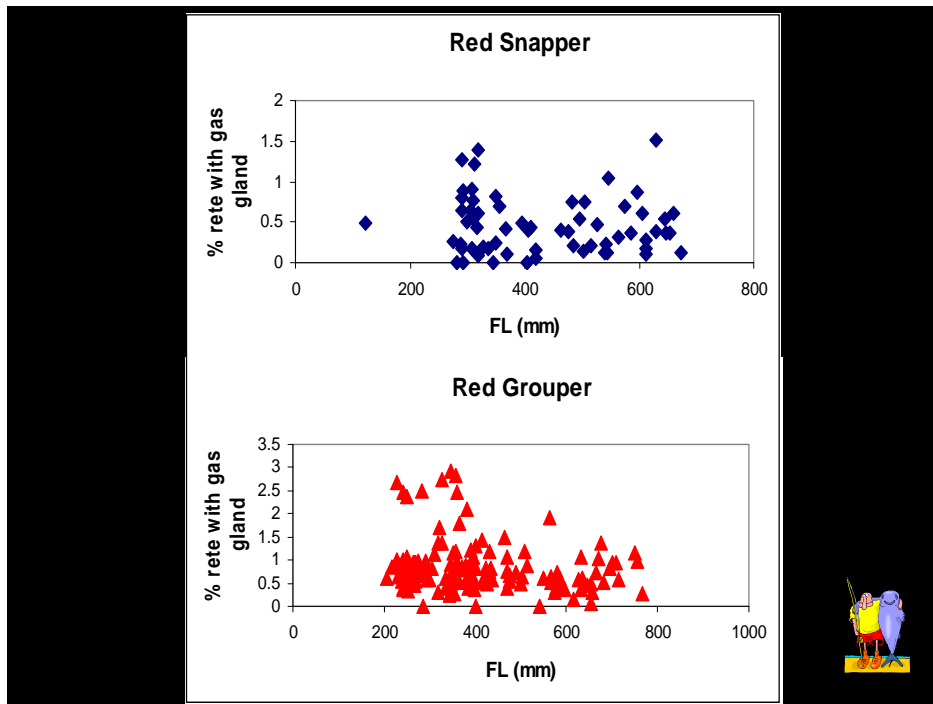
Figure 25. Comparison of percent of retal area found within the gas gland tissue of red snapper and red grouper swim bladder wall.

Smaller fishes of both species exhibited less hemorrhaging than larger fish, however; small red snapper swim bladders exhibited less hemorrhaging than red grouper at similar size and depths of capture (Figure 26).
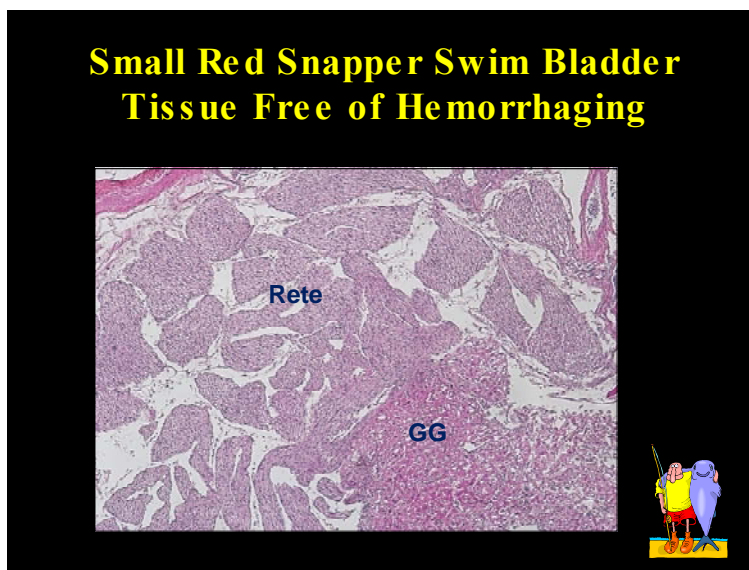
Figure 26. Histological section of red snapper swim bladder wall tissue showing normal rete and gas gland tissue.

35

Percentage of fish showing hemorrhaging in both rete and swim bladder tissue increased significantly with every 50 mm increase in length for both species (Figure 27). This supports cage study results reported by Wilson (1993) who found smaller red grouper held in cages survived rapid decompression better than larger fish, and those of Koenig's (2001) cage studies where he reported small red grouper and red snapper survived rapid decompression better than larger fish.
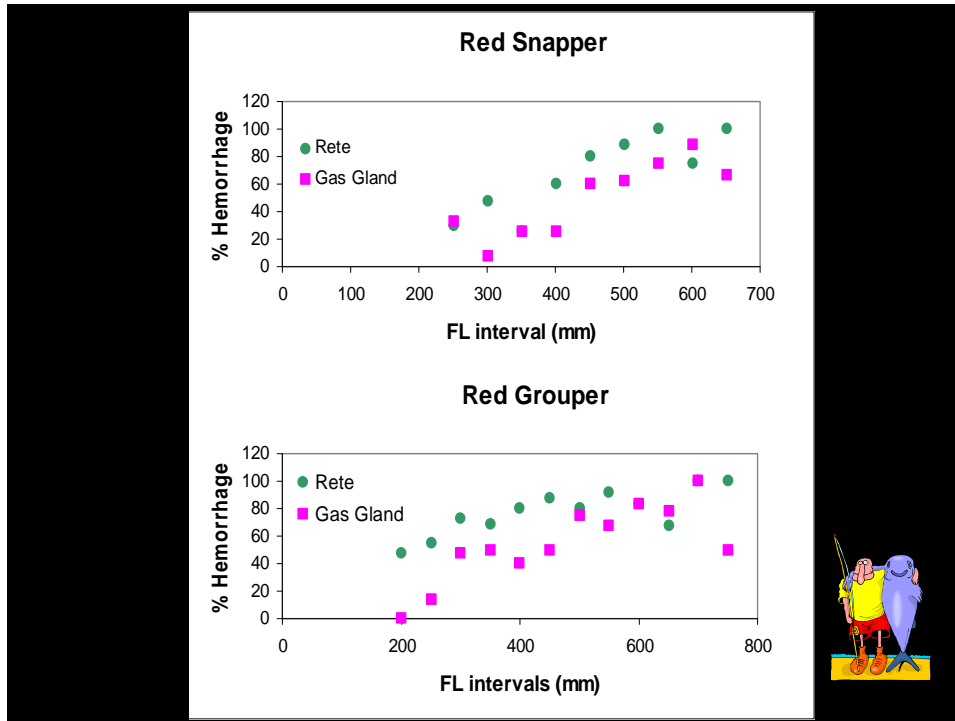
Figure 27. Comparison of percent of hemorrhage of rete and gas gland cells within the swim bladder walls of red snapper and red grouper by fish size (mm, FL).

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). 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 4).

Table 3. 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. No red grouper trials were held at 61 m.
.

		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 4. Acute and delayed mortalities of red snapper and red grouper from hyperbaric chamber tests.

	Acute	Delayed	Total mortalities	% acute	% delayed	Signs of trauma and fish
Red snapper	12	5	17	71.0	29.0	
Red grouper	8	0	8	100.0	0.0	

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 28) 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 29) that was unique to red grouper throughout the course of these experiments. Exopthalmia in red snapper can occur in either one or both eyes and not necessarily affect the brain.
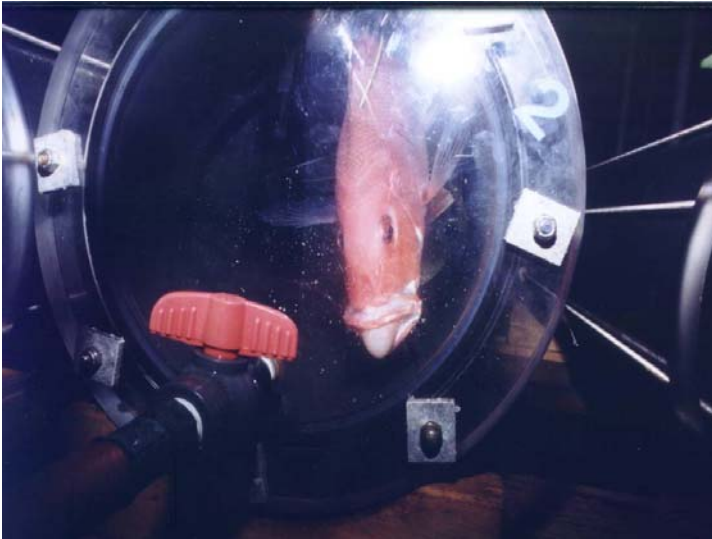
Figure 28. Red snapper exhibiting stomach prolapse following swim bladder rupture during simulated depth experiments using fish hyperbaric chambers.

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 29. 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 30). 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 30. Esophageal ring bruise caused by stomach prolapsed in a red snapper rapidly decompressed from 61m.

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) 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.

Table 5. 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).

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

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 (Figure 31). 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 32) 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 33). 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 34). 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.
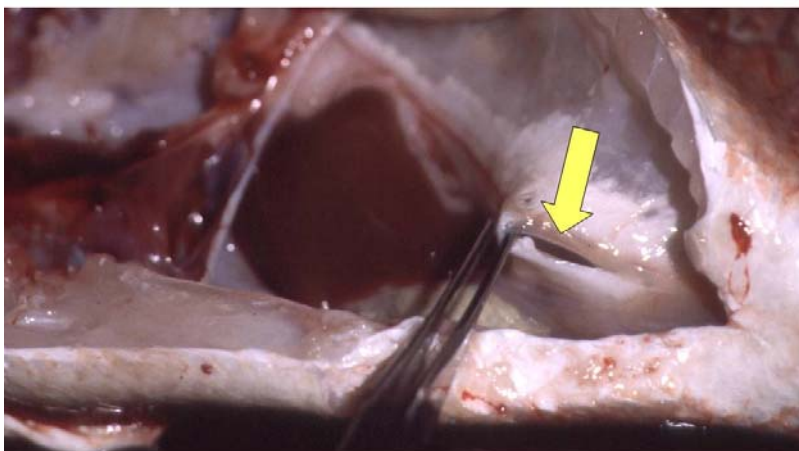
Figure 31. Red snapper swim bladder, 24 hours after rupture, showing signs of healing.
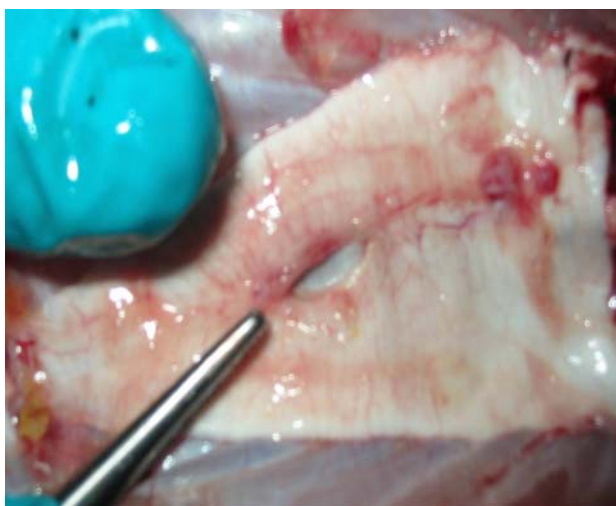
Figure 32. Red snapper swim bladder rupture site showing healing in a fish sacrificed two days after rapid recompression from the simulated depth of 62 m in hyperbaric chambers.
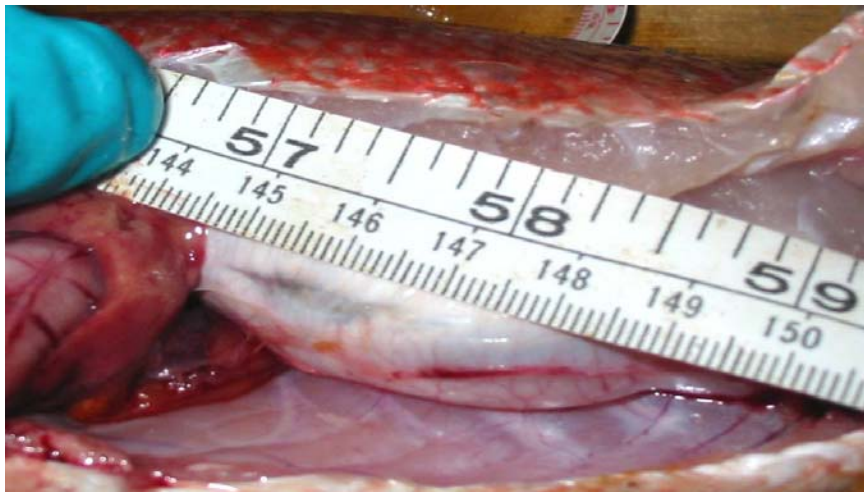
Figure 33. Red snapper swim bladder rupture scar three days after rupture
in 62 m hyperbaric chamber rapid decompression experiment.
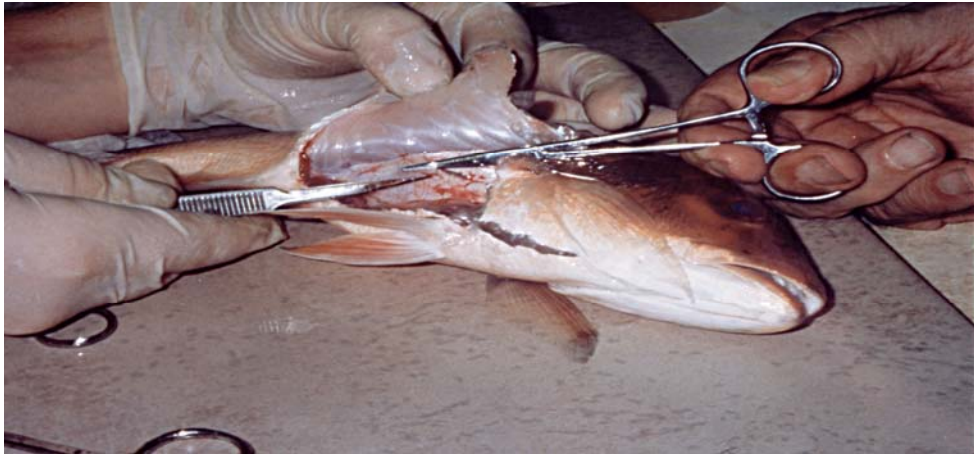
Figure 34. New swim bladder rupture from depth simulation of 21.3 m (tip of forceps) and healed scar (tip of scissors) from rupture at 21.3 m during capture one month previously.

Stomach Prolapse and Feeding

One of the most common external signs of swim bladder rupture was stomach prolapsed (Figure 35). 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 36 - 38). 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 35. Red snapper exhibiting stomach prolapse.

Post-experimental Fish Feeding

Species	Depth (m)	Time (hrs)
Red Grouper	21.3 27.4	2
	42.7	12-24
Red Snapper	21.3 27.4	1
	42.7	4

Figure 36. Number of hours to feeding following full stomach prolapse and stomach repositioning after simulated depth experiments in fish hyperbaric chambers.

45

To determine that the stomach was in the correct position and functioning properly a small subsample of experimental fish were necropsied (Figures 3-19 and 3-20).

Figure 37. Red snapper stomach one hour after stomach prolapse. Stomach is back in place and fish can feed normally.

Figure 38. Overall view of red snapper seven 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.
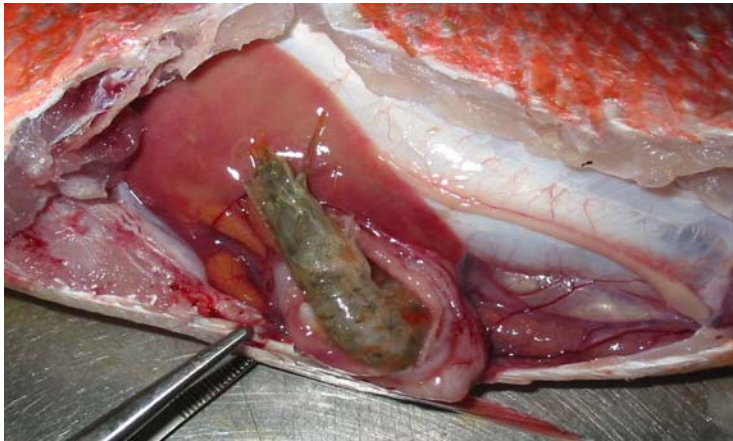
Fish Tag and Release

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 $(p=9.7 \times 10^{-19})$. 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) $(p=9.5 \times 10^{-6})$ (Table 6).

Table 6. 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) $\leq$ 38.1cm vs. > 38.1 cm
Red Grouper $\leq$ 38.1 cm	3308	194	5.9	9.7×10^{-19}
> 38.1 cm	1675	240	14.3	df =1
Red Snapper $\leq$ 38.1 cm	3957	333	8.4	9.47×10^{-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 7). 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. Another reason is predation in the Gulf of Mexico, especially bottlenosed dolphins in the northern Gulf of Mexico (Figure 39).

Table 7. 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=4.02x10^{-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

Figure 39. Bottlenosed dolphin about to feed on an undersized red snapper just discarded from a headboat fishing off Panama City, Florida.

Discussion

Acute Mortality – Hook Mortality

Red snapper exhibited severe obvious signs of trauma and high mortality from hooks. Necropsies of acute mortalities caught from headboats showed hook trauma was the leading cause of death. 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. Overall 64.3% of the total red snapper catch died from hook trauma. It appears hooking injuries are far more common and harmful to red snapper and have a much larger impact on red snapper survival than depth related effects at depths ranging 27.7-42.7 m

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 benefit 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

49

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 and jaw morphology reflected feeding methodology. 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 snapper have large 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 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.

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 red snapper demonstrating that they are capable of both a strong biting force and high velocity of jaw closure. 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).

Feeding Videos

Different feeding behavior predicated on dentition and jaw ecomorphology appears to be a 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

51

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 eco-morphology.

Additional research on various species is needed to confirm that J and circle hook mortality is heavily dependent on eco-morphology 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 eco-morphology 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, eco-morphology could be a useful tool in eco-management 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.

Acute Mortality- Barotrauma

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

53

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 $\geq$ 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 but 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 $\leq$ 42 m, many survived when held at 1 atm pressure if vented. In contrast, red grouper never survived rapid decompression from simulated depths of $\leq$ 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 Alexander 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 $p=9.7x10^{-19}$; red snapper $p=9.47x10^{-6}$). 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 3-30). 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.

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).

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).

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).

Experiments designed to gain an understanding of how J and circle hooks affected red snapper mortality were discussed. Necropsy results from headboat client caught fish showed red snapper suffered high acute hook trauma with 49.1% mortality resulting from hooking, almost equaling all other sources (50.9%) of red snapper mortality combined. Similar to acute hook mortality rates, red snapper deaths from latent hook mortality (29%) were also high. The null hypothesis tested using data from a tag/release study that there would be no difference in recapture rates of red snapper caught on circle versus J hooks was rejected. 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 was influenced by 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 could influence hook mortality. Circle hooks are not a panacea and do not enhance survival of red snapper.

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. 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. Fish swim bladders rupture with rapid change of pressure of 1 atm of pressure (10 m). Data from hyperbaric chamber studies showed that red snapper can easily survive rapid decompression from 21 m and 27 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 if vented (Burns et al. 2004). Results of these investigations were compared with data from red snapper fish tagging studies. At sea, lethal and semi-lethal effects of barotraumas also began at around 42 m.

Although red snapper survive rapid changes in depth better than some other reef fishes such as 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. 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 snapper mortality from hooks and barotrauma, there are no simple answers regarding the minimum size rule. Hook mortality can affect small red snapper as well as larger legal sized fish because of their large gape and circle hooks do not show favorable results for red snapper. This is unfortunate as red snapper suffer high hook mortality. 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 favors survival of larger fish. 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.

References

Albin, D. and K.A. Karpov. 1998. Mortality of lingcod, *Ophinodon elongatus*, related to capture by hook and line. *Marine Fisheries Review* 60(3):29-34.

Ault, J.S., S.G. Smith, J.A. Bohnsack, J. Luo, D.E. Harper and D.B. McClellan. 2006. Building sustainable fisheries in Florida's coral reef ecosystem: positive signs in the Dry Tortugas. *Bulletin of Marine Science* 78(3):633-654.

Ault, J.S., J.A. Bohnsack, S.G. Smith and J. Luo. 2005. Towards sustainable multispecies fisheries in the Florida USA coral reef ecosystem. *Bulletin of Marine Science* 76(2):595-622.

Ault, J.S., J.A. Bohnsack and G.A. Meester. 1997. A retrospective (1979-1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fishery Bulletin* 96(3):395-414.

Ayvazian, S.G., B.S. Wise and G.C. Young. 2002. Short-term hooking mortality of tailor (*Pomatomus saltatrix*) in Western Australia and the impact on yield per recruit. *Fisheries Research* 58:241-248.

Bacheler, N.M. and J.A. Buckel. 2004. Does hook type influence the catch rate, size, and injury of grouper in a North Carolina commercial fishery? *Fisheries Research* 69:303-311.

Bartholomew, A. and J.A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* 15:129-154.

Bendock, T. and M. Alexandersdottir. 1993. Hooking mortality of Chinook salmon released in the Kenai River, Alaska. *North American Journal of Fisheries Management* 13:540-549.

Bettoli, P.W., C.S. Vandergoot and P.T. Horner. 2000. Hooking mortality of saugers in the Tennessee River. *North American Fisheries Management* 20:833-837.

Bettoli, P.W. and R.S. Osborne. 1998. Hooking mortality and behavior of striped bass following catch and release angling. *North American Journal of Fisheries Management* 18:609-615.

Blaxter J.H.S. and P. Tytler. 1972. Pressure discrimination in teleost fish. p. 417- 443. *In*: *The Effects of Pressure on Organisms.* Symposia of the Society for Experimental Biology (ed.) Cambridge: At the University Press, London NW 1 2 DB

Bohnsack, J.A. 2000. A comparison of the short-term impacts of no-take marine reserves and minimum size limits. *Bulletin of Marine Science* 66:635-650.

Bohnsack, J.A. and J.S. Ault. 1996. Management strategies to conserve marine biodiversity. *Oceanography* 9(1):73-82.

Brown-Peterson, N.J., K.M. Burns and R.M. Overstreet. 2006. Swim bladder morphology differences in red snapper and red grouper. Abstracts of the Joint Meeting of Ichthyologists and Herpetologists, New Orleans, Louisiana, July 6-11, 2006. p. 61

Bruesewitz, S., D. Fletcher and M. Divens. 1996. Hooking mortality of walleye caught from deep water. Washington Department of Fish and Wildlife Research Report No. IF96-07, 7 p.

Burns, K.M. and N.F. Parnell. In prep. Comparison of hook mortality between red snapper, *Lutjanus campechanus*, and red grouper, *Epinephalus morio*, in the eastern Gulf of Mexico and Atlantic Ocean off Florida, with emphasis on differences in feeding behavior and jaw morphology.

Burns, K.M., N.J. Brown-Peterson, R.M. Overstreet, J. Gannon, P. Simmons, J. Sprinkle and C. Weaver. 2008. Evaluation of the Efficacy of the Current Minimum Size Regulation for Selected Reef Fish Based on Release Mortality and Fish Physiology. Mote Marine Laboratory Technical Report No. 1176 (MARFIN Grant # NA17FF2010). 75 p.

Burns, K.M. and B.D. Robbins. 2006. Cooperative long-line sampling of the west Florida shelf shallow water grouper complex: Characterization of life history, undersized bycatch and targeted habitat. Mote Marine Laboratory Technical report No. 1119. 46 p.

Burns, K.M., N.J. Brown-Peterson, R.M. Overstreet, J.G. Gannon, J.M. Sprinkel, B.D. Robbins, and C.A. Weaver. 2006. Geographic comparison of age, growth, reproduction, movement, and survival of red snapper off the state of Florida. Mote Marine Laboratory Technical Report No. 1147.

Burns, K.M., N.F. Parnell and R.R. Wilson. 2004. Partitioning release mortality in undersized red snapper bycatch: comparison of depth vs. hooking effects. Mote Marine Laboratory Technical Report No. 932. 36 p.

Burns, K.M., C.C. Koenig, and F.C. Coleman**.** 2002. Evaluation of multiple factors involved in release mortality of undersized red grouper, gag, red snapper, and vermilion snapper. Mote Marine Laboratory Technical Report No. 814. (MARFIN grant # NA87FF0421).

Burns, K.M. and V. Restrepo. 2002. Survival of Reef Fish after Rapid Depressurization: Field and Laboratory Studies. p. 148-151. I*n:* Lucy, J.A. and A.L. Studholme (eds.) *Catch and Release in Marine Recreational Fisheries*. American Fisheries Society, Symposium 30, Bethesda, Maryland.

Burns, K. 2001a. Venting of some bottom fish aids survival. *Salt Water Sportsman Annual Pro Issue*. May 2001.

Burns, K.M. 2001b. Fish venting. Mote Marine Laboratory. Available: http://isurus.mote.org/research/cfe/fish-bio-how-to-vent-a-fish.html (January 2006).

Castriota, L., Finoia M.G. and F. Andaloro. 2005. Trophic interactions between *Xyrichtys novacula* (Labridae) and juvenile *Pagrus pagrus* (Sparidae) in the central Mediterranean Sea. *Electronic Journal of Ichthyology* 2:54 -60.

Chopin, F. S., T. Arimoto and Y. Inoue. 1996. A comparison of the stress response and mortality of sea bream *Pagrus major* captured by hook and line and trammel net. *Fisheries Research* 28:277-289.

Clifton, K.F. and P.J. Motta. 1998. Feeding morphology, diet, and ecomorphological relationships among five Caribbean labrids (Labridae, Teleostei). *Copeia* 1998:953-966.

Coleman, F.C., W.F. Figueira, J. S. Ueland and L.B. Crowder. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* 305(5692):1958-1959.

Collins, M.R. J.C. McGovern, G.R. Sedberry, H.S. Meister and R. Pardieck. 1999. Swim bladder deflation in black sea bass and vermilion snapper: potential for increased post-release survival. *North American Journal of Fisheries Management.* 19:828-832.

Cooke, S.J. and C.D. Suski. 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodiversity and Conservation* 14:1195-1209.

Cooke, S.J., and I.G. Cowx. 2004. The role of recreational fishing in global fish crises. *BioScience* 54(9):857-859.

Cooke S. J. and C.D. Suski. 2004. Are circle hooks an effective tool for conserving marine and freshwater recreational catch-and-release fisheries? *Aquatic Conservation: Marine and Freshwater Ecosystems* 14:1-28.

Cooke, S.J., B.L. Barthel and C.D. Suski. 2003a. Effects of hook type on injury and capture efficiency of rock bass, *Ambloplites rupestris*, angled in south-eastern Ontario. *Fisheries Management and Ecology* 10:269-271.

Cooke, S.J., C.D. Suski, B.L. Barthel, K.G. Ostrand, B.L. Tufts and D P. Philipp. 2003b. Injury and mortality induced by four hook types on bluegill and pumpkinseed. *North American Journal of Fisheries Management* 23:883-893.

Cooke, S.J., C.D. Suski, M.J. Siepker and K.G. Ostrand. 2003c. Injury rates, hooking efficiency and mortality potential of largemouth bass (*Micropterus salmoides*) captured on circle hooks and octopus hooks. *Fisheries Review* 61:135-144.

Davis, M.W. and B.L. Olla. 2001. Stress and delayed mortality induced in Pacific halibut by exposure to hooking, net towing, elevated seawater temperature and air: implications for management of bycatch. *North American Journal of Fisheries Management* 21:725-732.

Dextrase, A.J. and H.E. Ball. 1991. Hooking mortality of lake trout angled through the ice. *North American Journal of Fisheries Management* 11:477-479.

Diggles, B.K. and I. Ernst. 1997. Hooking mortality of two species of shallow-water reef fish caught by recreational angling methods. *Marine Freshwater Research* 48:479-483.

Doi, T., T. Nakamura, M. Yokota, T. Maruyama, S. Watanabe, H. Noguchi, Y. Sano and T. Fujita. 2004. Hooking mortality and growth of caught and released Japanese charr *Salvelinus leucomaenis* and masu salmon *Oncorhynchus masou masou* in experiment ponds. *Nippon Suisan Gakkaishi* 70(5):706-713.

Dubois, R.B., T.L. Margenau, R.S. Stewart, P.K. Cunningham and P.W. Rasmussen. 1994. Hooking mortality of northern pike angled through ice. *North American Journal of Fisheries Management* 14:769-775.

Eberhardt, L.L. and J.M. Thomas. 1991. Designing environmental field studies. *Ecological Monographs* 6(1):53-73.

Falterman, B. and J.E. Graves. 2002. A Preliminary Comparison of the Relative Mortality and Hooking Efficiency of Circle and Straight Shank ("J") Hooks Used in the Pelagic Longline Industry. p. 80-87. *In:* Lucy, J.A. and A.L. Studholme (eds.). *Catch and release in marine recreational fisheries.* American Fisheries Society, Symposium 30, Bethesda, Maryland.

Fänge, R. 1996. Physiology of the swim bladder. *Physiological Review*. 46:299-322.

Feathers, M.G. and A.E. Knable. 1983. Effects of depressurization upon largemouth bass. *North American Journal of Fisheries Management* 3:86-90.

Franks, J.S. 2003. First record of goliath grouper, *Epinephelus itajara*, in Mississippi coastal waters with comments on the first documented occurrence of red grouper: *Epinephelus morio*, off Mississippi. *Gulf and Caribbean Fisheries Institute* 56:295-306.

Gitschlag, G.R. and M.L. Renaud. 1994. Field experiments on survival rates of cages and released red snapper. *North American Journal of Fisheries Management* 14:131-136.

GMFC (Gulf of Mexico Fishery Management Council). 1981b. Amendment to the Reef Fish Fishery Management Plan, Gulf of Mexico Fishery Management Council, 2203 N. Lois Avenue, Suite 1100, Tampa, Florida 33607.

Goodyear, C.P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. NMFS/SEFSC Contribution MIA-95/96-05. 171 p.

Gulf of Mexico Fishery Management Council Reef Fish Stock Assessment Panel. 2002. September, 2002 Report of the Reef Fish Stock Assessment Panel. A report of the September 17-19, 2002 meeting. Available from the Gulf of Mexico Fishery Management Council, 301 North, Suite 1000, Tampa, Florida 33619.

Hernandez, P. and P.J. Motta. 1997. Trophic consequences of differential performance: ontogeny of oral jaw-crushing performance in the sheepshead, *Archosargus probatocephalus* (Teleostei, Sparidae). *Journal of Zoology* (London) 243:737-756.

Huber, D.R., Eason, T.G., Hueter, R.E., and P.J. Motta. 2005. Analysis of bite force and mechanical design of the feeding mechanism of the durophagous shark *Heterodontus francisci*. *Journal of Experimental Biology* 208:3553-3571.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54(2):187-211.

Jarvis, E.T. and C.G. Lowe. 2008. The effects of barotrauma on the catch-and-release survival of southern California nearshore and shelf rockfish (Scorpaenidae, *Sebastes* spp.). *Canadian Journal of Fisheries and Aquatic Science* 65:1286-1296.

Jones, F.R.H. and N.B. Marshall. 1953. The structure and functions of the teleostean swimbladder. *Biological Bulletin* 28:16-83.

Julliard, R., N.C. Stenseth, J. Gjøsæter, K. Lekve, J. Fromentin and D.S. Danielssen. 2001. Natural mortality and fishing mortality in a coastal cod and population: a release-recapture experiment. *Ecological Applications* 11(2):540-558.

Koenig, C. 2001. Preliminary results of depth-related capture-release mortality of dominant reef fish in the eastern Gulf of Mexico. Special report to the Gulf of Mexico Fishery Management Council.

Kwak, T.J. and M.G. Henry. 1995. Largemouth bass mortality and related causal factors during live-release fishing tournaments on a large Minnesota lake. *North American Journal of Fisheries Management* 15:621-630.

Lee, W.C. and E.P. Bergersen. 1996. Influence of thermal and oxygen stratification on lake trout hooking mortality. *North American Journal of Fisheries Management* 16:175-181.

Lindsay, R.B., R.K. Schroeder and K.R. Kenaston. 2004. Hooking mortality by anatomical location and its use in estimating mortality of spring Chinook salmon caught and released in a river sport fishery. *North American Journal of Fisheries Management* 24:367-378.

Loftus, A.J. 1991. Puncturing air bladders: successful release method? SFI Bulletin No. 426 p. 3.

Lucy, J.A. and M.D. Arendt. 2002. Short-Term Hook Release Mortality in Chesapeake Bay's Recreational Tautog Fishery. p. 114-117. *In:* Lucy, J.A. and A.L. Studholme (eds.). *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 30, Bethesda, Maryland.

Lukacovic, R. and J.H. Uphoff. 2002. Hook location, fish size, and season as factors influencing catch-and-release mortality of striped bass caught with bait in Chesapeake Bay. p. 97-100. *In*: Lucy, J.A. and A. L. Studholme (eds.) *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 30, Maryland.

Machlis, L., P.W.D. Dodd and J.C. Fentress. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. *Zeitschrift für Tierpsycologie* 68:201-214.

Malchoff, M.H. and S.W. Heins. 1997. Short-term hooking mortality of weakfish caught on single-barb hooks. *North American Journal of Fisheries Management* 17:477-481.

Malchoff, M.H., J. Gearhart, J. Lucy and P.J. Sullivan. 2002. The Influence of Hook Type, Hook Wound Location, and Other Variables Associated with Post Catch-and-Release Mortality in the U.S. Summer Flounder Recreational Fishery. p. 101-105. *In:* Lucy, J.A. and A.L. Studholme (eds.). *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 30, Bethesda, Maryland.

Manooch, III, C.S. 1977. Foods of the red porgy, *Pagrus pagrus* Linnaeus (Pisces: Sparidae), from North Carolina and South Carolina. *Bulletin of Marine Science* 27(4):776-787.

Marshall, N.B. 1970. 'Poissons sans poids'. *The Life of Fishes*. Universe Books. New York. p. 67-80.

Meester, G.A., A. Mehrotra, J.S. Ault and E.K. Baker. 2004. Designing marine reserves for fishery management. *Management Science* 50(8):1031-1043.

Meester, G.A., J.S. Ault, S.G. Smith and A. Mehrotra. 2001. An integrated simulation modeling and operations research approach to spatial management decision making. *Sarsia* 86(6):543-558.

Millard, M.J., S.A. Welsh, J.W. Fletcher, J. Mohler, A. Kahnle and K. Hattala. 2003. Mortality associated with catch and release of striped bass in the Hudson River. *Fisheries Management and Ecology* 10:295-300.

Mitsuyasu, M. and D. Fluharty. 2004. Ecosystem planning. p. 184-189. *In*: Witherell, D. (ed.). *Managing our nation's fisheries: past, present and future.* Proceedings of a conference on fisheries management in the United States held in Washington, D.C., November 2003. 254 p.

Motta, P.J. 1984. Mechanics and functions of jaw protrusion in teleost fishes: a review. *Copiea* 1984(1):1-17.

Mullaney, Jr., M.D. and L.D. Gale. 1966. Ecomorphological relationships in ontogeny: anatomy and diet in gag, *Mycteroperca microlepis* (Pisces: Serranidae). *Copeia* 1:167-180.

Murphy, M.D., R.F. Heagey, V.H. Neugebauer, M.D. Gordon and J.L. Hintz. 1995. Mortality of spotted seatrout released from gill-net or hook-and-line gear in Florida. *North American Journal of Fisheries Management* 15:748-753.

National Marine Fisheries Service. 2002. Status of red grouper in United States waters of the Gulf of Mexico during 1986-2001. Sustainable Fisheries Division Contribution

SFD-01/02-175, Southeast Fisheries Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 33149.

Neal, J.W. and D. Lopez-Clayton. 2001. Mortality of largemouth bass during catch-and-release tournaments in a Puerto Rico reservoir. *North American Journal of Fisheries Management* 21:834-842.

Nelson, K.L. 1998. Catch-and-release mortality of striped bass in the Roanoke River, North Carolina. *North American Journal of Fisheries Management* 18:25-30.

Overton, A.S. and J. Zabawski. 2003. Release mortality of Undersized Fish from the Snapper/Grouper Complex odd the North Carolina Coast. Final Report to North Carolina Sea Grant Fisheries Resources Grant Program 03-FEG-21 18 p.

Pelster, B. 1997. Buoyancy. p. 25-42. *In:* Evans, D. (ed.) *The Physiology of Fishes 2nd edition*. CRC Press.

Pew Oceans Commission. 2003. America's living oceans – charting a course for sea change. Available at http://www.pewtrusts.org/pdf/env_pew_oceans_final_report.pdf

Porch, C.E. 1998. Estimating Atlantic bluefin tuna mortality from the release and recapture dates of recovered tags. International Commission for the Conservation of Atlantic Tunas, Collected Volume of Scientific Papers, SCRS/98/65, Miami, Florida.

Porter, H.T. and P.J. Motta. 2004. A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Marine Biology* 145:989-1000.

Prince, E.D., M. Ortiz, and A. Venizelos. 2002. A Comparison of Circle Hook and "J" Hook Performance in Recreational Catch-and-Release Fisheries for Billfish. p. 66-79. *In:* Lucy, J.A. and A.L. Studholme (eds.) *Catch and Release in Marine Recreational Fisheries*. American Fisheries Society, Symposium 30, Bethesda, Maryland.

Queensland, Facility Management Association (FMA), Australia. 1989. Maximizing survival rates of released fish, how to release fish with inflated air bladders.

Randall, J.E. and B.P. Bishop. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* (Miami). 5:665-847.

Render, J.H. and C.A. Wilson. 1994. Hook-and-line mortality of caught and release red snapper around oil and gas platform structural habitat. *Bulletin of Marine Science* 55:1106-1111.

Render, J.H. and C.A. Wilson. 1996. The effect of gas bladder deflation on mortality of hook-and-line caught and released red snappers: implications for management. p.244-253. *In:* Arreguin-Sanchez, F., J.L. Munro, M.C. Balgos and D. Pauly (eds.) *Biology and culture of tropical groupers and snappers.* International Center for Living, Aquatic Resources Management Conference Proceedings 48, Makati City, Philippines.

Rogers, B.L., C.G. Lowe, E. Fernández-Juricic and L.R. Frank. 2008. Utilizing magnetic resonance imaging (MRI) to assess the effects of angling-induced barotraumas on rockfish (Sebastes). *Canadian Journal of Aquatic Science* 65:1245-1249.

Rummer, J.L. and W.A. Bennett. 2005. Physiological effects of swim bladder overexpansion and catastrophic decompression on red snapper. *Transactions of the American Fisheries Society* 134:1457-1470.

Rummer, J.L. 2007. Factors affecting catch-and-release (CAR) mortality in fish: insight into CAR mortality in red snapper and the influence of catastrophic decompression. p. 123-144. *In*: Patterson, W.F., III, J.H. Cowan, Jr., G.R. Fitzhugh, and D.L. Nieland, (eds.). *Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico*. American Fisheries Society, Symposium 60, Bethesda, Maryland.

Schirripa, M.J. and K.M. Burns. 1998. Growth estimates for three species of reef fish species in the eastern Gulf of Mexico. *Bulletin of Marine Science* 61:581-591.

Schirripa, M.J,, K. Burns and J.A. Bohnsack. 1993. Reef fish release survival based on tag and recovery data. SEFC, Miami Laboratory, Contribution No. MIA 92/93, 34 p.

Schisler, G.J. and E.P. Bergersen. 1996. Postrelease hooking mortality of rainbow trout caught on scented artificial baits. *North American Journal of Fisheries Management* 16:570-578.

SEDAR 7. 2004. Red snapper data workshop report. SEDAR. New Orleans, Louisiana. 88 p.

SEDAR 12. 2006. Stock assessment report of Gulf of Mexico red grouper. Stock Assessment Report 1 SEDAR. St. Petersburg, Florida. 64 p.

Shasteen, S.P. and R.J. Sheehan. 1997. Laboratory evaluation of artificial swim bladder deflation in largemouth bass: potential benefits for catch-and-release fisheries. *North American Journal of Fisheries Management* 17:32-37.

Skomal, G.B., B.C. Chase and E.D. Prince. 2002. A Comparison of Circle Hook and Straight Hook Performance in Recreational Fisheries for Juvenile Atlantic Bluefin

Tuna. 2002. p. 57-65. *In:* Lucy, J.A. and A.L. Studholme (eds.). *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 30, Bethesda, Maryland.

Sobel, J. and C. Dahlgren. 2004. Marine Reserves A Guide to Science, Design, and Use. Island Press. 1718 Connecticut Ave., Suite 300, NW, Washington, D.C. 383 p.

Systat Software Inc. 2004. Sigmaplot version8.02a. Richmond, California.

Tagart, J. 2004. Policy perspectives on bycatch. p. 196-201. *In*: Witherell, D. (ed.) *Managing Our nation's Fisheries: Past, Present and Future.* Proceedings of a conference on fisheries management in the United States held in Washington, D.C., November 2003. 254 p.

Taylor, M.J. and K.R. White. 1992. A meta-analysis of hooking mortality of nonanadromous trout. *North American Journal of Fisheries Management* 12:760-767.

Theberge, S. and S. Parker. 2005. Release methods for rockfish. Oregon Sea Grant, Corvallis, Oregon, No. ORESU-G-05-001.

Tomasso, A.O., J.J. Isely and J.R. Tomasso. 1996. Physiological responses and mortality of striped bass angled in freshwater. *Transactions of the American Fisheries Society* 125:321-325.

Trumble, R.J. and S.M. Kaimmer, and G.H. Williams. 2002. Review of the Methods Used to Estimate, Reduce, and Manage Bycatch Mortality of Pacific Halibut in the Commercial Longline Groundfish Fisheries of the Northeast Pacific. p. 88-96 *In:* Lucy, J.A. and A.L. Studholme (eds.). *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 30, Bethesda, Maryland.

U.S. Commission on Ocean Policy. (2004). An Ocean Blueprint for the 21st Century. Final Report. U.S. Commission on Ocean Policy, Washington, D.C. 676 p. Available at http://www.oceancommission.gov/documents/full_color_rpt/welcome.html.

Wainwright, P.C. 1991. Ecomorphology: experimental functional anatomy for ecological problems. *American Zoologist* 31(4):680-693.

Wainwright, P.C. and B.A. Richards. 1995. Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fish* 44:97-113.

Wainwright, P.C., L.A. Ferry-Graham, L.A., T.B. Waltzek, A.M. Carroll, C.D. Hulsey, and J.R. Grubich. 2001. Evaluating the use of ram and suction during prey capture by cichlid fishes. *Journal of Experimental Biology* 204(Pt 17):3039-3051.

Ward-Campbell, B.M.S. and F.W.H. Beamish. 2005. Ontogenetic changes in morphology and diet in the snakehead, *Channa limbata*, a predatory fish in western Thailand. *Environmental Biology of Fishes* 72:251-257.

Weaver, D.C. 1996. Feeding ecology and ecomorphology of three sea basses (Pisces: Serranidae) in the Gulf of Mexico. Master's Thesis. University of Florida, Gainesville, Florida

Weaver, D.C. 2001. Feeding ecology and functional morphology of western Atlantic groupers (Serranidae: Epinephelinae). Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia. 8 p.

Westneat, M.W. 1995. Phylogenetic systematics and biomechanics in ecomorphology. *Environmental Biology of Fishes* 44:263-283.

Westneat, M.W. 2003. A biomechanical model for analysis of muscle force, power output and lower jaw motion in fishes. *Journal of Theoretical Biology* 223:269-281.

Westneat, M.W., M.E. Alfaro, P.C. Wainwright, D.R. Bellwood, J.R. Grubich, J.L. Fessler, K.D. Clements and L.L. Smith. 2005. Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proceedings of the Royal Society B* 272:993-1000.

Wilde, G.R., M.I. Muoneke, P.W. Bettoli, K.L. Nelson and B.T. Hysmith. 2000. Bait and temperature effects on striped bass mortality in freshwater. *North American Journal of Fisheries Management* 20:810-815.

Wilde, G.R. 2009. Does venting promote survival of released fish? *Fisheries* 34(1):20-28.

Wilson, R. 1993. An *in –situ* study of the survivorship of the undersized bycatch in the red grouper fishery. MARFIN grant # NA17FF0387-01. 39 p.

Wilson, R.R. and K.M. Burns. 1996. Potential survival of released groupers caught deeper than 40 m based on shipboard and *in situ* observations, and tag-recapture data. *Bulletin of Marine Science* 5(1):234-247.

Witherell, D. editor. 2004. Managing our nation's fisheries: past, present and future. Proceedings of a conference on fisheries management in the United States held in Washington, D.C., November 2003. 254 p.

Wood, C.M., D.T. Turner and M.S. Graham. 1983. Why do fish die after severe exercise? *Journal of Fishery Biology* 22:189-201.

Zar, J.H. 1999. *Biostatistical Analysis*. 4th edition. Prentice Hall, New Jersey.

Zimmerman, S.R. and E.A. Bochenek. 2002. Evaluation of the Effectiveness of Circle Hooks in New Jersey's Recreational Summer Flounder Fishery. p. 106-109. *In:* Lucy, J.A. and A.L. Studholme (eds.). *Catch and Release in Marine Recreational Fisheries.* American Fisheries Society, Symposium 30, Bethesda, Maryland.