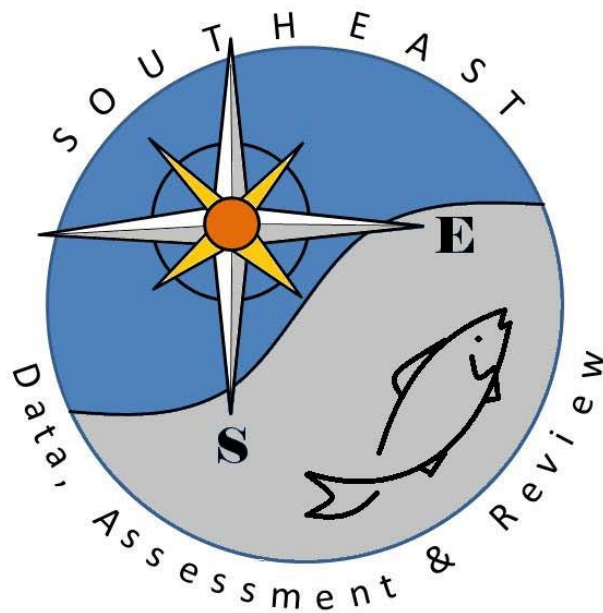# Survival of Red Grouper (*Epinephalus morio*) and Red Snapper (*Lutjanus campechanus*) Caught on J-Hooks and Circle Hooks in the Florida Recreational and Recreational-for-Hire Fisheries

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SURVIVAL OF RED GROUPER (*EPINEPHALUS MORIO*) AND RED SNAPPER (*LUTJANUS CAMPECHANUS*) CAUGHT ON J-HOOKS AND CIRCLE HOOKS IN THE FLORIDA RECREATIONAL AND RECREATIONAL-FOR-HIRE FISHERIES

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ABSTRACT

We documented survival of released sublegal red grouper, *Epinephalus morio* (Valenciennes, 1828), and red snapper, *Lutjanus campechanus* (Poey, 1868), caught on circle and J-hooks by recreational anglers in Florida waters. Immediate hook mortality was 20.0% for red grouper and 49.1% for red snapper. Delayed (5 d) hook mortality from blood loss of J-hook nicked internal organs differed between red grouper (7%) and red snapper (29%). Delayed mortality from starvation was observed for five emaciated red snapper with severed esophagi from prior hook injuries. Different survival rates were correlated with feeding behavior, jaw morphology, and prey residence time. Mean (±SD) prey residence time in the mouth was significantly longer for red grouper (6.62 ± 0.42 s) than red snapper (3.73 ± 0.29 s) possibly resulting in more red grouper being mouth hooked than red snapper, which were more likely to swallow bait and become gut hooked. Jaw morphology and feeding behavior may predict release survival for other species. Tag recapture rates used as a surrogate for survival were significantly higher for tagged red grouper initially caught on circle hooks (14.0%, *n* = 121 recaptures; 863 tagged) than on J-hooks (7.3%, *n* = 287 recaptures; 3935 tagged). Conversely, recapture rates were significantly higher for red snapper initially caught on J-hooks (12.5%, *n* = 269 recaptures; 2145 tagged) than circle hooks (8.1%, *n* = 258 recaptures; 3172 tagged). Mandatory regulations implementing the use of circle hooks when targeting all reef fish species may not provide the intended conservation benefits.

Red grouper, *Epinephelus morio* (Valenciennes, 1828), and red snapper, *Lutjanus campechanus* (Poey, 1868), support important commercial and recreational fisheries in the Gulf of Mexico and along the southeast US coast. In 2009, combined commercial and recreational landings of red grouper in the Gulf of Mexico were >2,267,000 kg, while combined landings for red snapper were >3,175,000 kg, (N Farmer, NMFS–SERO, pers comm). Increased numbers of both species are being caught and released in both the commercial and recreational fisheries and estimating survival of released fish is difficult, but essential, for accurate stock assessments. Commercial discards in 2008 were reported to be 741,021 individuals in the red grouper fishery and 884,629 in the red snapper fishery. In the recreational-for-hire sectors 3,092,028 live red grouper and 132,534 dead discards were reported for 2008. For red snapper 2,220,910 live red snapper and 828,373 dead discards were reported for 2008 (SEDAR–12 2009, SEDAR–7 2009).

Minimum size rules have required more releases of recreational and commercial undersized fishes in the United States (Cooke and Cowx 2004, Bartholomew and Bohnsack 2005). Coleman et al. (2004) found recreational fishing contributed significantly to mortality in various marine fisheries, including red snapper. Although

numerous factors can affect post-release mortality (Gitschlag and Renaud 1994, Lee and Bergersen 1996, Davis and Olla 2001, Lucy and Arendt 2002), hook trauma is a primary cause (Render and Wilson 1994, Bartholomew and Bohnsack 2005). Identifying mechanisms contributing to hook mortality and possible ways to circumvent them represents a potentially valuable contribution to fisheries management.

The present study examines acute and latent J-hook mortality for red grouper and red snapper to assess if differences in hook mortality were due to differences in jaw size, morphology, and feeding behavior. For each species, jaw lever ratios were determined and feeding behavior was analyzed. The relationship of fish dentition, jaw morphology, and feeding behavior to diet has been well established (Mullaney and Gale 1966, Motta 1984, Wainwright 1991, Hernandez and Motta 1997, Porter and Motta 2004). Fish feeding behavior was filmed in the laboratory to determine feeding type and relate feeding behavior to jaw morphology.

Due to a perception that circle hooks are beneficial for all fish species, they have become popular in recreational and recreational-for-hire fisheries. Circle hooks have been promoted as an effective means of reducing mortality for released hook-and-line caught fish. However, fish survival varies among species (Cooke and Suski 2004). Studies have shown reduced mortality for some species (Falterman and Graves 2002, Prince et al. 2002, Skomal et al. 2002), minimal or no benefit for other species (Malchoff et al. 2002, Zimmerman and Bochenek 2002, Cooke et al. 2003a,b), and severe injury to others (Cooke et al. 2003c). A comparison between hook types (J and circle) was conducted to determine if circle hooks have potential as a tool to reduce the trauma described in the species comparisons.

Methods

Acute Mortality.—Potential causes of acute (i.e., immediate) mortality were assigned to moribund fishes that died during or just after being caught from depths ranging 10–43 m during 1999 and 2003. Twenty moribund red grouper and 171 red snapper caught on J-hooks during J-hook-and-line fishing trips aboard headboats fishing off Sarasota, Panama City, Daytona, and St. Augustine, Florida, were placed in ice slurries and transported to the laboratory for necropsy.

In the laboratory, fish eyes, fins, gills, heart, liver, spleen, swim bladder, stomach, urinary bladder, and skin were examined for gross trauma and anomalies. Organ position within the body cavity was noted as well as any gross distortion or discoloration of organ tissues, ruptures or tears in tissues, presence of gas bubbles, and hemorrhaging. Trauma and any anomalies encountered were noted and documented using a digital still-camera. Based on necropsy findings, mortality was attributed to one of three categories: hook injury, barotrauma, or "other" causes. The "other" category included mortality presumably caused by high temperature, improper venting, or generalized stress.

Latent Mortality–Direct Observations.—In total, 46 live red grouper and 241 live red snapper collected during fishing trips were transported to the laboratory, held 1 mo for observation, and treated for parasites. Fishes were maintained in 3406-L tanks with a recirculating filtration system that included mechanical (filter floss), chemical (carbon), biological (fluidized bed), and ultraviolet (light) components. Water quality was monitored daily to ensure 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. Fishes were fed until sated twice daily on a diet that consisted of live shrimp and cut squid and/or fish. Water quality, quantity of food consumed, fish condition, and any tank treatments such as partial water changes were recorded in a daily log.

Dentition and Jaw Lever Ratios.—Comparisons were made of red grouper and red snapper jaw type, size, shape, and dentition. Because jaw morphology can change with ontogeny, carcasses of adult red grouper [542–691 mm fork length (FL)] and red snapper (510–870 mm FL) were obtained from commercial fish houses and used to examine dentition and jaw morphology. Measurements were used to mathematically describe the main physical mechanism involved in feeding behavior. Measurements of mouth gape, jaw processing (flesh removal), and tooth counts were made following Weaver (2001). Closing and opening jaw lever ratios were calculated following Wainwright and Richards (1995). Care was taken to ensure consistent measurements were taken at the same location for each fish.

Feeding Behavior.—Feeding behavior of two groups (355–406 mm FL) of healthy red grouper (eight fish per group) and red snapper (15 fish per group), acclimatized in the laboratory for 1 mo, were filmed in separate 3406-L tanks to determine feeding type and relate feeding behavior to jaw morphology. Fishes were maintained and observed in groups because experience indicated that captive red snapper remained healthier and acted normally when multiple fish were kept together. Numbers imprinted on fish tags were too small to be read on video recordings, so individual fish could not always be identified during the trials. However, an attempt was made to prevent reexamination of animals based on individual characteristics, such as differences in fish size, color, and other physical characteristics. For consistency, 36 large (approximately 10 cm) brown shrimp, *Farfantepenaeus aztecus* (Ives, 1891), were offered as food during each trial. Fishes were fed prior to the trials to reduce aggression during observations. To provide an opportunity to observe feeding by the other fish, dominant red grouper were segregated from less dominant individuals after they had fed. Only 14 of the 57 red grouper and 25 of 56 red snapper feeding sequences were complete and retained for analysis because fishes either swam out of the field of view before swallowing or other fish obstructed the view.

Two cement blocks positioned perpendicular to each other were left overnight in tanks where the cameras were to be stationed. The next day, after fish had habituated to the presence of the cement blocks, the blocks were removed and replaced with a SeaViewer Sea Drop® model 650 color video camera (lateral orientation) and a Sony VX2000® camera in an Amphibico® housing (head on orientation). Both cameras recorded concurrently in color in mini DVD format. The video feed was viewed remotely on a laptop computer positioned away from the tanks. To keep action within the cameras' fields of view, a live shrimp was tethered with either 4-lb breaking strength monofilament fishing line or a rubber band to a 1.8 kg diving weight placed at the intersect point of the recording fields of the two submerged cameras. DVDs of the feeding videos at normal, 50%, and 37.5% speed were made using Turtle Beach Video Advantage® PCI model 1500-1 multi-media video capture software.

Observation objectives were to determine feeding behavior type (ram feeding, suction, biting with oral manipulation, etc.) and determine the length of time prey was retained in the predator's oral cavity before swallowing, but not to measure strike and prey capture kinematics. Prey residence time was determined by counting the number of frames s^{-1} (based on a standard of 29 frames s^{-1}) from initial prey capture to confirmed swallow while viewing the original videotape with Adobe Premiere Pro 2.0® software. Prey processing times were compared using a *t*-test.

Fish Tagging.—Red grouper (1990–2007) and red snapper (1999–2007) were caught using hook-and-line and tagged by Mote Marine Laboratory (MML) staff, student interns, and volunteers, as well as by charter boat and headboat captains and crew, and private recreational fishers throughout the eastern Gulf of Mexico and off the southeastern Florida coast (Fig. 1). Tags, tagging kits, and instructions were provided by MML. Instructions provided were to insert the single-barbed, Hallprint® plastic dart tags at a 45° angle next to the anterior portion of the dorsal fin by inserting the barb between pterygiophores. Large (13.5 cm) tags were used on fish measuring ≥304 mm FL and small tags on fish <304 mm FL. Data recorded included: tagging date, gear, tag number, time of day, bait used, water depth, FL in inches, fish condition
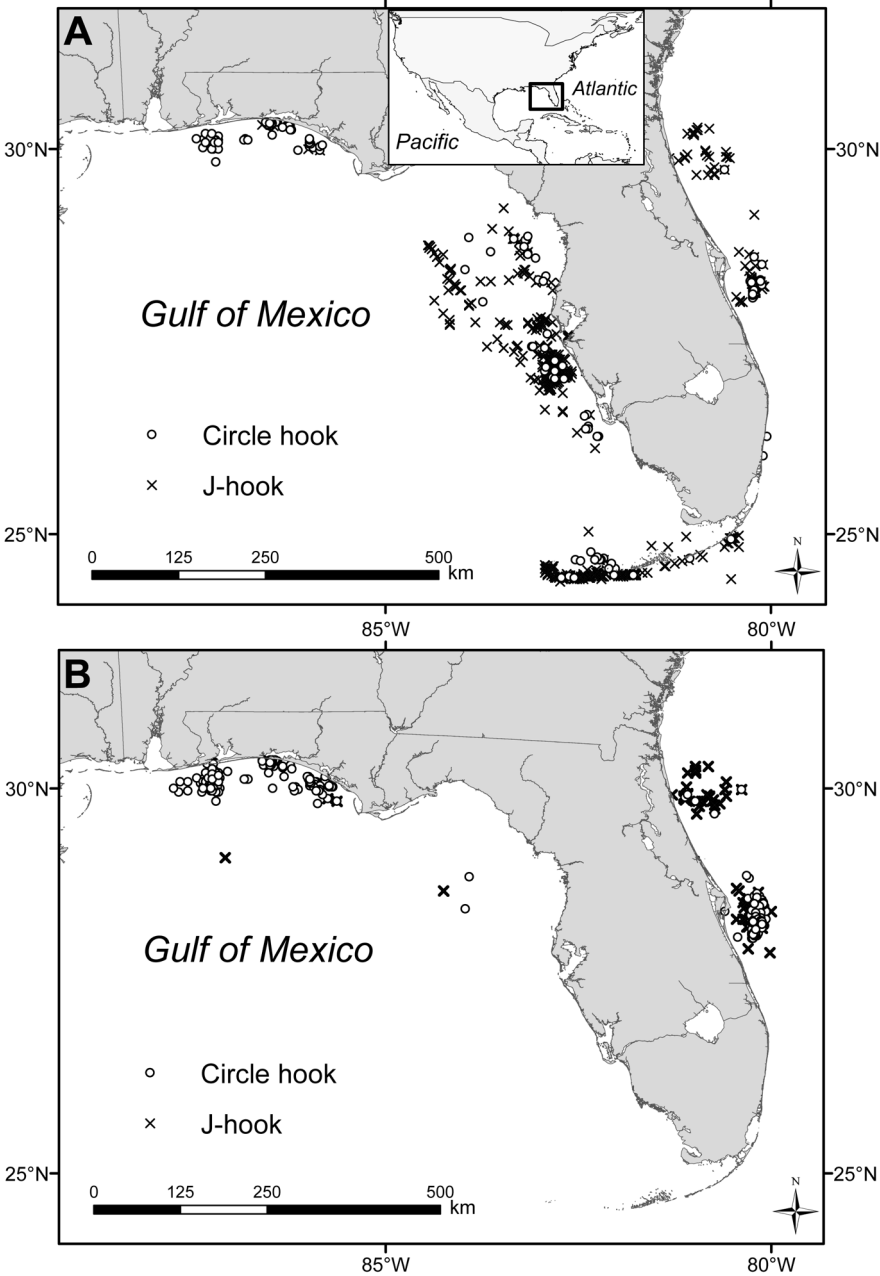
Figure 1. Tag and release sites for (A) red grouper (*Epinephalus morio*) and (B) red snapper *(Lutjanus campechanus).* Circles correspond to fishes caught on circle hooks. Crosses correspond to fishes caught on J-hooks.

upon release, time the fish was out of the water, whether or not fish was vented, and the capture location to the nearest minute of latitude and longitude.

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 caudally through the body wall 2.5–5.1 cm posterior to the tip of the pectoral fin of the bloated fish and held in place until most of the expanded swim bladder gases were released from the fish's body cavity.

Tags included the tag number and a toll free, dedicated telephone number at MML. The telephone was answered personally during work hours and an answering machine recorded tag return information on weekends, holidays, and evenings. 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 into a Paradox® database and were proofed by a second individual against the original data sheet. A tag lottery was held at the end of each year. Both the tagger and the person who returned the tag each received US$100.

Recaptures of red grouper and red snapper initially caught on circle hooks and J-hooks were compared to test the hypothesis of no difference in recaptures by hook type. Volunteer taggers from the private and recreational-for-hire sectors were provided with 4/0 zero-offset circle hooks (Eagleclaw®) and supplied their own J-hooks. There was no attempt to standardize J-hook size. 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 tag equal numbers of fish by J-hooks or circle hooks, but was only successful for red snapper. Within a species, relative recapture rate by hook type was considered a proxy for relative survival. A log-likelihood G test was used to test for differences between recapture rates for fishes caught on J-hooks and circle hooks.

Results and Discussion

Acute Mortality.—All immediate hooking mortalities for the 20 red grouper (9.6% of all captures) and 171 red snapper (13.6% of all captures) examined suggested severe blood loss at the time of capture. Hook injuries included lacerations to internal viscera, gills, and the esophagus. In severe cases, organs were destroyed. The specific injury site was associated with hook orientation when swallowed. Upward oriented hooks punctured or lacerated the liver. Hooks oriented downward typically 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). Depth-related barotrauma injuries included severe exophthalmia, visible gas bubbles in the gills, viscera, and blood vessels. Another key sign of barotrauma was stomach prolapse and extrusion through the oral cavity caused by the expansion of swim bladder gases. The "other" category associated with acute mortality included generalized stress, heat, and improper venting with diving knives or ice picks that did not release swim bladder gases or unknown causes.

Damage from J-hooks was responsible for 20.0% of the acute mortality of red grouper and 49.1% for red snapper (Fig. 2). Barotrauma accounted for 13.5% of red snapper acute mortality, which increased with depth (Fig. 3). It was not readily apparent why J-hook mortality increased with depth. It may be that there was a synergistic effect with barotrauma, a longer time to land the fish allowing the hook to do more damage or some other factor. No acute mortalities were observed for red grouper that were caught at shallower depths than red snapper. Mortality was attributed to "other" factors for 80.0% of red grouper and 37.4% of red snapper.
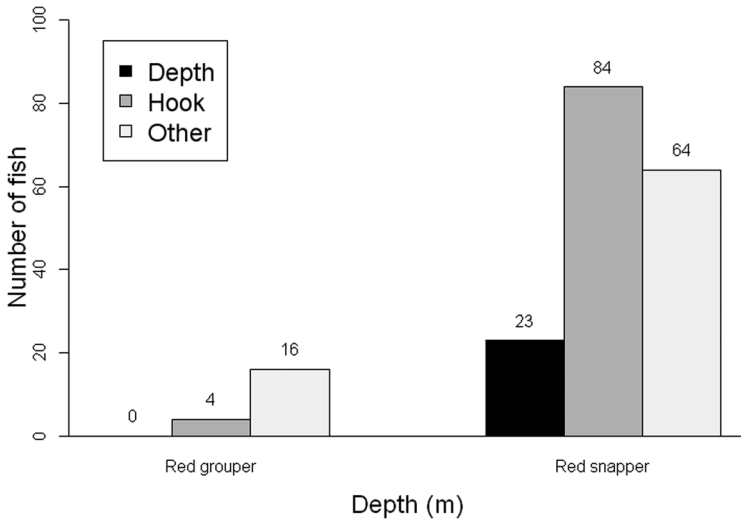
Figure 2. Comparison of number and attributed cause of acute shipboard mortalities for red grouper (*n* = 20) and red snapper (*n* = 171). Total number of fish caught during these trips was 56 red grouper and 266 red snapper. Depth includes barotrauma injuries, "hook" represents hooking injuries, and "other" included heat stress, excessive handling, improper venting, and undetermined causes.

Latent Mortality.—Delayed "latent" hook mortality was 7% for red grouper and 29% for red snapper. Only three of the 45 live sublegal (i.e., <50.8 cm) sized red grouper caught on J-hooks and transported to the laboratory died of hook injuries. Unlike the red grouper, of 241 sublegal-sized (i.e., <50.8 cm in the western North Atlantic and <40.6 cm in the Gulf of Mexico) red snapper caught on J-hooks and transported to the laboratory, 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 fish appeared healthy during transport, acted normally, and fed well the first 2 d of captivity. On the third day, they lost their bright red color and ceased feeding and swimming. Death occurred on day five. Necropsies revealed hook damage to vital organs occurred when a J-hook nicked a small area of a vital organ (usually the heart or liver) and suggested that fish slowly bled to death. Blood from the nicked organ pooled in the ventral coelom. The remaining 42 red grouper and 103 red snapper survived, grew, and thrived during captivity in the absence of hook damage.

Evidence of latent hook mortality from starvation was noted for five emaciated, pale sublegal-sized red snapper caught during fishing trips. Necropsies revealed these fish had been previously hooked and the hooks had longitudinally severed part of the esophagus resulting in the lower esophagus becoming a disconnected tube of necrotic tissue. A lack of blood, the amount of necrotic tissue, and the absence of any apparent disease indicated that these fish were starving possibly because damage to the esophagus made them incapable of swallowing food. The wounds did not appear recent; elapsed time between initial trauma and subsequent recapture was unknown.
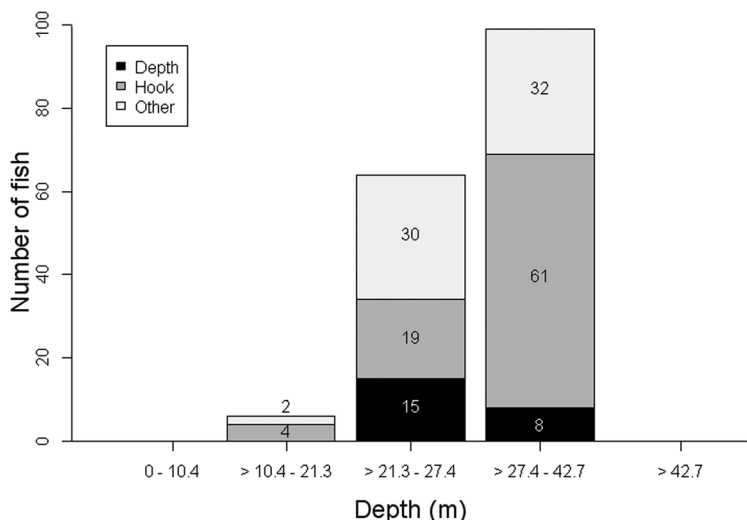
Figure 3. Attributed cause of red snapper mortality by depth. Depth includes barotrauma injuries, "hook" represents hooking injuries, and "other" included heat stress, excessive handling, improper venting, and undetermined causes.

Dentition and Jaw Lever Ratios.—Differences in dentition and jaw morphology between species reflects differences in feeding strategies and prey type (Mullaney and Gale 1966, Wainwright and Richards 1995, Hernandez and Motta 1997, Porter and Motta 2004). Red grouper had a mean of 526 small teeth in their upper jaw and 201 in their lower jaw arranged in rows on the dentary and premaxilla (Fig. 4). Larger canine teeth were located on the frontal margin of the upper and lower pre-maxilla. Some teeth were caudally rotated to facilitate grasping and holding prey during initial prey capture and preventing prey escape before swallowing. The oral jaw is used for initial prey capture and pharyngeal jaw processes prey, which are swallowed whole (N Parnell, Georgia Tech, pers comm).

Red snapper have larger teeth in both jaws and fewer fixed teeth in the lower jaw. This dental arrangement is indicative of a predator that feeds on soft-bodied prey like fish and squid (Weaver 2001). Red snapper had a mean of 616 teeth in the upper and 93 in the lower jaw. Large canine teeth are present in the upper jaw, but absent in the lower jaw. Red snapper also had fewer teeth and greater space between teeth in the bottom jaw than red grouper (Fig. 4).

Red grouper had a larger gape than red snapper of similar length. The rear margin of the red grouper dentary was extended because of the increased height of the ascending process and the extension of the posterioventral region creating a wide mandible compared to red snapper which have a shorter and narrower ascending process. The different jaw shapes are a major factor in determining biomechanical jaw functioning and feeding behavior (Wainwright and Richards 1995, Westneat 1995, 2003, Huber et al. 2005, Westneat et al. 2005). Lower jaw depression begins the buccal expansion responsible for prey capture. Jaw lever ratios were 0.17 closing/0.24
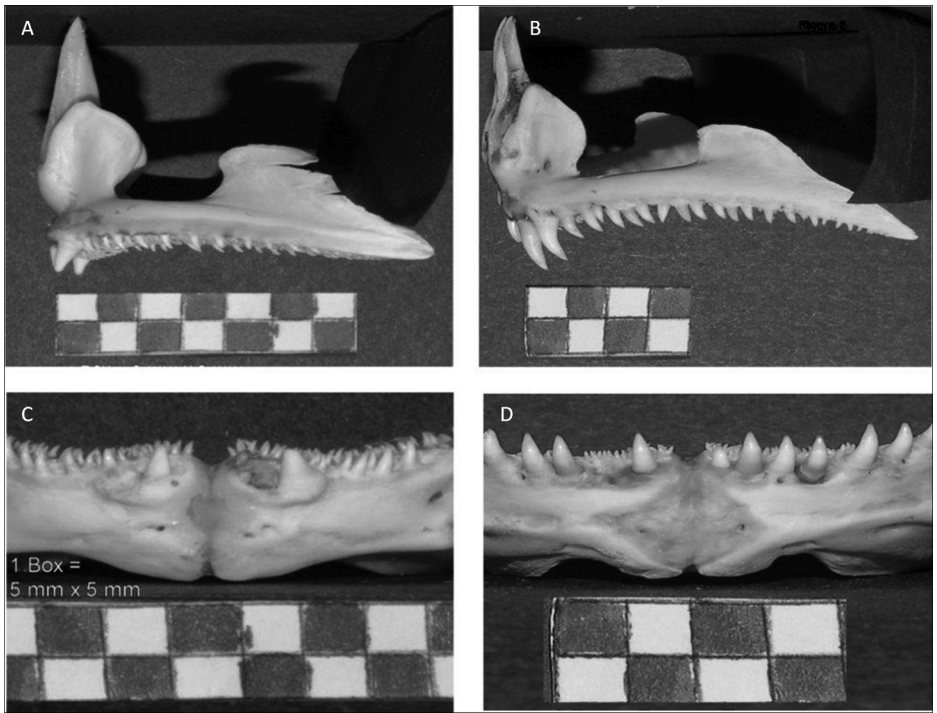
Figure 4. Comparisons of upper (A, B) and lower (C, D) jaw dentition for red grouper (A, C) and red snapper (B, D). Each square is 5 × 5 mm.

opening for red grouper and 0.32 closing/0.22 opening for red snapper, which indicated distinctly different feeding types: red grouper are suction feeders and red snapper are biters. The high lever closing ratio translates into decreased velocity of jaw opening but increased jaw strength while a high lever opening ratio for red grouper represents increased velocity (Wainwright and Richards 1995). Suction feeders draw prey into their mouths by creating negative hydraulic pressure produced by buccal cavity expansion and the simultaneous expulsion of water through the opercula, which requires substantial jaw strength (Wainwright and Richards 1995, Westneat 1995). The red snapper jaw lever ratio provides greater biting force, which allows deep penetration of the large sharp canines in the upper jaw to grip, immobilize, and slash prey. Also, fewer teeth spaced apart in the lower jaw enhances tooth penetration into soft bodied prey (Weaver 2001).

Adult red grouper feed on many species of fishes and octopods, as well as a variety of crustaceans (GMFMC 1981). Weaver (1996) found that crustaceans dominate the diet of juvenile red grouper, while the adult diet consist of 50% fishes and 50% crustaceans. The red snapper diet differs markedly. Shrimp are the most common prey of juvenile red snapper. After age one they become more piscivorous and usually feed on fish and squid (GMFMC 1981). 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 (KMB, pers obs), which is consistent with the use of canine teeth for slashing and biting prey.

Figure 5. Red grouper exhibiting suction feeding behavior. Note full buccal extension as the entire shrimp is drawn into the fish's mouth.

Feeding Behavior.—Both red grouper and red snapper are aggressive feeders, but video recordings revealed marked dissimilarities in feeding behavior including differences in the manner in which prey was approached, captured, and consumed. Red grouper exhibited hierarchal feeding when prey were introduced into their tank, in which the dominant (lighter-colored) fish fed first and often guarded prey, preventing other red grouper from feeding. In contrast red snapper formed a tight school and hesitated to approach prey until one fish began to approach, at which point all fish swam toward the prey.

Video analyses revealed that red grouper were ambush suction feeders. They approached and examined prey, and then drew it in by suction through the expansion of their large buccal cavity (Fig. 5). Prey were orally manipulated (mouthed) and swallowed whole. 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 never tried to remove prey from another grouper's mouth. At times, tethered shrimp were expelled from the grouper's mouth because its teeth did not sever the monofilament tether. In these instances, expelled shrimp were observed to be alive, apparently unharmed, and if not for the tether, capable of escape, suggesting oral teeth were not involved in processing prey. Expelled shrimp were recaptured either by the original fish or by a nearby fish, especially if it was of higher dominance.

In contrast, red snapper approached prey via high velocity lunges with open mouths and bit the prey using their canine teeth to sever the monofilament tether and often severing the shrimp into two parts (Fig. 6). Red snapper immediately swam away
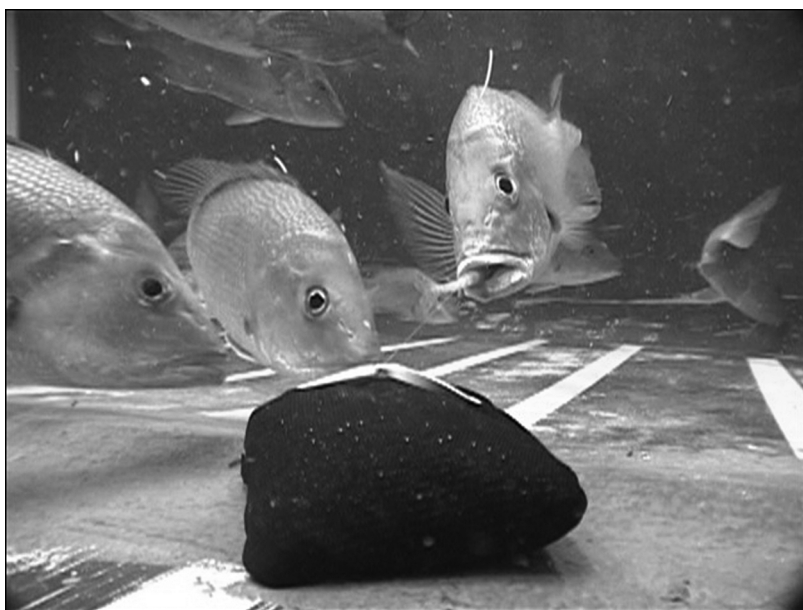
Figure 6. Red snapper exhibiting biting feeding behavior. Fish was in the process of biting a shrimp in half before swallowing.

from the prey capture site following prey acquisition. When shrimp were severed, the first snapper took part and a second immediately took what remained. Some red snapper tried to steal prey protruding from other fish's mouths. Successfully feeding fish immediately swam away to escape being challenged by other fish trying to steal prey.

The null hypothesis of no difference between species in terms of prey residence time was rejected. Mean prey residence time within a fish's mouth before swallowing was significantly faster for red snapper ($\leq$3.74 s $\pm$ 95% CI, n = 25) than red grouper ($\leq$6.62 s $\pm$ 95% CI, n = 14; t-test: P < 0.001). Data were found to be normal (P = 0.157) and variances homogenous (P = 0.489). Because fishing with J-hooks requires the angler to set the hook, the longer prey residence time in the mouth before swallowing gives anglers more time to set the hook before the bait is swallowed. The result is that red grouper are more likely to be mouth-hooked and less seriously injured than red snapper with a shorter prey residence time. Also, for red grouper, the pharyngeal jaws create the tug on the line that an angler feels when setting a J-hook. Setting the hook often jerks a hook out of the pharyngeal jaws and into the mouth or jaw where it becomes lodged.

Fish Tagging Results.—Between 1 November, 2001, and 30 September, 2007, 4798 red grouper and 5317 red snapper and were tagged and released at depths ranging $\geq$5 to $\leq$99 m. Most red grouper were caught and recaptured at depths ranging 12–21 m and 22–31 m. Red snapper captures and recaptures were more evenly spread over a broader depth range from 12.5–21.3 m to 21.6–30.5 m and from 30.8 to 61.0 m. Initial capture depths were between 21.7 and 42.7 m for most tagged red snapper compared to 10.4 and 21.3 m for red grouper. Minimum size limits during this study for red grouper were 508 mm total length (TL) in all areas and 508 mm TL for

Table 1. Number of red grouper and red snapper tagged and recaptured by hook type showing that hook differences are significant for both species since the 95% CIs do not overlap.

Species	Hook type	Tagged	Recaptured	Mean (%)	95% CI (low–high)
Red grouper	Circle	863	121	14.0	11.9–16.5
	J	3,935	287	7.3	6.5–8.1
Red snapper	Circle	3,172	258	8.1	7.2–9.1
	J	2,145	269	12.5	11.2–14.0

red snapper in the Atlantic and Florida Keys and 406 mm TL in the Gulf of Mexico. Tagged red grouper ranged in size from 146 to 889 mm FL; red snapper ranged from 152 to 686 mm FL.

The recapture rate for tagged red grouper initially caught on J-hooks was 7.3% and was significantly lower than the 14.0% recapture rate for circle hooks (G-test: $P < 0.0001$, Table 1). The opposite pattern was observed for red snapper. Recapture rates for red snapper were significantly higher on J-hooks (12.5%) than circle hooks (8.1%; G-test: $P < 0.0001$, Table 1).

In conclusion, the present study shows that differences in immediate and delayed hook mortality between red grouper and red snapper caught on J-hooks were influenced by differences in depth of capture, species feeding behavior, and jaw morphology. Although red grouper and red snapper are aggressive feeders, observations revealed differences in feeding behavior and prey residence time within the mouth that could potentially influence hooking location. Red grouper draw entire prey into their mouth and orally manipulate its orientation before swallowing it whole. The result is that red grouper are more likely to be hooked in the mouth. In contrast, red snapper usually bite and swallow pieces of prey and are more likely to ingest the bait and become gut hooked.

Results indicate that release mortality estimates based solely on visual assessment at time of capture are likely to greatly underestimate delayed mortality, which could have significant ramifications in stock assessments. The low hook mortality results observed for red grouper are consistent with Bacheler and Buckel (2004) who reported similar grouper mortality rates and noted that grouper were usually jaw hooked and experienced higher mortality from barotrauma than hook mortality. The higher recapture rates observed for red grouper caught on circle hooks also is consistent with Bacheler and Buckel (2004), who reported that gut-hooked grouper had higher mortality when captured on J-hooks than with circle hooks. For red snapper, hook trauma was a chief cause of mortality, which increased with capture depth.

The observed differences in recapture rates between red grouper and red snapper may be partially accounted for by the fact that most red snapper were caught in deeper water than red grouper. Barotrauma from depth is known to be an important mortality factor, although other factors may have contributed to this difference. Unlike grouper, red snapper mortality was significantly higher on circle hooks than J-hooks. It is possible that the 4/0 zero-offset circle hooks used in our study did not provide conservation benefits for red snapper because they were too small and could be easily swallowed. Larger circle hooks too large to swallow may have produced different results (see Patterson et al. 2012).

The present study is unique in its attempts to examine and understand the importance of feeding behavior and jaw lever rates and morphology as factors that influence release mortality and survival associated with J-hooks and circle hooks.

It indicates that observed differences in recapture rates by hook type for red grouper and red snapper may be influenced by species differences in feeding behavior, dentition, jaw lever ratios, and jaw morphology. Such differences appear to be major factors responsible for differences in hook mortality between red grouper and red snapper and could potentially be used to predict outcomes for other species.

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