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ARTICLE

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Abstract

Red Snapper *Lutjanus campechanus* are the most economically important reef fish in the Gulf of Mexico and a heavily targeted fishery. When brought to the surface from deep water, this species often suffers pressure-related injuries collectively known as barotrauma. This trauma results in high discard mortality and has affected recovery of the fishery. In laboratory experiments using hyperbaric chambers, we assessed sublethal effects of barotrauma and subsequent survival rates of Red Snapper after capture events from pressures corresponding to 30 and 60 m deep. We then evaluated the use of rapid recompression and venting to increase survival and improve recovery after release in this controlled environment. Vented fish in simulated surface release and rapid-recompression treatments had 100% survival. Fish released at the surface that were not vented had 67% survival after decompression from 30 m but only 17% survival from 60 m, while nonvented rapidly recompressed fish had 100% survival from 30 m and 83% survival from 60 m. Fish that were vented upon release at the surface showed significantly better ability to achieve an upright orientation and evade a simulated predator. Results showed clear benefits of venting or recompression. Our data also show strong depth effects resulting in increased barotrauma injuries, more impaired reflexes, and greater mortality as depth increases. Overall, our data support venting or rapid recompression as effective tools for alleviating barotrauma symptoms, improving predator evasion, and increasing overall survival.

The mortality of released fish has long been a concern for fisheries managers, especially in fisheries with high discard rates (Harrington et al. 2005; Davis and Ottmar 2006; Hochhalter and Reed 2011). Discard mortality is often due to stress associated with hooking, exhaustion, air exposure, vision damage from sunlight, rapid thermal change (experienced at the thermocline), and handling injuries (Davis and Olla 2001; Brill et al. 2008; Campbell et al. 2010b). The widespread problem of discard mortality

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has prompted fisheries scientists to seek improved methods to quantify, predict, and reduce mortality, but there is still a paucity of data for many fisheries, especially reef fish fisheries (Davis and Ottmar 2006; Pollock and Pine 2007; Hochhalter and Reed 2011).

The major stressors experienced during capture of deep-dwelling physoclistic species are collectively known as barotrauma, which results from swim bladder gas expanding during a forced ascent (Gravel and Cooke 2008; Brown et al. 2009; Dowling et al. 2010). This occurs because as pressure decreases, gas expands exponentially. Fish suffering from barotrauma may exhibit symptoms including distension of the abdomen, stomach eversion from the buccal cavity, intestinal protrusion from the anus, and eyes bulging from the head (exophthalmia); these injuries can be lethal (Burns et al. 2004; Rummer and Bennett 2005; Campbell et al. 2010b). These visible signs constitute part of an extensive suite of internal and external injures, including swim bladder rupture and organ displacement and compression, that can be caused by barotrauma (Rummer and Bennett 2005; Hannah et al. 2008) and result in high discard mortality.

In addition to mortality estimates and outward signs of pressure-related injuries, barotrauma is also quantified by measuring sublethal effects that can alter behavior and increase vulnerability to predation (Campbell et al. 2010a, 2010b). Sublethal effects include injuries (e.g., stomach eversion and exophthalmia), impairment to reflexes, and impairment of behavioral responses (Davis and Ottmar 2006; Campbell et al. 2010a). Once released, fish with expanded swim bladders are very positively buoyant and may have difficulty orienting, submerging, and avoiding a predatory attack (Brown et al. 2010). Compounding the problem, some predators such as dolphins (family Delphinidae) have been observed following fishing vessels and appear to have associated boats with this easy prey source (Burns et al. 2004). Therefore, a fish that may otherwise have recovered from capture and release may not survive given their reduced ability to escape predation.

Several techniques have been proposed to improve survival and recovery for fish species that undergo barotrauma (Hochhalter and Reed 2011). One is to reduce the volume of the expanded gasses. The two primary methods used to accomplish this are swim bladder deflation with a venting tool (Wilde 2009) and rapid recompression (Brown et al. 2010). A venting tool is a hollow needle that is used to puncture the fish's abdomen and swim bladder wall (Render and Wilson 1994). With the swim bladder volume reduced, the fish is more likely and able to return to depth when released (Render and Wilson 1996). Studies on the efficacy of venting have found differing results, and proper venting technique is likely a major factor in successfully employing this method (reviewed by Wilde 2009). A more recent method for relieving barotrauma is rapid recompression of the gasses (Jarvis and Lowe 2008; Brown et al. 2010) by returning the fish to depth (Brown et al. 2010). This method is relatively noninvasive, but depending on the technique used for recompression, typically requires more time and effort to perform than venting. A wide variety of devices are used to release fish at depth, including cages and barbless hooks attached to heavy weights (descender hooks) (Brown et al. 2010; Hochhalter and Reed 2011). Most recently developed are specialized release hooks and pressure-activated lip-grips that release fish at specified depths (SeaQualizer).

The management of Gulf of Mexico Red Snapper *Lutjanus campechanus* has been hindered by the lack of survival estimates of discards and evaluation of barotrauma relief methods. This species is the most economically important reef fish in the Gulf of Mexico (Cowan et al. 2010) and supports major commercial and recreational fisheries, as well as playing a key ecological role as a higher trophic level predator in Gulf of Mexico reef habitats (Wells et al. 2008). Red Snapper are routinely caught between 30 and 60 m deep, can live as deep as 110 m, and commonly experience barotrauma when captured (Manooch et al. 1998; Rummer and Bennett 2005). This species has been overfished since at least the mid-1980s and has been subjected to intensive management (Diamond and Campbell 2009; Cowan 2011), though recently the stock has seen drastic improvement and populations are rebounding (NMFS 2012). Nonetheless, Red Snapper management remains controversial, and much of the debate revolves around the impact of regulatory discards (Cowan 2011). Compounding this problem are very shortened seasons; these restricted fishing windows, coupled with increasing fish abundance, result in an even higher discard rate. Thus, data are sorely needed to quantify the mortality of regulatory discards and assess tools and techniques that may increase the populations of deep-dwelling species that are undergoing stock rebuilding plans, especially in the Gulf of Mexico and the Atlantic coast. Additional evaluations of the efficacy of venting or rapid recompression will aid fisheries managers in developing effective strategies to promote survival and recovery.

A principal obstacle in understanding the effects of pressure-related injuries is the inability to document the fate of released fish. Laboratory experiments using hyperbaric chambers provide a controlled setting to evaluate mortality, barotrauma effects, and relief procedures while controlling for confounding events. A hyperbaric chamber can be used to simulate the pressures fish experience at selected depths (Rummer and Bennett 2005). Thus, to better document the best practices and methods to ameliorate the effect of barotrauma to Red Snapper, we undertook this study to (1) estimate the survival rates of Red Snapper that have experienced decompression events, (2) evaluate the relative effectiveness of venting and rapid recompression to increase survival and improve recovery after release, including evasion responses from a simulated predator, and (3) quantify the sublethal effects of barotrauma on Red Snapper, including injuries (e.g., stomach eversion and exophthalmia) and reflex impairment.

TABLE 1. Experimental design for conducting barotrauma studies on Red Snapper and the resulting impairment and percent survival. Surface release = fish that were released into an open-air holding tank. Rapid recompression = fish that were returned to a hyperbaric chamber and rapidly recompressed to the same pressure from which they were previously decompressed. Relative impairment for each treatment is shown through a mean barotrauma reflex score (mean BtR) ± SE; a higher number indicates greater impairment.

| | 0 m (control) | | | | 30 m | | | | 60 m | | | |
| | Surface release | | Rapid recompression | | Surface release | | Rapid recompression | | Surface release | | Rapid recompression | |
Measurement	Vented	Not vented	Vented	Not vented	Vented	Not vented	Vented	Not vented	Vented	Not vented	Vented	Not vented
Sample size (n)	5	4	5	5	6	6	6	6	6	6	6	6
Mean BtR	0.036	0	0	0	0.227	0.212	0.197	0.242	0.288	0.424	0.242	0.288
SE	0.020	0	0	0	0.040	0.040	0.040	0.060	0.030	0.080	0.080	0.060
% Survival	100	100	100	100	100	67	100	100	100	17	100	83

METHODS

Fish collection and maintenance.—Red Snapper were collected by hook and line from depths of 20–40 m from reef sites southeast of Port Aransas, Texas, during May and November 2012. Average fish length ± SE was 356 ± 5 mm. Upon capture, all fish were vented with a Team Marine PV 2 Angler Series Pre-Vent tool and placed in a flow-through live-well system for transport to the laboratory. Venting was performed by inserting the hollow needle into the abdomen at a 45° angle approximately 4 cm behind the base of the pectoral fin. A total of 67 fish were used in these experiments with six replicates in each treatment group and either four or five fish in control groups (Table 1).

Experiments took place at the Texas A&M AgriLife Research Mariculture Laboratory in Port Aransas, where fish were kept in three indoor tanks with flow-through filtered seawater (5,600 L, 3.7 m in diameter, 1.2 m high). Water temperature in the holding tanks and the outflow pipe from the hyperbaric chamber was measured repeatedly during each experimental trial. Mean ± SD temperature was 25 ± 2°C. The photoperiod cycle was 12 h light : 12 h dark. Water quality parameters, including nitrates, nitrites, pH, and ammonia levels, were monitored daily. Fish were treated prophylactically on arrival with a 60-s freshwater dip, and holding tanks were treated with 0.25 mg/L copper sulfate every other day for 8 d to remove any ectoparasites or gill trematodes (Burns et al. 2004; Rummer and Bennett 2005). Initially, fish were fed a natural diet of squid *Loligo* spp., shrimp *Penaeus* spp., and Rough Scad *Trachurus lathami*, but over a 2-week period all fish were converted to a pelleted diet (Rangen brood trout diet; 41% protein, 14% lipid, 6.4-mm size) and fed to satiation three times per week (R. Phelps, Auburn University, personal communication). Fish were allowed to acclimate and recover for a minimum of 14 d prior to experiments (Rummer and Bennet 2005; Campbell et al. 2010a). This recovery period was chosen because ruptured swim bladders in Red Snapper have been shown to heal within 4 d of capture (Burns et al. 2004). Almost all fish survived the initial collection and were behaving and feeding normally within 24 h. Any fish that appeared unhealthy was excluded from experimental trials.

Hyperbaric chambers were used to simulate pressure at depth. Chambers were cylindrical and constructed of high-pressure-tolerant Schedule 80 PVC pipe with circular acrylic end plates held in place with threaded rods 30 mm in diameter. Each had a volume of 83 L, was 98.5 cm in length and 38 cm in diameter, and had a front opening diameter of 15 cm (Wilson and Burns 1996). Utilitech 1/2-hp, 8-GPM, 3-wire, 230-V submersible well pumps were used to pressurize the chamber. By gradually closing the outflow valve, pressure built up inside the chamber in a controlled manner (see Rummer and Bennett 2005 for a similar design.) Pressure meters on the chambers were calibrated using a dive computer while pressurizing the system. Visual observations of fish were made through the clear acrylic end plates.

Acclimation to pressure and decompression.—To examine the effects of barotrauma on Red Snapper, fish were first recompressed to depth and after 30 h rapidly decompressed to simulate a catch-and-release event. First, individual Red Snapper were randomly assigned to pressure treatments that corresponded to depths of 0, 30, and 60 m. Depth levels were reflective of the range of common capture depths in this fishery in the Gulf of Mexico (Rummer and Bennett 2005; Campbell et al. 2010a). After fish were transferred to the chambers, pressure was maintained at 1 atm (surface) for at least 1 h. Pressure was then gradually increased at intervals of approximately 24.1 kPa/h for 30-m (302 kPa) depth treatments and 41.4 kPa/h for 60-m (604 kPa) depth treatments over 13–15 h. These rates were slow enough to minimize stress indicators such as rapid gilling and constant fin movement to retain upright orientation. Once at the desired depth, fish were kept at that pressure for an additional 16 h. Fish maintained neutral buoyancy and required little to no fin movement to maintain their position (Wilson and Smith 1985; Rummer and Bennett 2005). Fish were decompressed at a rate of 1 m/s, which is similar to the rate of ascension Red Snapper experience when caught by hook and line (Campbell et al. 2010a). Control fish were held prior to the experiments in an identical manner to pressurized treatments; however, they were placed in the chambers that were

not pressurized. Four chambers were used to provide replicate testing.

Assessment of barotrauma injuries and reflex responses.— After decompression, individuals were removed from the chambers and examined for sublethal effects using a condition index modified from Campbell et al. (2010a). The condition index used was the barotrauma reflex (BtR) score, and all injuries and reflex responses recorded were binary (1 = unimpaired state, 0 = impaired state). A total of 11 injury and reflex measurements were recorded for each fish. The six barotrauma-related injuries were as follows: (1) enlarged abdomen that was hard to the touch (tightened swim bladder), (2) intestinal protrusion from the anus, (3) stomach eversion into the buccal cavity, (4) subcutaneous hemorrhaging, (5) exophthalmia (eyes bulging), and (6) inactivity. The five reflex responses tested were as follows: (1) gag, (2) opercular, (3) dorsal spine, (4) hypaxial-muscle flex, and (5) vestibular-ocular. The gag response was measured by inserting a 7-mm × 15-cm cylindrical plastic probe into the fish's esophagus and an unimpaired response (score of 1) was recorded if the fish contracted its jaw or tried to expel the probe. An unimpaired opercular response was noted if the fish was actively moving its gill flaps. The dorsal spines were pushed down with the probe and considered uninhibited if they reextended into the erect defense position. A response of 1 was recorded for hypaxial response if the subject demonstrated hypaxial-muscle contraction (tail flapping) after prodding with the probe. Vestibular-ocular response was tested by moving the fish's cranium along its lateral axis and was considered unimpaired if the fish's eyes rotated to refocus on the human observer.

The BtR scores were calculated using the following equation (Campbell et al. 2010a):

$$BtR = 1 - \left[\left(\sum \text{individual responses} \right) \Big/ \text{total responses possible} \right].$$ (1)

A BtR score close to 1 indicated high levels of impairment, while a score close to 0 indicated low impairment. After BtR indices were evaluated, total length was recorded and the fish was tagged with an external T-bar Floy tag. The entire process took between 1 and 3 min, and handling time was recorded for each individual.

Barotrauma relief procedures and behavior tests.—Fish were assigned to one of four treatment groups: (1) VSR (vented surface release) = vented with a hollow metal venting tool and then released at the surface, (2) NSR (nonvented surface release) = released at the surface without venting, (3) VRR (vented and rapidly recompressed) = vented as above but returned to the hyperbaric chambers and repressurized to their depth group (0, 30, or 60 m) within 1–2 min, and (4) NRR (nonvented and rapidly recompressed) = returned to the hyperbaric chambers without venting and repressurized to their depth group (0, 30, or

60 m) within 1–2 min (Table 1). Control fish underwent one of the four treatments but did not undergo pressure changes inside the chambers. The treatment of fish that were vented and rapidly recompressed received both relief methods (venting and recompression). While it is unlikely both methods would be used on the same fish in the field, this treatment was included to ensure a fully crossed experimental design.

Red Snapper in the surface release treatments (VSR, NSR) were transferred into one of the aquaculture system tanks (1.2 m deep), where they underwent behavior tests. Handling time from exiting the chamber to release in the tank was between 1 and 3 min and was recorded for each individual. Release directly into a tank represents the treatment that a fish would experience when discarded overboard from a fishing vessel. Immediately after entering the water (time zero), and after 5 and 15 min, the subject was examined for upright orientation and tested for the ability to evade a simulated predator, for a total of six measurements. Similar to BtR indices, these measurements were binary and an unimpaired response (score of 1) was recorded if a fish was upright and swimming normally, as opposed to sideways or upside down (score of 0). At each time interval, predatory attack simulations were done by quickly thrusting a dip net towards the fish, and an unimpaired response was recorded if the individual was able to evade capture. Behavior test scores were calculated the same way as the BtR score (equation 1) but using the six behavior measurements. After behavioral tests, fish were monitored for mortality after 1 and 3 h and then checked again the next morning (16 h after release). To evaluate any delayed mortality or long-term sublethal barotrauma effects, all fish were monitored in holding tanks for at least 21 d after experiments.

Fish in rapid-recompression treatments (VRR, NRR) were returned to the hyperbaric chambers and rapidly recompressed to their depth group (0, 30, or 60 m), which took 1 to 2 min. Rapidly recompressed fish were monitored inside the chamber over the next 1 to 3 h for immediate mortality and checked again the following morning (after approximately 16 h). It was not possible to subject rapidly recompressed fish to behavioral tests. Recovery for longer-term observation required us bringing fish in the chambers back to surface pressure while avoiding barotrauma. Thus, over the next 3 d, pressure in the chamber was slowly returned to 1 atm. This allowed sufficient time to avoid barotrauma, while minimizing stress associated with being inside the chamber (e.g., not feeding for several days). Fish were monitored for at least 3 weeks after the experiments to evaluate any delayed mortality or long-term effects from barotrauma.

Data analysis.—Statistical analyses were run on survival data, behavior test scores, and BtR scores to determine the effects of different treatments. A binary exact logistic regression was used to determine differences in treatment in predicting survival (Derr 2000). This technique is more robust for small sample sizes than a regular logistic regression model (Hirji et al. 1987). Behavior test scores were analyzed using a two-way analysis of variance (ANOVA) with depth (0, 30, and 60 m) and venting as main effects ($\alpha = 0.05$). The distribution of the

residuals was analyzed using the UNIVARIATE procedure, and data were transformed (fourth root) to reduce heteroscedasticity. A significant depth × venting interaction was observed, so a priori linear contrasts were used to test for significant differences in behavior test scores between the following: (1) vented and nonvented, (2) 0 and 30 m, (3) 0 and 60 m, and (4) 30 and 60 m (α = 0.05). To evaluate sublethal effects of barotrauma from different decompression depths, BtR scores were analyzed using a one-way ANOVA. Significant main effects of the ANOVA were further analyzed using Tukey's honestly significant difference post hoc test. Additionally, a linear regression was used to test for any effects of fish length on BtR score. A two-sample t-test was also run on all fish BtR scores, comparing whether fish that were surface released or rapidly recompressed had differing initial impairment before release. All statistical analyses were conducted using SAS 9.2 software.

RESULTS

Survival

Red Snapper that were vented or recompressed showed higher survival then nonvented or nonrecompressed fish. Fish that underwent vented rapid recompression (VRR) and vented surface release (VSR) both had 100% survival (Table 1), while fish subjected to nonvented rapid recompression (NRR) had 92% survival and nonvented surface release (NSR) had 58% survival. Control (0 m) fish within all four treatments had 100% survival. Fish with the lowest overall survival were in the NSR group. But there was also a depth effect, with lower survival from deeper depths; 67% and 17% survival in fish decompressed from 30 and 60 m, respectively (Table 1). The NRR treatment group had 100% survival from 30 m and 83% survival from 60 m (Table 1). Since all vented fish survived, venting was not used as a variable for determining survival in the exact logistic regression. Rapid recompression significantly improved overall survival (vented and nonvented) compared with surface release ($P < 0.05$; Table 2). The odds ratio of the exact logistic regression showed that a fish that was rapidly recompressed, vented or nonvented, was 9.7 times more likely to survive than one released at the surface (Table 3). Rapidly recompressed fish showed high survival regardless of venting treatment. There was also a significant effect of depth on survival ($P < 0.05$; Table 2). All mortality was observed in the first few hours posttreatment, and those that survived quickly resumed normal swimming behavior. Fish were monitored for at least 3 weeks, and no delayed mortality from barotrauma occurred past 18 h of the decompression event. All fish began eating normally within 1 or 2 d after the completion of their experimental trial.

Sublethal Effects of Barotrauma

While vented fish clearly showed higher survival than nonvented individuals, vented fish also showed less behavioral impairment due to barotrauma after surface release into a tank. Behavior tests were only performed on surface release treatments because it was not possible to subject rapidly recompressed fish to the tests while they were "compressed" inside the hyperbaric chambers. A significant interaction was found between depth and venting treatments (Table 4), therefore, a one-way main-effects ANOVA was used to compare several treatment combinations (Table 4). A priori linear contrasts showed that vented fish had significantly lower (less impaired) scores than nonvented fish (ANOVA: $F = 30.59$, df = 1, $P < 0.0001$; Figure 1, Table 4). Generally, vented fish were able to swim normally and avoid the dip nets at all three time intervals (after 0, 5, and 15 min) (Table 5). In contrast, nonvented fish showed difficulty achieving an upright orientation and their increased buoyancy caused them to float upside down in the tank, with no response to the dip net. There was no improvement in the condition of nonvented fish after 15 min, and most fish were still inverted at the surface after 60 min.

Depth was significant, but it was not as influential on behavioral impairment as venting. A priori linear contrasts showed that 0-m (control) treatments had significantly lower behavior test scores than 30-m (ANOVA: $F = 22.07$, df = 1, $P < 0.0001$) or 60-m ($F = 17.13$, df = 1, $P < 0.0003$) treatments (Figure 1; Table 4). However, there was no significant difference between 30- and 60-m depths ($F = 0.37$, df = 1, $P = 0.5491$; Figure 1; Table 4). Control fish all had behavior test scores of 0. While venting clearly correlated with improved behavior metrics, decompression depth did not significantly affect them.

TABLE 2. Results of conditional exact tests showing survival of Red Snapper subjected to decompression. The effects tested were depth (0-m control, 30 m, and 60 m) and release type (surface release or rapid recompression); mid = discrete distribution mid P-value.

| | | | Conditional exact tests | |
| | | | P-value | |
Effect	Test	Statistic	Exact	Mid
Depth	Score	6.94	0.0280	0.0254
	Probability	1.93	0.0383	0.0357
Release	Score	5.45	0.0442	0.0340
	Probability	0.02	0.0442	0.0340

TABLE 3. Odds ratio results from the exact logistic regression for survival of Red Snapper subjected to decompression.

| | | 95% Confidence limits | | |
Parameter	Odds ratio	Lower	Upper	P-value
Depth 0 m	8.69	1.090	∞	0.0407
Depth 30 m	4.06	0.563	50.3	0.2110
Release: rapid recompression	9.70	1.040	490.0	0.0442

TABLE 4. Analysis of variance (ANOVA) results for the effects of depth and venting on behavioral impairment (as measured by mean behavior test score) of Red Snapper that have been decompressed from depth. A significant depth × venting interaction was observed, and a priori linear contrasts were used to test for significant differences in behavior test scores between vented and nonvented fish, between 0 and 30 m, between 0 and 60 m, and between 30 and 60 m. Mean behavior tests scores evaluated the ability of a fish to maintain an upright orientation and evade a simulated predator after being decompressed, vented or not, and then released in an open-water tank.

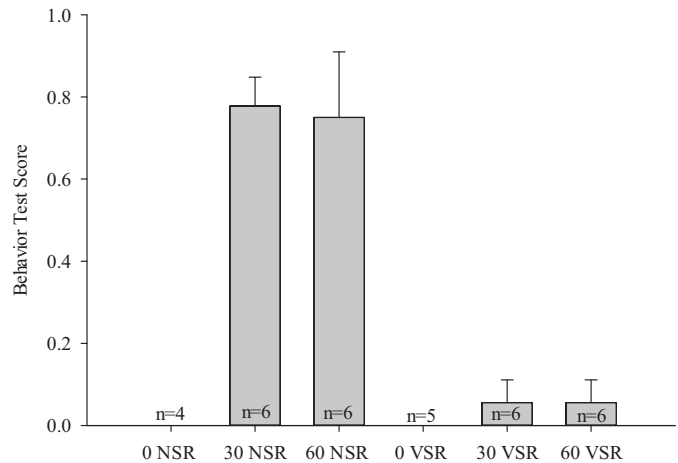| Test	df	SS[a]	F	P
ANOVA				
Depth	2	1.64	12.58	0.0001
Venting	1	1.99	30.59	<0.0001
Depth × venting	2	0.93	7.11	0.0033
Residual	27	1.76		
Linear contrasts				
Main effects	5	5.03	15.4	<0.0001
Vented versus nonvented	1	1.99	30.59	<0.0001
0 m versus 30 m	1	1.44	22.07	<0.0001
0 m versus 60 m	1	1.12	17.13	0.0003
30 m versus 60 m	1	0.02	0.37	0.5491
Residual	32	6.79		

[a]Sum of squares.

FIGURE 1. Relative behavior impairment, as shown by mean behavior test scores, among treatments of Red Snapper that were decompressed from depths of 0 (control), 30, and 60 m and then vented and surface released (VSR) into an open holding tank or not vented and surface released (NSR). Mean behavior tests scores evaluated fish ability to maintain an upright orientation and evade a simulated predator after release. A higher score indicates greater behavior impairment. A priori linear contrasts were used to test for significant differences in mean behavior test scores among depth and venting treatments. Significant differences among treatment groups are shown in Table 4. Error bars indicate standard error.

Red Snapper were evaluated for barotrauma injuries and reflex responses through the BtR index when they were removed from the chambers, and decompression depth did have a significant effect on BtR score. There were significant differences among depths (ANOVA: $F = 35.52$, df = 2, $P < 0.001$), and Tukey's post hoc tests found that 0-, 30-, and 60-m depths were all significantly different from each other (Figure 2). Mean BtR score ± SE of fish decompressed from 60 was 0.32 ± 0.03, from 30 m was 0.27 ± 0.02, and from 0 m was 0.017 ± 0.01. To ensure that the fish that were run through the experiment first (vented treatments) had similar initial impairment to fish done later in the experiment (rapidly recompressed treatments) before release, a two-sample t-test was run on all fish BtR scores comparing the two groups. The BtR scores of fish that were later surface released were not significantly different from fish that were later rapidly recompressed (t-test: $t = 1223$, df = 33, $P = 0.197$). Additionally, fish in all treatments were similar in size, and a linear regression showed no relationship between fish length and BtR score ($t = 42.92$, df = 15, $r^2 = 0.002$, $P = 0.9234$).

TABLE 5. Percent occurrence of Red Snapper exhibiting impaired behavioral responses after decompression from depth and release at surface (ambient) pressure in each venting and depth (0, 30, or 60 m) treatment combination. Behavioral responses were tested at 0, 5, and 15 min after release. Each value represents the percent occurrence that a fish had an abnormal orientation (could not stay upright and swim normally) or could not evade a simulated predator at that time interval and treatment combination.

|	Surface release					
	Vented			Nonvented		
Measurements	0 m	30 m	60 m	0 m	30 m	60 m
Sample size (n)	5	6	6	4	6	6
Impaired behavioral responses (%)						
Abnormal orientation; 0 min	0	17	17	0	33	50
Failed to evade predator; 0 min	0	17	17	0	33	67
Abnormal orientation; 5 min	0	0	0	0	100	83
Failed to evade predator; 5 min	0	0	0	0	100	83
Abnormal orientation; 15 min	0	0	0	0	100	83
Failed to evade predator; 15min	0	0	0	0	100	83
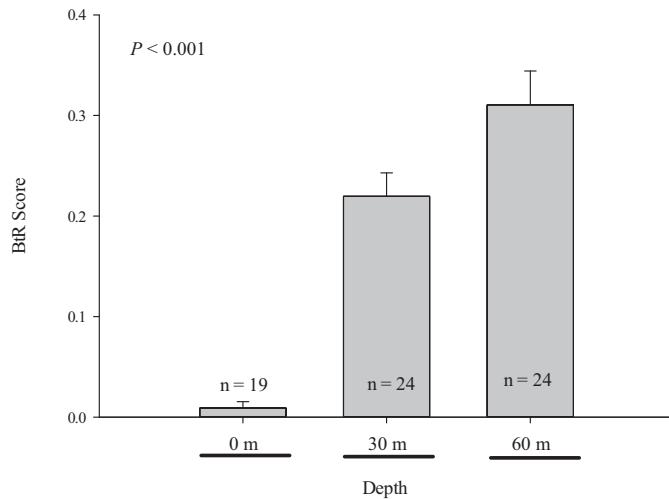
FIGURE 2. Relative impairment from decompression injuries, as shown by barotrauma reflex (BtR) scores, of Red Snapper that had been decompressed from a depth of 0, 30, or 60 m. Columns that do not share a horizontal line are significantly different ($\alpha = 0.05$). Error bars indicate standard error.

The percent occurrence of specific barotrauma symptoms and impaired reflex responses increased with greater depth but varied by individual (Table 6). Most noncontrol fish showed at least one sublethal barotrauma symptom. A tightened swim bladder (enlarged abdomen) and stomach eversion were the most frequent symptoms (Table 6). All fish assigned to rapid-recompression treatments had tightened bladders (Table 6). Exophthalmia was observed in only fish subjected to 60-m depth treatments. Fish frequently failed the gag, opercular, and dorsal spine reflexes.

There was only one fish that did not display the vestibular-ocular response, and the hypaxial-muscle flex was usually observed, showing 17% or less impairment per treatment group (Table 6). Control fish (0 m) rarely showed impairment, though lack of gag reflex and opercular response was observed in a small percentage (11%) of controls.

DISCUSSION

Our findings show that both venting and rapid recompression have the potential to increase survival and to improve recovery of regulatory discarded Red Snapper. Fish in the vented surface-released and rapid-recompression treatment groups had the highest survival, while nonvented surface-released fish had the lowest. All vented fish survived during the minimum of 21 d that they were monitored after decompression, regardless of depth. These results indicate that venting a surface-released fish or rapidly recompressing it will increase the probability of surviving barotrauma.

This study improves on several of the limitations and issues seen in field studies on venting and illustrates that, when performed correctly, venting is a beneficial practice. However, the practice of venting fish has been controversial. Wilde (2009) reviewed studies on 21 species and concluded that, in general, venting did not increase survival. Included in Wilde's (2009) review were four studies involving Red Snapper, which were all conducted in the field. Two showed a positive effect of venting (Gitschlag and Renaud 1994; Render and Wilson 1994) and two showed a negative effect (Render and Wilson 1996; Burns et al. 2002). While all four provide valuable contributions, our updated methods specifically targeted the effects of

TABLE 6. Percent occurrence of Red Snapper exhibiting barotrauma and impaired reflex responses after decompression from depths of 0, 30, or 60 m. After decompression fish were released at surface (ambient) pressure into an open holding tank or rapidly recompressed (all barotraumas symptoms and reflex responses were recorded before release and were not influenced by release treatment). Venting treatments within each depth group are not shown separately because symptoms and reflex responses were recorded before a fish was vented.

Measurements	Surface release			Rapid recompression		
	0 m	30 m	60 m	0 m	30 m	60 m
Sample size (n)	9	12	12	10	12	12
Barotrauma symptoms (%)						
Tightened bladder	0	92	92	0	100	100
Stomach eversion	0	42	75	0	33	58
Intestinal protrusion	0	0	8	0	17	17
Exophthalmia	0	0	25	0	0	0
Subcutaneous hemorrhage	0	8	42	0	0	0
Inactivity	0	0	8	0	8	17
Impaired reflex responses (%)						
Gag	11	58	50	0	33	33
Opercular	11	8	50	0	17	25
Dorsal spine	0	33	25	0	25	25
Vestibular-ocular	0	0	8	0	0	0
Hypaxial-muscle flex	0	0	8	0	8	17

venting (while others focused on hook size, fish length, season, etc.), used a more even sample size among treatments, and standardized problematic venting methods while in a controlled setting for determining survival. Additionally, previous work showing a negative effect of venting (Render and Wilson 1996) was performed at relatively shallow capture depths (<21 m), where barotrauma is not as severe. At greater capture depths, where the fishery routinely occurs (SEDAR 2009), our results show venting dramatically improves survival. Venting may not be necessary for all fish, but our findings and previous work suggest that this determination should be made individually for each species and that for Red Snapper venting can improve survival.

The results from our study show that rapidly recompressing Red Snapper can be successful in mitigating barotrauma symptoms and improving survival. This technique guarantees return to depth of capture without the invasive needle puncture associated with venting. The high survival rates from rapid recompression that we found are encouraging for the development of effective barotrauma relief procedures and are similar to results from other studies examining rapid recompression on other species prone to barotrauma (Hannah et al. 2008; Hochhalter and Reed 2011). However, there are other factors to consider in developing management practices. Our laboratory study simulated returning fish to the pressures from which they were decompressed. However, it excluded factors that would be present in the field, including the actual device that would return the fish to its capture point. It is possible that stress associated with struggling against a hook as the fish moves up and down the water column and the amount of time spent at the surface while a recompression device is attached may counteract some of the benefits of recompression or could even attract predators. However, venting is a relatively invasive procedure, and there is a possibility of introducing infection, though none was seen in our study. Our venting tools were not disinfected to simulate field conditions, and we do not advise venting a fish that will be rapidly recompressed. Nonetheless, our treatment that included both venting and recompression (an unlikely process in field) showed slightly higher survival than the nonvented rapid-recompression group. Others studies have shown similar survival success with rapid recompression on species prone to barotrauma. Yelloweye Rockfish *Sebastes ruberrimus* released at depth with descender hooks showed a much higher probability of survival than those released at the surface (Hochhalter and Reed 2011). Rockfishes *Sebastes* spp. inhabit rocky reef habitats at similar depths as Red Snapper (Hannah et al. 2008). A study on several California rockfish species found that rapid recompression significantly increased discard survival and that the length of time spent at the surface and the differential in seafloor and sea surface temperatures were the most significant predictors of short-term mortality (Jarvis and Lowe 2008).

Long-term survival results from this experiment were similar to those found in previous field studies on survival of released Red Snapper (Gitschlag and Renaud 1994; Diamond and Camp-

bell 2009). These studies also concluded that Red Snapper mortality from barotrauma generally occurs within 48 h or less, and in this study there was no mortality after 18 h of decompression. Gitschlag and Renaud (1994) conducted a caged study in which fish were monitored by scuba divers for 10–15 d. They reported that 90% of all deaths occurred during the first 24 h and 95% occurred within 48 h. Diamond and Campbell (2009) performed similar research using caged fish and scuba divers to observe the effects of barotrauma after release. Similarly, they showed virtually all mortality occurred within the first 48 h. Some scientists have hypothesized that injuries incurred from decompression might affect feeding or other life processes and that delayed mortality might occur several days to weeks after capture and release (Rummer and Bennett 2005). Our results did not show any long-term negative effects of decompression resulting in mortality; all fish in this study began eating normally 1 to 2 d after completion of the experiment, and some did so immediately. Thus, based on all of these findings, barotrauma-related mortality in Red Snapper seems to occur rapidly, and if the fish survives the first 48 h there is minimal risk of mortality. This further underscores the value of either venting or rapid recompression to return the fish to depth to maximize survival.

In this study, postrelease behavior tests showed that barotrauma injuries can cause disorientation and failure to evade a simulated predator when fish are released at the surface, particularly if fish were not vented. Based on the behaviors we observed in nonvented fish (alive but floating and unresponsive), it is unlikely that a fish exhibiting these impairments could escape a predator in the wild. A major cause of discard mortality of reef fish is predation by dolphins, barracudas *Sphyraena* spp., and sharks (families Carcharhinidae and Sphyrnidae) (Burns et al. 2004). Dolphins can associate fishing activities with increased feeding opportunities (Burns et al. 2004; Powell and Wells 2011). We observed that some nonvented fish survived and their swim bladders slowly equilibrated after several hours floating at the surface. If we had considered failure to escape a simulated predator as a proxy for mortality, then none of the nonvented surface-released fish from 30 m would have survived after 5 min, and 83% of the fish from 60 m would also have died. Surprisingly, behavioral impairment was lower in the 60-m nonvented treatment than in the 30-m nonvented treatment after 5 and 15 min. It is possible some fish in the deeper-depth treatments had ruptured swim bladders and gas escaped the body, allowing for improved swimming ability (i.e., trapped gasses were expelled and did not keep them floating at the surface) within the first 15 min, but these internal injuries eventually resulted in death. Fish in our study could not recompress naturally due to the restricted depth of the tank (1.2 m), and it is possible that tank shallowness affected even their willingness to attempt to submerge, but the majority of nonvented fish were floating at the surface within seconds, highly impaired and not attempting to submerge. While not all previous studies support the use of venting, if it allows fish to submerge to their preferred

water depth, then venting may increase survival due to the high vulnerability to predation.

Fish captured from greater depths showed a direct relationship with increased mortality and higher BtR scores; thus, as fishing depth increases, there is a greater need to either vent or rapidly recompress fish. The nonvented surface-released fish in the 30-m treatment had a nearly four times higher rate of survival than those in the 60-m group, and the only death in either of the rapid-recompression treatments was from 60 m. More severe barotrauma symptoms, such as exophthalmia and intestinal protrusion, were seen primarily in the 60-m depth treatments, suggesting that these injuries are likely to manifest only with greater gas expansion in the fish's abdomen (Rummer and Bennett 2005). Several other studies have also concluded that Red Snapper captured from deeper waters can be expected to have more frequent and more severe injuries as space decreases in the body cavity (Gitschlag and Renaud 1994; Rummer and Bennett 2005; Campbell et al. 2010a).

Benefits and Limitations of a Laboratory Study

Conducting this study in a laboratory allowed us to observe long-term survival of fish and control outside variables to focus on treatment effects, but all laboratory studies have certain limitations that may not be seen under field conditions. There are also particular conditions that were not replicated for this laboratory environment that can affect fish survival (e.g., no predators), suggesting that survival here is under "ideal" conditions. Other factors such as hooking trauma, handling time, and temperature stress were not considered. Multiple studies, including unpublished acoustic telemetry data from our laboratory, have found that warmer sea surface temperatures during the summer months significantly decrease the survival of discarded fish (Jarvis and Lowe 2008; Diamond and Campbell 2009; Campbell et al. 2010b). Our experiment occurred over a constant temperature, and future studies should consider how temperature differentials between seafloor and sea surface, particularly stratification in the water column, may affect mortality or influence other sublethal effects. It is likely that greater differentials between the temperature in the chambers and the temperature of the surface release waters in this study could have increased mortality, which further necessitates the need for venting or rapid recompression to allow the fish to quickly submerge to cooler waters. The other factors related to capture are all potential causes for mortality, but we argue venting or rapid recompression is effective for improving survival. Additionally, fish in our study were acclimated to depth in the chambers over a 30-h period, which is not as long as the time used in a previous Red Snapper hyperbaric study (Rummer and Bennett 2005), though longer than the time used by Campbell et al. (2010a). While fish decompressed from 60 m clearly had more severe barotrauma injuries than those in the 30-m group, it is possible that the fish from 60 m were not fully acclimated to depth within 30 h. However, if time at depth was an issue, survival rates after full acclimation in this group likely would have been even

lower and the benefits of venting or rapid recompression would probably be even more pronounced. Finally, to control for any effect of fish size, we used only relatively small fish compared with the maximum size of adult Red Snapper. We selected for this size because it was below the minimum regulatory size of fish permitted for retention. It is certainly possible that venting or rapid recompression may affect larger fish differently. Certainly, future studies should focus on how size relates to discard mortality. These potential limitations clearly point toward the need to follow up with controlled field studies to ascertain the full effect of barotrauma-related mortality in the Red Snapper fishery.

Management Implications and Conclusions

The findings from this study indicate that venting and rapid recompression are both very viable methods of increasing the survival of Red Snapper regulatory discards. Fisheries managers should encourage the use of either of these two techniques to aid in the recovery of this important fishery. Venting a fish and releasing it at the surface showed the best survival, and both rapid-recompression treatments had very high survival, which mirrors the results shown with this method in other species (Jarvis and Lowe 2008; Hochhalter and Reed 2011). However, there are several factors that should be considered when developing management practices. Proper venting-tool use and technique are an essential part of making this procedure an effective management strategy, and public outreach education on the subject would likely improve the fate of vented-and-released regulatory discards, as improper venting techniques are common, even by scientists. Rapid recompression does not require anatomical knowledge to be done properly and is a relatively noninvasive procedure, but in the field this technique may not be as practical as venting. Our observations show that venting, sometimes referred to as the "pop-and-drop" method, takes a relatively short amount of time (typically ≤ 1 min). Attaching a fish to a recompression device and returning it to depth takes several minutes and requires dedicated gear and personnel. However, there are a wide variety of descending devices that can be tailored to different conditions and angler skill. Nonetheless, our findings suggest comparable results can be achieved with either method. While these methods may have certain limitations, we conclude the benefits outweigh the costs.

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