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Factors Affecting Catch and Release (CAR) Mortality in Fish: Insight into CAR Mortality in Red Snapper and the Influence of Catastrophic Decompression

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Abstract.—The red snapper *Lutjanus campechanus* fishery is arguably one of the most important in the Gulf of Mexico, but habitat destruction, climate change, and serial overfishing has resulted in significant population declines in red snapper and other high-profile fisheries species. The red snapper fishery may be one of the best examples where management strategies that promote catch and release (CAR) have failed. Populations have not recovered despite CAR management strategies, likely because CAR mortality is high; however, the basis for CAR mortality is unclear. Numerous studies associated with fishing-induced mortality were reviewed in an attempt to make generalizations as to how red snapper and other high-profile fisheries species respond to CAR. A framework for understanding CAR mortality in red snapper and other species was constructed based on four pillars: retrieval conditions, species and size relationships, handling, and release conditions. Each of these fishing factors was examined as to relative impact toward CAR. A predictive model was generated from all available data on CAR mortality. For a deep-water fish like red snapper, the underlying problem is directly related to capture depth, particularly injuries related to rapid swim bladder (SB) overinflation and catastrophic decompression syndrome (CDS). If not immediately lethal, depth-related injuries may have long term effects on growth and immune function that could go unnoticed and are unaccounted for in traditional field studies; all other fishing factors will only intensify this baseline impairment. Management plans are typically built under the assumption that CAR mortality is below 20%, but it is widely accepted that this is a gross underestimate. Modeling from this review suggests that, in red snapper, mortality may be as low as 20% but only if fish are caught between 0 and 20 m depths. This is not the case, and CAR mortality may reach 100% if fish are retrieved from deeper than 110 m. Current CAR management strategies are ineffective, and not enough information exists to impose maximum fishing depths. Given these limitations, a logical approach would be to restrict particular areas such that fish populations can be protected from all fishing and CAR activity, therefore protecting age, size, and sex classes and ratios. For fish species like red snapper, where overfishing is widespread and CAR mortality is high, or other species where CAR is unclear and a thorough investigation as to depth-related CAR mortality has not been performed, strategies based on space (i.e., marine protected areas and no-take reserves), rather than time or numbers (i.e., season closures, size limits, bag limits, etc.), have the greatest potential for overall conservation and sustainability and should be strongly considered.

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Introduction

The Gulf of Mexico red snapper *Lutjanus campechanus* fishery developed in the mid 1800s and advanced alongside technology over almost two centuries; the red snapper has since become an icon species of the Gulf of Mexico (Moran 1988; Schirripa and Legault 1999). Recreational catch often surpasses the 2,000 metric ton annual commercial catch in the U.S., and the fishery as a whole is worth over $40 million U.S. annually (Schirripa and Legault 1999; Stevens 2004; SEDAR 7 2005). However, red snapper, as well as many other reef species, are overfished relative to established benchmarks for resource sustainability and have been declared "severely overfished" and appear on "species to avoid" lists (Helm and Smullen 1997; Stevens 2004; Ault et al. 2005). Historically, a fishery could be sustainable when populations have a spatial refuge from the fishery (Pauly et al. 2002). Although red snapper are traditionally caught from deep waters, which may offer some protection from the fishery, they are also caught near shore and exercise high site fidelity, making them an easy target for exploitation and necessitating management strategies for adequate protection (Moran 1988; Schirripa and Legault 1999; Coleman et al. 2000; Pritchard 2005). Stringent regulations such as season closures, bag limits, and size limits, implemented since 1990, have increased the proportion of red snapper caught that are subsequently released in the recreational fishery to over 50%, a 10-fold increase since the early 1980s (Figure 1). However, these strategies have failed to reverse the decline in red snapper populations, likely because not enough red snapper survive the catch and release process (Schirripa and Legault 1999; GMFMC 2000; Stevens 2004; Rummer and Bennett 2005).

Catch-and-release (CAR) fishing has been historically viewed as an approach toward conservation and ethical sustainability, but fisheries management strategies such as season closures, quotas, bag limits, and size limits that have been implemented in the recreational and commercial red snapper fisheries for almost two decades also promote CAR activity (Schirripa and Legault 1999; Casselman 2005; Cooke et al. 2005). Time closures and quotas are ineffective strategies, as they temporarily shift pressure to other species, and red snapper may still be caught and suffer release mortality in those fisheries (Stevens 2004; Coleman et al. 2000; GMFMC 2000). Bag limits can be problematic if fishing trips are not limited or the number of anglers increases (Coleman et al. 2000). Size limits and species prohibition strategies are only practical for hardy species in shallow-water systems, and few management plans are in place to preserve size, age, social structure, or the natural sex ratios of reef fish like red snapper (Coleman et al. 2000). The key to a successful CAR management strategy is that fish actually survive the CAR experience, which may be unlikely (Casselman 2005; Rummer and Bennett 2005). CAR-related mortality is reported to range from 16 to 30% depending on species, gear, depth, and season, but may be even higher (Figure 2) (Davis 2002; Stevens 2004; Casselman 2005).

According to Muoneke and Childress' 1994 review, CAR accounts for less than 15% mortality in lake trout and pikes occasionally exceeds 30% among drums, basses, trouts, and catfishes, but averages 68% among brown trout *Salmo trutta*, bluegill *Lepomis macrochirus*, crappie *Pomoxis annularis*, striped bass *Morone saxatilis*, and coho salmon *Oncorhynchus kisutch* (Muoneke and Childress 1994). Data from the 118 CAR studies involving over 120,000 fish in Casselman's (2005) review displayed average CAR mortality at 16.2% (Casselman 2005). Bartholomew and Bohnsack reported a comparable 18% average after reviewing 53 CAR studies; although averages for release mortality were described

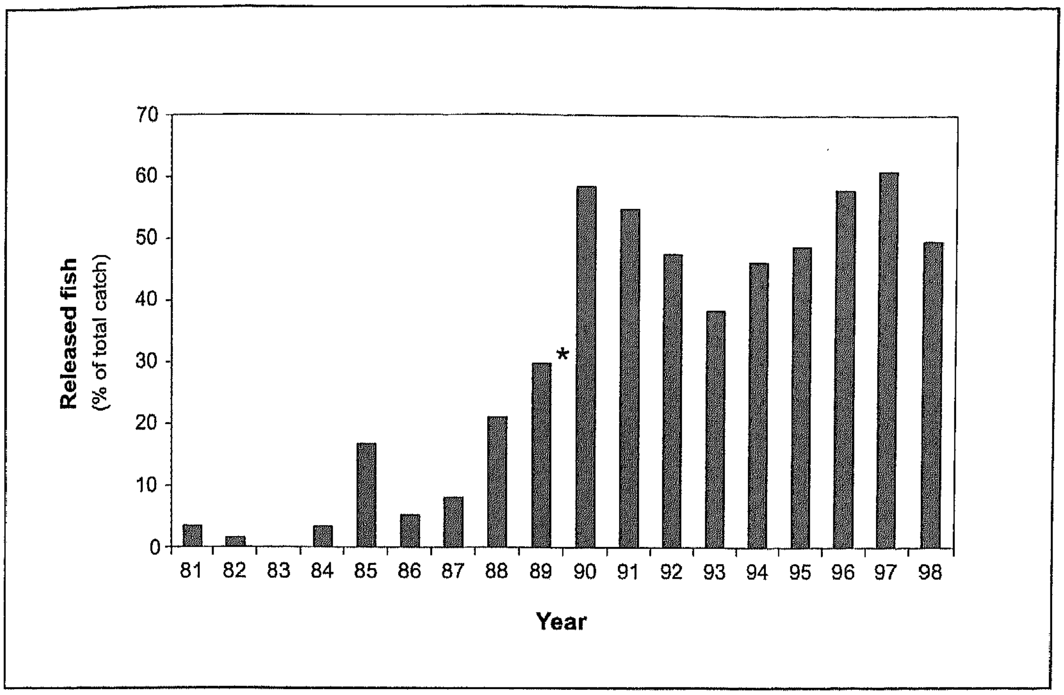

Figure 1. Estimated fractions of red snapper *Lutjanus campechanus* caught and released by recreational anglers between 1981 and 1998 in the Gulf of Mexico. The asterisk demarcates the onset of regulatory practices. Modified from Shirripa and Legault 1999.

as heavily skewed, varying substantially by species and within species, and ranging from 0 to 95% (Bartholomew and Bohnsack 2005). For red snapper, specifically, Porch and colleagues estimate release mortality to average approximately 46%, ranging 15–88% in both recreational and commercial fisheries combined (reviewed in SEDAR 7 2005). A framework for understanding the relative importance of factors responsible for CAR mortality and the underlying causes does not yet exist, hence the wide range in mortality rates reported (Figure 2) and the multitude of factors influencing overall CAR mortality. The purpose of this work was first to build a framework for understanding the factors that ultimately lead to CAR mortality in fish in general, and second, to integrate information into a predictive model to be used in assessing the interactions between factors that further affect CAR mortality. Not only will this approach give insight as to how red snapper respond to CAR but also how CAR mortality can be understood in other species as well.

Methods

I. Qualitative Approach

To approach CAR mortality qualitatively, a framework was built starting with the four general fishing factors that attribute to CAR mortality: retrieval conditions, species and size, handling, and release conditions (Figure 3). Based on data from over 200 studies investigating at least 40 species (Figure 2), the framework was expanded to include sub-elements under each of the four fishing factors (Figure 3). Some of the sub-elements outlined have been the focus of other studies (e.g., hook type and location, retrieval time and depth, swim bladder (SB) physiology and

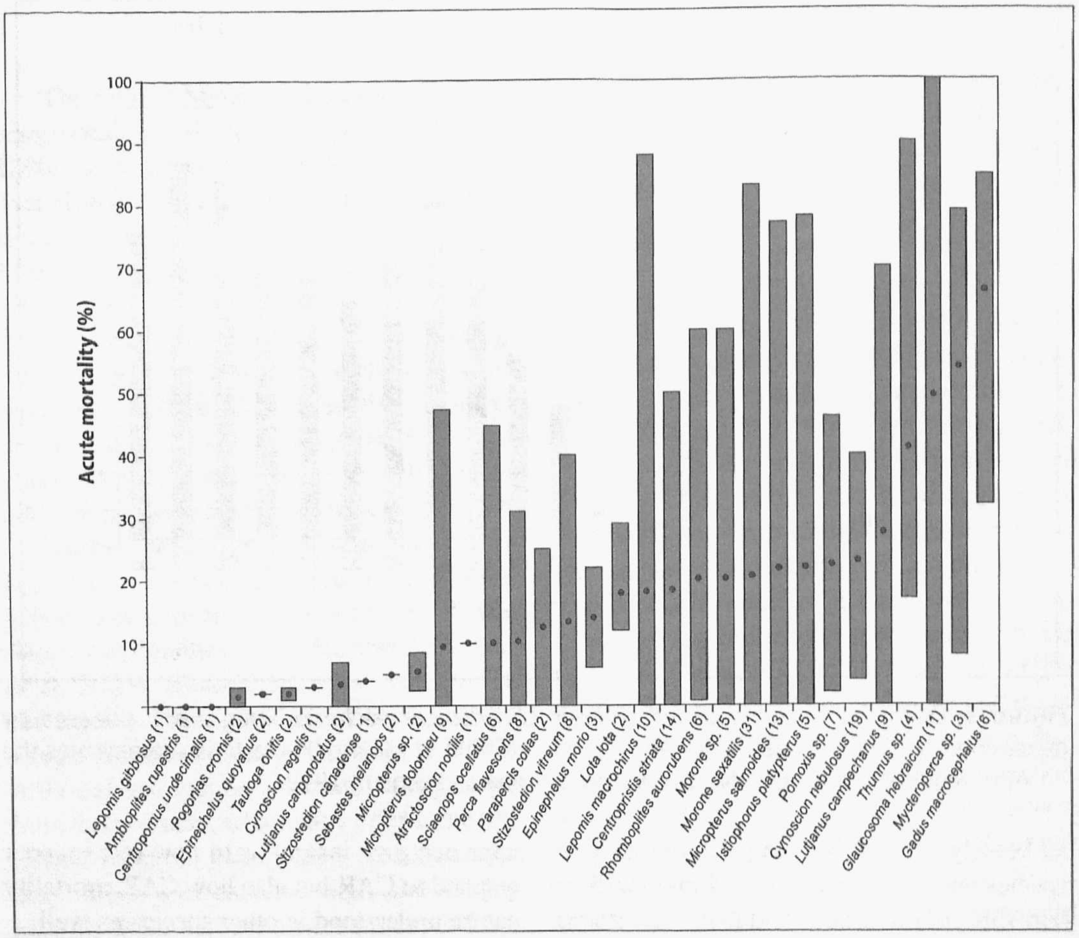

Figure 2. Summary of CAR mortality rates (%) in various physoclistous fish species. Means are derived from the average mortality reported from each study considered, but the bar extends to include the highest and lowest rates published for each species. The number in parentheses, following the species name, represents the number of studies considered. Data were compiled from reviews by (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Casselman 2005) and studies by (Beggs et al. 1980; Fable 1980; Low 1981; Bugley and Shepherd 1991; Lee 1992; Bruesewitz et al. 1993; Gitschlag and Renaud 1994; Render and Wilson 1994; Murphy et al. 1995; Keniry et al. 1996; Render and Wilson 1996; Wilson and Burns 1996; Shasteen and Sheehan 1997; Bettoli and Osborne 1998; Nelson 1998; Collins et al. 1999; Bettoli et al. 2000;Cooke et al. 2001; Cooke et al. 2002a; Cooke et al. 2002b; Cooke et al. 2003a; Cooke et al. 2003b; Aalbers et al. 2004; Neufeld and Spence 2004; Cooke et al. 2005; Millard and Mohler 2005; Bettinger et al. 2005; Rummer and Bennett 2005; St. John and Syers 2005; Nichol and Chilton 2006)

morphology, air exposure, tactile protocol, temperature, and predation); others, like life history, health, capture history, reproductive stage, and diet and prandial status have not been as easily addressed (Figure 3). Acute effects, when identifiable, were documented for each factor but demarcated with a question mark when data were unavailable. The latent effects of CAR (including mortality) that have been investigated thus far were listed as the final component of the framework.

II. Quantitative Approach

The framework devised to describe the various factors responsible for CAR mortality was integrated into a predictive model that was generated to assess the influence of and potential interactions between factors on CAR mortality as a whole. Ideally, a suite of data from one comprehensive study where CAR mortality in red snapper was investigated and all parameters were examined equally would be used. A statistical model could then be developed to predict mortality in red snapper caught from a specific depth under various conditions. Unfortunately, a comprehensive study on red snapper does not yet exist. CAR mortality data in red snapper were used when available, but when necessary, average mortality rates from studies on other species were used as well. Assuming that each of the factors examined significantly affects mortality, a predictive model that can be validated and tested statistically was generated.

While it is possible to assume that certain factors will result in increased mortality, it is difficult to predict whether relationships are linear and which factors interact with others, resulting in multiplicative, rather than additive effects. However, it is known that stressors, in general, are often additive or multiplicative but rarely subtractive (Wedemeyer et al. 1990). The seven parameters that have been most heavily investigated in the literature were considered for the model and regarded as having additive effects on mortality. The seven parameters used include capture depth, venting, retrieval rate, hook type, surface to depth temperature differential, presence of surface predators, and handling and hook location. Only studies where one parameter was explicitly monitored or factors were investigated independently were utilized. Handling and hook location were integrated into the model as one factor because, aside from studies where deeply embedded hooks were not removed prior to fish release (i.e., line was cut instead of removing hook), it is assumed that handling time would increase if the hook was embedded deeply.

The following model describes the effects of the seven factors on general CAR mortality. Y_i is a binary variable measuring whether fish i is dead (1) or alive (0) when inspected after exposure to one of the seven parameters investigated. The first parameter, capture depth$_i$, is the depth (measured in meters) from which fish i was retrieved; percentages (0–100%) were assigned to each depth to represent corresponding mortality rates for each retrieval depth investigated. The second parameter, venting$_i$, is a binary variable recording whether fish i was vented (1) or not (0); percentages were assigned to vented (1) and unvented (0) fish to represent corresponding mortality rates. Thirdly, retrieval rate$_i$ is a binary variable and records the relative rate at which fish i was brought to the surface, either slow enough for acclimation to neutral buoyancy, which depends on species and was typically only observed in research-based collections where commercial and recreational fishing gear was not used, or fast, similar to commercial fishery retrieval rates; percentages were assigned to slow (0) and fast (1) rates to represent corresponding mortality rates. Fourth, hook type$_i$ is a binary variable recording if fish i was captured with

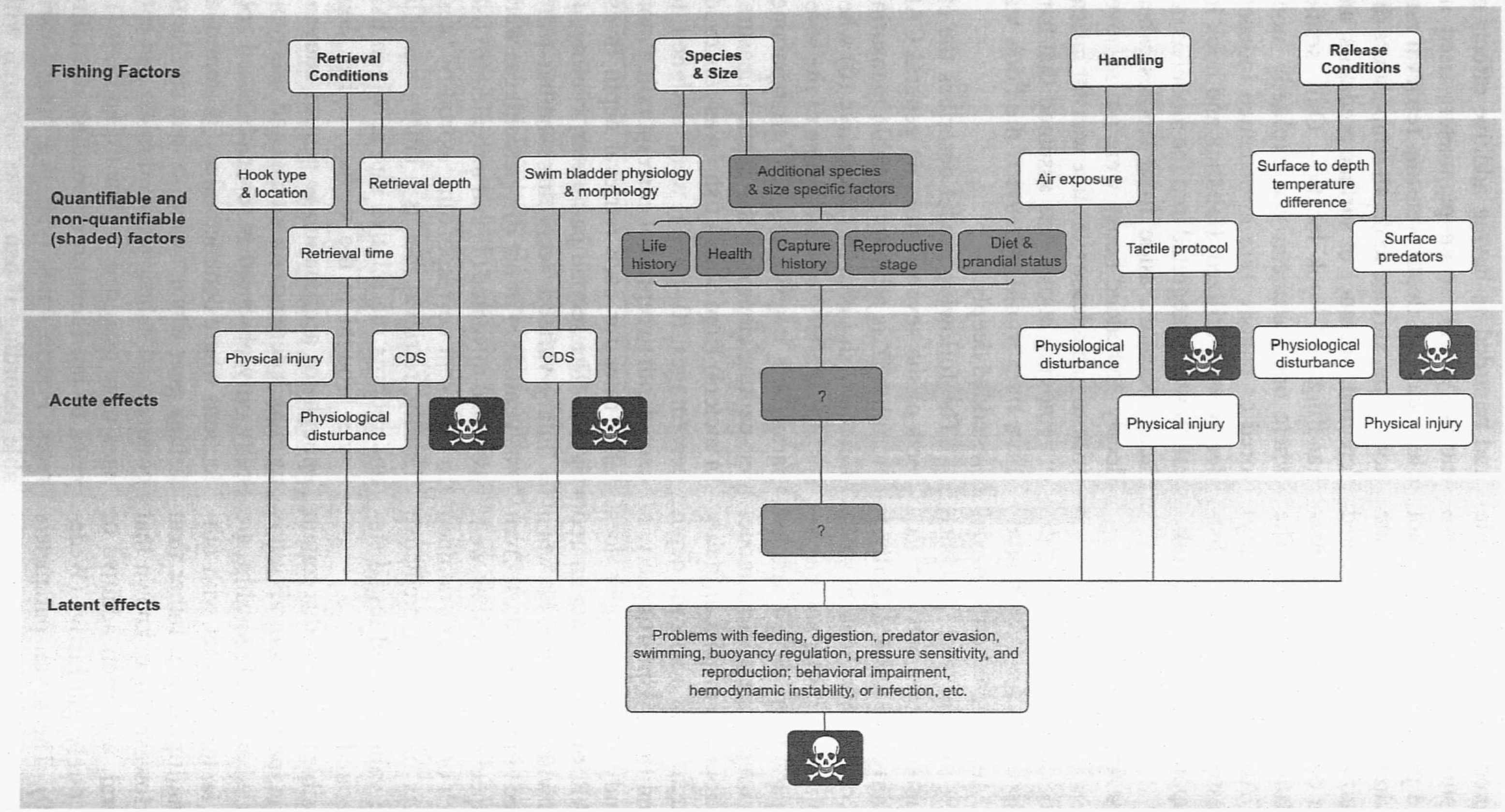

Figure 3. Framework for understanding catch and release (CAR) mortality based on four main fishing factors (top panel), eight parameters most commonly investigated as well as five factors that are not easily identifiable or quantifiable (second panel), and the acute and latent effects of CAR (third and fourth panels). Boxes shaded in gray represent uncertainties in the overall understanding of each factor's contribution to CAR, and black boxes with skull and crossbones represent probable mortality from the respective aspect of CAR or acute effects related to CAR.

a J hook (1) or circle hook (0); perecentages were assigned to each hook type to represent each corresponding mortality rate. Fifth, water temperature$_i$ is a binary variable recording the relative temperature of surface waters either being warm or outside the species' optimal temperature range (1), or cool or optimal for that particular species upon release (0); percentages were assigned to each temperature differential to represent mortality rates. The sixth parameter, predation$_i$, is a binary variable recording if there were surface predators present (1) or not (0) when fish i was released; percentages were assigned to the presence or absence of surface preadators to represent corresponding mortality rates. Finally, the seventh parameter, handling time & hook location$_i$, is a binary variable that combines both parameters and is (1) for long handling time and visceral hook location and (0) for short handling time and superficial hook location; percentages were assigned to each category to represent corresponding mortality rates. The model, which predicts Y_i, whether fish i is dead or alive, using a-h as constants and ε_i as the error term, was calculated using SigmaStat statistical program Version 3.0 (Systat Software Corp, Richmond, California, USA) and assumes that mortality increases with depth. The power of the test for each parameter (i.e., the probability of accepting an incorrect H_0 [coefficient is 0] when H_1 [coefficient is the estimated value] is true) was calculated at $\alpha = 0.05$. When power is low (<0.40) a nonsignificant result ($P > 0.05$) is inconclusive. The predictive model is as follows:

$$Y_i = \frac{\exp\begin{pmatrix} a + b^*\textbf{Capture depth}_i + c^*\ \textbf{Venting}_i + d^*\ \textbf{Retrieval rate}_i + e^*\ \textbf{Hook type}_i \\ + f^*\textbf{Water temperature}_i + g^*\textbf{Predation}_i + h^*\ \textbf{Handling \& hook location}_i \end{pmatrix}}{1 + \exp\begin{pmatrix} a + b^*\textbf{Capture depth}_i + c^*\ \textbf{Venting}_i + d^*\ \textbf{Retrieval rate}_i + e^*\ \textbf{Hook type}_i \\ + f^*\textbf{Water temperature}_i + g^*\textbf{Predation}_i + h^*\ \textbf{Handling \& hook location}_i \end{pmatrix}} + \varepsilon_i$$

Given that, (1) data from an array of species were utilized for this model, (2) no two studies were executed identically, and (3) no study incorporated every factor of interest, the approach to modeling utilized for this contribution is not statistically concrete. However, it is critical that, even if only a theoretical predictive tool at this point, we have a starting point for future studies investigating CAR mortality in red snapper and other species.

Results and Discussion

I. Qualitative Approach

Fishing Factors: Retrieval conditions

Hook type/location.—Hook type and location have been the most thoroughly examined factors in CAR mortality studies and the leading causes for CAR mortality in shallow water species, including red snapper retrieved shallower than 30 m (Muoneke and Childress 1994; Watterson et al. 1998; GMFMC 2000; Burns et al. 2004). Fishing style, fish size, species feeding mode, and species mouth morphology necessitate an array of hook types (shape and barb presence/numbers) and sizes (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Casselman 2005; Cooke et al. 2005). Circle hooks generally result in lower mortality rates (0–34%) than other hook shapes because they are rarely swallowed (Cooke et al. 2003b; Cooke et al. 2005; Millard and Mohler 2005). For this reason, circle hooks are recommended for red snapper as well as many other species. However, circle hooks require more time to remove and eye hooking, which may permanently impair vision, is common (Cooke et al. 2003b; Cooke et al. 2005; Millard and Mohler 2005). J-hooks are easier to set and remove compared to circle hooks but result in higher mortality rates (0–46%) because they are more prone to embed deeply, resulting in damage to heart, liver, gill arches, kidneys, and intestines (Cooke et al. 2005). Barbless hooks will not embed in a fish easily, and for that reason, are less desirable to anglers (Cooke et al. 2001). However, barbless hooks are easier to remove than barbed counterparts and therefore reduce handling time, tissue damage, and ultimately mortality rates (Cooke et al. 2001). Bait type may also result in differences in hooking mortality. Lunging behavior, common in carnivorous species like the red snapper, regularly results in esophageal hooking and therefore increased hook removal and air exposure time and chance of additional injury (Muoneke and Childress 1994; Wilde et al. 2000; Burns et al. 2004; Bartholomew and Bohnsack 2005; Casselman 2005). Some investigations, however find data on hooking-induced CAR mortality inconclusive (Aalbers et al. 2004; Bartholomew and Bohnsack 2005; St. John and Syers 2005). While hooking may rarely result in immediate mortality, latent effects of hooking and multiple hooking events should be considered, especially for red snapper and other long-lived and high site fidelity species that may encounter angling often (Bartholomew and Bohnsack 2005). Clearly, mortality related to hook type is related to how and where the hook penetrates the fish, bait type, and how difficult it is to remove the hook once the fish is retrieved from the water (Pelzman 1978; Murphy et al. 1995; Nelson 1998; Wilde et al. 2000; Aalbers et al. 2004; Burns et al. 2004; Lindsay et al. 2004; Bartholomew and Bohnsack 2005).

Retrieval time.—Acute and latent effects of retrieving a fish rely not only on specific details of hooking, as outlined above, but also on the degree and duration of struggle as the fish is brought to the surface (Gustaveson et al. 1991; Tufts et al. 1991; Ferguson and Tufts 1992; Cooke et al. 2001; Stephens et al. 2002; Cooke et al. 2003a; Suski et al. 2003; Bartholomew and Bohnsack 2005; Bettinger et al. 2005; Casselman 2005; Morrissey et al. 2005; Lupes et al. 2006). The physiological effects of play (how long it takes to retrieve a fish) have been well studied. Acute effects include changes in heart rate, cardiac output, blood pressure, ventilation rate, plasma parameters (e.g., catecholamines, corticosteroids, glucose, lactate, chloride, and osmolarity), respiratory and metabolic acid-base balance, and reductions in muscle energy stores. The acute physiological effects of retrieval may take several hours to return to baseline levels, potentially resulting in cellular and tissue damage, immune suppression, changes in behavior, and ultimately increased mortality (Beggs et al. 1980; Wood et al. 1983; Tufts et al. 1991; Muoneke and Childress 1994; Wells 1996; Davis 2002; Cooke et al. 2001; Manire et al. 2001; Cooke et al. 2003a; Cooke et al. 2003b; Bartholomew and Bohnsack 2005; Casselman 2005; Cooke et al. 2005; Cooke and Suski 2005). Despite the fact that the overall physiological response to retrieval and play has been clearly outlined, monitoring changes in physiological parameters upon capture, prior to release, and post release has not been found adequate for predicting mortality (Davis 2002).

Retrieval depth.—Countless field studies have considered gear types and retrieval times responsible for CAR mortality in shallow water species, but for a deep-water fish like red snapper, the fundamental concern with CAR is capture depth (Rummer and Bennett 2005). It is well known that, if a fish moves above the level at which it is in hydrostatic equilibrium with its environment, the decrease in hydrostatic pressure (1 atm for every 10 m of water) leads to an expansion of the SB

(Harden-Jones 1952). If ambient pressure is rapidly reduced, catastrophic decompression (CD) may result in SB overexpansion (Figure 4) or rupture and internal injuries, collectively referred to as catastrophic decompression syndrome (CDS) (Harden-Jones 1952; Keniry et al. 1996; Schmidt-Nielsen 1997; Collins et al. 1999; Neufeld and Spence 2004; Rummer and Bennett 2005; St. John and Syers 2005). Injuries associated with CDS can often be observed superficially, immediately as a fish is brought to the surface. In the field, researchers have observed that up to 50% of red snapper retrieved from depth possess superficial injuries, most of which were related to SB over-expansion (e.g., stomach eversion from the mouth and intestinal protrusion) (Gitschlag and Renaud 1994; Rummer and Bennett 2005). However, external symptoms of CDS in red snapper have not been found to be accurate predictors of mortality (Gitschlag and Renaud 1994; Rummer and Bennett 2005). The lack of correlation between external injuries and mortality is problematic in many other deep-water species as well. For example, Neufeld and Spence retrieved burbot (*Lota lota*) directly from depths ranging 13–31 m and found 22% of the fish died within 10 min, all of which exhibited varying degrees of CDS, but no trend could be established from superficial observations (Neufeld and Spence 2004). Necropsy results revealed severe internal injuries, and mortality was likely due to ruptured blood vessels, hemorrhaging, and hematomas in the pericardial region (Neufeld and Spence 2004). Information on CDS in red snapper has been uncovered largely through systematic laboratory experiments and thorough necropsy immediately following CD (Rummer and Bennett 2005). Cardiac injuries, including hemorrhaging and hematomas, that would likely be fatal in nature, were sustained by 18% of red snapper decompressed from pressures equivalent to 30 m and in 90% of red snapper decompressed from pressures corresponding to 110 m depth (Rummer and Bennett 2005). It is certain that external symptoms of CD account for only a slight proportion of the overall detriment sustained by the fish when retrieved from depth; therefore, the underlying causes for mortality can probably only be uncovered via thorough necropsy (Gitschlag and Renaud 1994; reviewed in Muoneke and Childress 1994; Keniry et al. 1996; Cooke and Suski 2005; Morrissey et al. 2005; Rummer and Bennett 2005; Nichol and Chilton 2006). Capture depth may be the most important factor influencing CAR mortality in deepwater species, but the response likely varies by species and fish size; this area of study has not yet received ample attention (Gitschlag and Renaud 1994; Keniry et al. 1996; Rummer and Bennett 2005; St. John and Syers 2005).

Fishing Factors: Species and size

Swim bladder physiology and morphology.—Studies on SB organization and physiology date back to the early 1800s. However, linking a species' SB physiology and morphology to CD-mediated overinflation and expansion patterns and ultimately the type and degree of injuries a fish sustains upon retrieval from depth, is a new area of study. It is known that species with closed (physoclistous) SBs are more prone to CD-related CAR mortality than species with open (physostomous) SBs, lacking functional SBs, or from surface or shallow (<5 m) waters (Davis 2002; Neufeld and Spence 2004; Bartholomew and Bohnsack 2005; Morrissey et al. 2005). Physostomes can rapidly remove excess gas by using the pneumatic duct as an escape valve and are therefore less likely to experience rapid SB overexpansion (Harden-Jones 1952). For the remainder of this review, however, the focus will be on physoclists, like red snapper, that must utilize the slow process of gas resorption into the blood to empty the SB. It may take several hours for the oval window to sufficiently resorb (re-

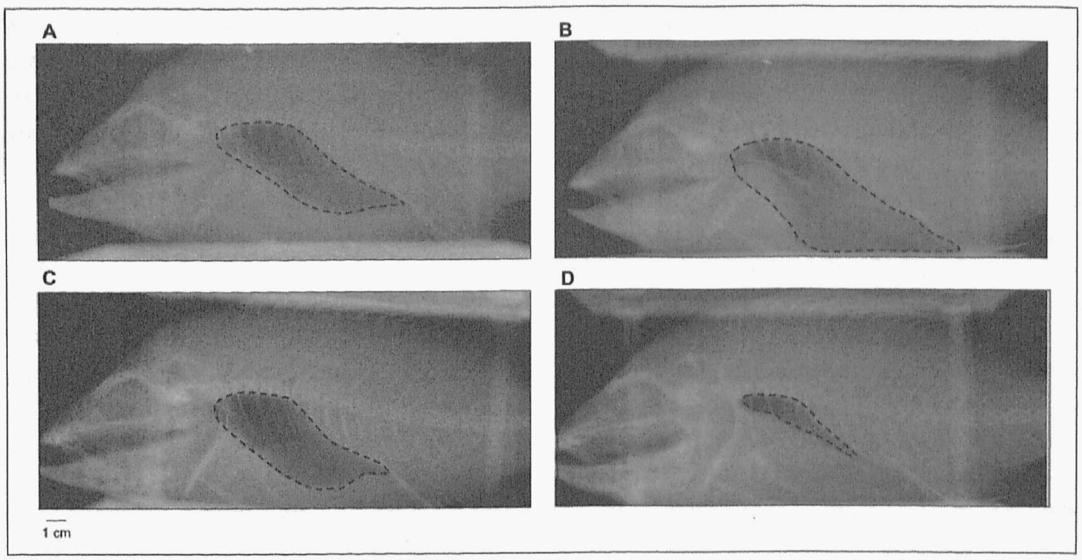

Figure 4. Lateral aspect X-ray images taken of red snapper acclimated to ambient pressure of 1atm (panels A and C). Panel B is following decompression of the fish from panel A. The fish from panel A was decompressed from a pressure of 6atm, a simulated depth of 50 m, at a rate of 0.1atm/s. Panel D represents the fish from panel C following decompression from a pressure of 12atm. An acclimation depth of 110 m was simulated, and decompression was executed at a rate of 0.1atm/s, during which time the fish's swim bladder ruptured. The broken line in each image demarcates the swim bladder boundary. Panels A and B were modified from Rummer and Bennett (2005), and panels C and D are images compiled from unpublished data from Rummer.

move) gas from the SB to maintain neutral buoyancy, and if pressure rapidly decreases, SB overexpansion will occur (Harden-Jones 1952; Keniry et al. 1996). Resorption rates are not as well characterized as SB secretion (filling) rates, and so most of our understanding is based on secretion data. Red snapper can acclimate to changes in depth (by filling the SB), while maintaining neutral buoyancy, at a rate no faster than 0.52 m per hour, a rate comparable to averages reported for other species, ranging 0.21–2.5 m per hour (Alexander 1972; Wittenberg and Wittenberg 1974; Ribbink and Hill 1979; Harden-Jones and Scholes 1985; Rummer and Bennett 2005). Secretion and resorption are mechanistically different and vary by species, but secretion rates are generally faster than if not equal to resorption rates, meaning 0.52 m per hour is a conservative estimate for resorption. This indicates that a red snapper would have to be retrieved from 50 m over a period of at least four days in order to avoid SB overexpansion upon retrieval. Healthy fish devoid of CDS have been retrieved from depth for research purposes when divers cage fish at depth and subsequently initiate a step-wise ascent over hours or days to bring fish to surface pressures without the risk of CD, but the protocol is clearly not feasible in recreational or commercial fisheries (Haight et al. 1993; Neufeld and Spence 2004).

The most obvious differences among SBs are at the morphological level. Differences in volume, shape, and elasticity vary by species and are also most pronounced between freshwater (FW) and seawater (SW) teleosts. If calculated relative to water density, the SB of a FW teleost occupies approximately 7% of the body volume, and the SB of a SW teleost occupies slightly less, approximately 5% of the body volume (Harden-Jones 1952; Alexander 1972; Alexander 1993). In line with this concept, red snapper SBs occupy an average 4.86% (n = 64) of the total body volume (Rummer, unpublished data). Expansion patterns depend on volume but also differ with SB shape. SB shape is typically ellipsoidal, as is seen in the red snapper, but several species defy this trend and possess multi-lobed or even heart-shaped SBs (Barimo 1998; Davenport 1999; Carpenter 2004; Rummer and Bennett 2005; Strand et al. 2005). Change in SB shape during CD is also influenced by the passive resistance generated from the SB wall and surrounding tissues (Harden-Jones 1952). A thick-walled SB, lacking substantial elastic properties, and therefore resisting expansion (e.g., *Gadus* spp.), may be more likely to tear or rupture than a thin-walled, less resistant SB (e.g. *Perca* spp.) (Harden-Jones 1952; Rogers et al. 1986; Nichol and Chilton 2006). SB rupture is rare in red snapper and has been observed in only 3% of fish in laboratory studies (Figure 4), which may give insight into the elasticity of red snapper SBs (Rummer and Bennett 2005; Rummer, unpublished data).

If SB rupture is common for a species, however, repair time is crucial. SB rupture has been observed in 90% of cod investigated and found to occur after pressure reductions greater than 50% or if fish are retrieved from deeper than 30 m (Harden-Jones 1952; Wilson Jr. and Smith Jr. 1985; Nichol and Chilton 2006). However, tears in cod SBs are repaired quickly, within 1–2 d; whereas, red snapper average 14 d, and other species may take longer than 4–8 weeks (Rankin et al. unpublished data; Rummer, unpublished data; Bruesewitz et al. 1993). Loss of SB function via rupture or overexpansion affects maneuverability that, in some species, can result in compensatory fin movements and a 20% increase in energy expenditure to maintain position in the water column (Harden-Jones 1952; Alexander 1972; Alexander 1993; Gitschlag and Renaud 1994). Reduced vertical migration rates and erratic recuperation behavior are common and probably related to SB volume leakage (Strand et al. 2005; Nichol and Chilton 2006). The SB is nature's solution to the buoyancy problem in teleosts and an anatomical and physiological feature potentially responsible for the extensive adaptive radiation of modern teleost fishes. However, the SB may also be the basis for the ultimate demise of red snapper and other high profile fisheries species in a CAR-based fishery. All things considered, capture depth is the underlying factor responsible for the greater part of CAR mortality, and so it is reasonable to begin species-specific CAR mortality investigations with an extensive understanding of SB physiology and morphology.

Additional species and size specific factors influencing CAR mortality.—Life history and reproductive stage, diet and prandial status, health, and capture history are aspects that can affect how a fish responds to the initial hooking and retrieval processes, SB expansion, as well as recovery post release. However, data are limited, contradictory, or only anecdotal. Depending on species, size may attribute to post release survival; large fish appear to descend faster, but small fish ultimately recuperate faster from the initial stress (Muoneke and Childress 1994; Nelson 1998; Wilde 1998; reviewed in Bartholomew and Bohnsack 2005; reviewed in Casselman 2005; Millard and Mohler 2005; Bettinger et al. 2005; Nichol and Chilton 2006). Other studies have found the opposite or no trend at all, further implying species dependence on size and survival relationships (Gitschlag and Renaud 1994; Bettoli and Osborne 1998; Wilde et al. 2000; Davis 2002).

Slight differences within a species attributed life history stage or reproductive status may affect post release survival both directly, by affecting hormone levels and the magnitude of the stress response, and indirectly via SB expansion patterns and internal organ displacement (Pankhurst and Dedual 1994; Machias and Tsimenides 1996). Ripe gonads in both male and female fish occupy a substantial portion of the body cavity and may alter SB expansion patterns and consequently, internal organ displacement. Intraspecific variations may be due to differences in gonad shape and size (large and tubular in females versus flat and thin in males). Fish with substantial body fat present in the abdominal cavity may also respond differently upon SB overexpansion; fat may insulate internal organs thus preventing or alleviating compaction injuries. However, excess abdominal body fat decreases available body cavity space for the SB to expand and may result in a lower threshold for when SB expansion-mediated displacement injuries shift to compaction injuries (Rummer and Bennett 2005). Postprandial physiological parameters could magnify the physiological stress associated with exhaustive exercise experienced by the fish upon retrieval as well, but little information exists to expand on this point (Busk et al. 2000; Hicks and Bennett 2004). Finally, multiple CAR events increase the probability of severe injuries (Nichol and Chilton 2006). Whether this increase is due to unhealed physical injuries or the chronic effects of a previous physiological disturbance has yet to be investigated (Nichol and Chilton 2006). A thorough understanding of species and size relationships relative to CAR and factors affecting mortality is needed.

Fishing Factors: Handling

Air exposure.—The time interval during which a fish is brought to the surface and returned to the water is crucial to post release survival in red snapper as well as many other species. Burns et al. (2002) suggest a direct relationship between short surface intervals and increased likelihood for post release survival. Air exposure can be detrimental to many species but is a necessary component of the de-hooking and release process. Rock bass, *Ambloplites rupestris*, exposed to air for less than one minute require up to two hours to fully recover (Cooke et al. 2001). However, Bettoli and Osborne (1998) found air exposure to be unrelated to CAR mortality in striped bass, *Morone saxatilis*. Air temperature, rather than exposure time, more strongly influences CAR mortality in striped bass and sablefish, *Anoplopoma fimbria* (Bettoli and Osborne 1998; Lupes et al. 2006). Stress parameters (plasma cortisol and glucose) were significantly elevated, and the immunological response was suppressed in sablefish exposed to elevated air temperatures (Lupes et al. 2006). Direct cause for release mortality cannot be easily defined and generalizations cannot yet be made, but it is clear that air exposure (time and temperature) negatively affects post release survival.

Tactile protocol.—Excessive handling and use of landing nets when fish are retrieved and released can cause physical injury and physiological stress (reviewed in Casselman 2005). Many protocols however, recommend handling a fish long enough to vent the over-expanded SB with a cannula or hypodermic needle prior to releasing the fish (Keniry et al. 1996; Wilson and Burns 1996; Burns et al. 2002). The technique alleviates compression on internal organs and allows an otherwise positively buoyant fish to quickly return to depth (Keniry et al. 1996; Wilson and Burns 1996; Burns et al. 2002). Results from some venting studies remain inconclusive, and some data suggest the process is detrimental (Gotschall 1964; Bruesewitz et al. 1993; Render and Wilson 1994 & 1996). The venting process will undoubtedly increase handling time and air exposure, and many investigators recommend avoiding venting for those reasons (reviewed in Casselman 2005). Properly venting a fish requires knowledge of the species' internal anatomy and, if done improperly, can result in increased mortality due to infection or damage to vital organs (Parrish and Moffitt 1993). By and large, if a fish exhibits a noticeably expanded SB or external symptoms of SB overexpansion that would necessitate venting, the fish has already sustained displacement and compaction injuries, and all other fishing factors will only amplify this baseline level of insult.

Fishing Factors: Release conditions

Difference between depth and surface water temperature.—CAR mortality in many species positively correlates with the temperature differential between conditions at depth of capture and the surface temperatures (Muoneke and Childress 1994; Murphy et al. 1995; Nelson 1998; Wilde 1998; Wilde et al. 2000; Bartholomew and Bohnsack 2005; Bettinger et al. 2005; Campbell et al. unpublished data). Warm surface waters can account for up to an additional 7–31% increase in mortality in Lutjanids, Percids, and Serranids (Fable 1980; Low 1981; Bugley and Shepherd 1991; Gitschlag and Renaud 1994; Muoneke and Childress 1994; Keniry et al. 1996; Wilson and Burns 1996; Shasteen and Sheehan 1997; Collins et al. 1999; Bartholomew and Bohnsack 2005; Casselman 2005; Rummer and Bennett 2005). Mortality is likely due to a suppressed immunological response, as signified by elevations in plasma lactate and glucose, indicative of cortisol release (Gustaveson et al. 1991; Lupes et al. 2006). Elevated surface water temperatures also correlate with low dissolved oxygen, which could be detrimental to released fish when at a high respiratory demand (reviewed in Bartholomew and Bohnsack 2005). Delayed mortality may be reduced by holding fish in recovery tanks prior to release or releasing fish into cages that are subsequently lowered to an intermediate depth (Matteson and Hannah, unpublished data; Gitschlag and Renaud 1994; Shasteen et al. 1997; Bettinger et al. 2005; St. John and Syers 2005). However, recovery tanks and recompression cages may only allow time for fish to recover from physiological stress. If fish sustain internal organ damage, although it may be to a lesser extent if fish are immediately recompressed, the latent effects may manifest themselves after physiological parameters have returned to baseline levels.

Surface predators.—Birds, large fish, and marine mammals commonly prey on injured, released red snapper and may account for 20% CAR mortality when fish are retrieved from 20 to 30 m depths (Parker 1985; Rummer and Bennett 2005). Although perceived high, predation has not been thoroughly investigated because experimental protocol either determine predation via surface observations or release fish into cages where predation is not a risk (Parker 1985; Gitschlag and Renaud 1994; Davis 2002; Burns et al. 2004; Bartholomew and Bohnsack 2005). In fact, Diamond and colleagues still measured 71% CAR mortality in cage-released red snapper retrieved from 45 m depths (Diamond and Campbell, unpublished data). Fish that are vented prior to release are able to avoid surface predators directly, as they are no longer positively buoyant and therefore able to freely swim back to depth (Parker 1985; Davis 2002; Burns et al. 2004; Bartholomew and Bohnsack 2005). Although Burns et al. (2002) retrieved small red snapper from 55 m, vented them, and then released them into cages, they still recorded 70% mortality. The venting procedure will also alleviate predation indirectly by decreasing the fish's target strength, making the fish a less obvious target for echo-locating predators than if the SB was overinflated and target strength high (Love 1969, 1971, and 1977; Keniry et al. 1996; Collins et al. 1999). Caged release and sinker-mediated release techniques have been recommended for releasing CD fish so that venting is not necessary and the risk of predation and detrimental surface water conditions can be assuaged, but the reality of CDS as a result of retrieval depth remains an issue and will compromise survival over the long term.

II. Quantitative Approach

The ultimate goal is to be able to utilize the framework outlined in Figure 3 for designing future experiments to understand the basis for CAR mortality in red snapper and other fish species. The full theoretical logistic regression model (Table 1) included all parameters as significant contributions toward mortality, even though some were less significant than others (e.g., venting; $p = 0.023$, predation; $p = 0.049$, and handling time and hook location; $p = 0.035$). A likelihood ratio test (test statistic 77.680) of the theoretical model showed that the model was an adequate fit ($P < 0.001$) of the response variable. The ability of the theoretical model to correctly predict Y_i (whether the fish was alive or dead) was 98% (with 1.5% of live fish predicted to be dead while 22.9% of dead fish were predicted as alive). Given the limitations in data available, mortality rates from an array of species were used in conjunction with red snapper specific data to generate this predictive model as a starting point for future investigations.

To most effectively communicate CAR mortality data used to generate the predictive model for this review, the baseline mortality rate (%) as a function of capture depth was plotted (Figure 5) (Rummer and Bennett 2005). The remaining six parameters were factored in, one by one until all were integrated into the mortality curve, represented by the curve furthest to the left on the graph (Figure 5). For comparison, a capture depth dependent mortality curve, according to a comprehensive set of field data collected by

Table 1. Parameter estimates for the predictive model built to describe whether a fish would be alive or dead as a result of capture depth, venting, retrieval rate, hook type, surface to depth temperature differential, surface predators, and handling time and hook location (first column). The constant and coefficients (± standard error) for the model are represented in the first and second columns respectively. The Wald statistic, which is the coefficient divided by the standard error and describes how significantly each independent variable predicts the dependent variable (mortality), is represented in the third column. The odds ratio (95% confidence interval), which represent the lower and upper ends of the confidence interval in which the true odds ratio lies, is reported in the fourth column. *P* values (fifth column) were calculated from the Wald statistic and based on chi-square distribution with one degree of freedom. When *P* values are small ($P < 0.05$), this indicates high probability that the independent variables affect the dependent variable (mortality).

Variable	Coefficient (S.E.)	Wald statistic	Odds ratio (95% C.I.)	P
% Mortality	(*a*) -3.133 (0.385)	66.252	0.044 (0.021-0.093)	<0.001
Capture depth	(*b*) 0.062 (0.012)	29.023	1.064 (1.040-1.088)	<0.001
Venting	(*c*) 1.777 (0.780)	5.184	5.911 (1.287-27.279)	0.023
Retrieval rate	(*d*) 2.710 (0.693)	15.299	15.027 (3.865-58.427)	<0.001
Hook type	(*e*) 2.965 (0.684)	18.803	19.399 (5.078-74.104)	<0.001
Water temperature	(*f*) 3.815 (0.691)	30.462	45.391 (11.710-175.946)	<0.001
Predation	(*g*) 1.532 (0.783)	3.833	4.628 (0.998-21.458)	0.049
Handling time and hook location	(*h*) 1.677 (0.795)	0.795	5.347 (1.125-25.424)	0.035

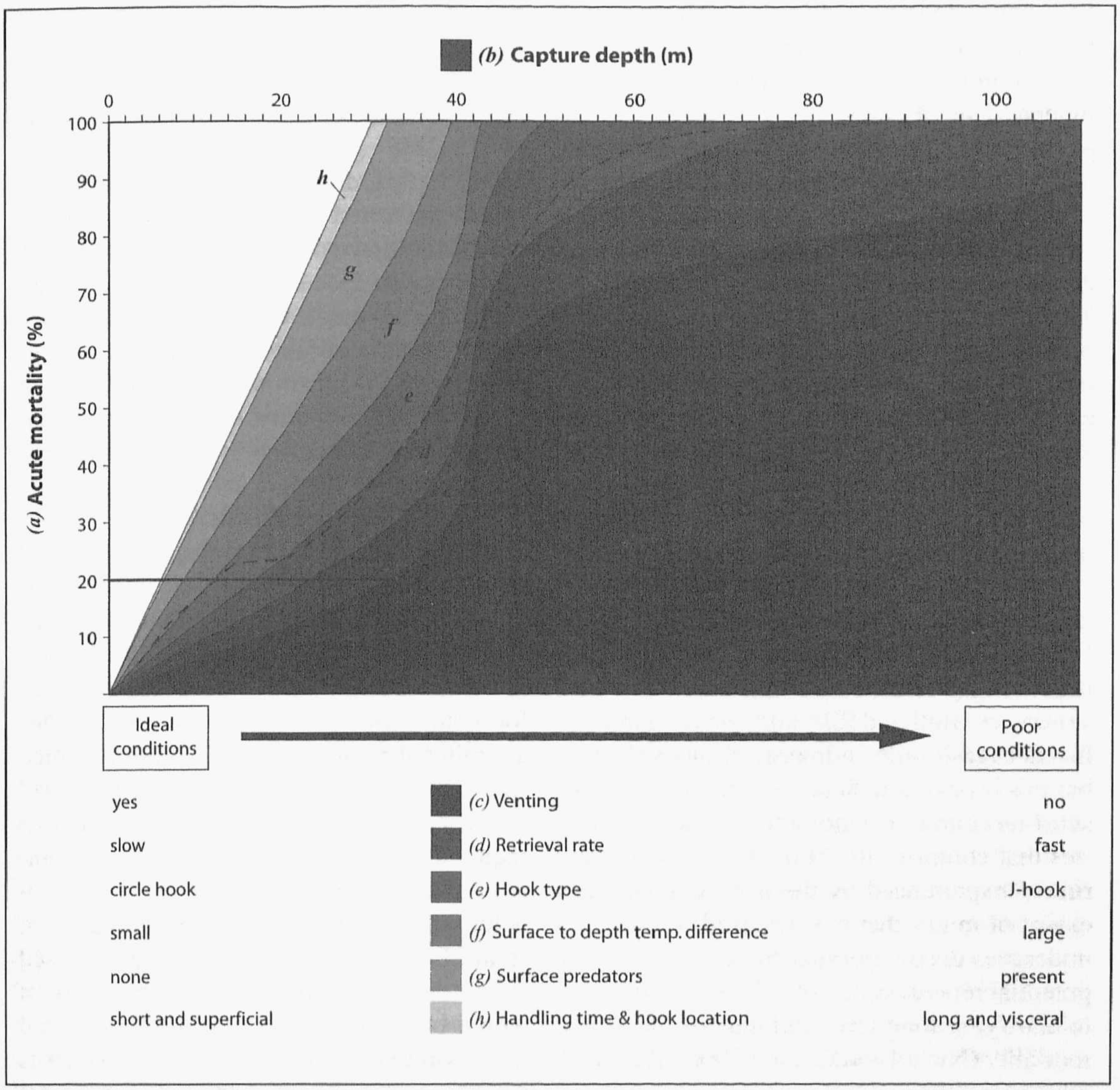

Figure 5. Graphical display of mortality (%) represented by (*a*) as a function of capture depth (m) represented by (*b*) in red snapper *Lutjanus campechanus* (Rummer and Bennett 2005) as well as six other factors represented as (*c–h*), when information from the logistical regression analysis performed for this review was incorporated into overall catch and release (CAR) mortality. Each additional factor affecting CAR was considered additive to the baseline mortality associated with capture depth and treated as a binary variable, e.g. poor and ideal conditions; data were compiled from information on CAR in other freshwater and seawater physoclist species as well as red snapper. See text in figure for further details. Note: The letters used to demarcate the dependent variable of percent mortality (*a*) and seven independent variables (*b–h*) were to maintain consistency with the abbreviations for the logistical regression model. The heavy dashed line represents actual field data from research on the Westralian jewfish, *Glaucosoma hebraicum*, used as a reference and for verifying the model with existing field data on a non red snapper species (St. John and Syers 2005). The solid horizontal line parallel to the *x*-axis at 20% represents the generally accepted mortality rate based on CAR mortality.

St. John and Syers (2005) on Westralian jewfish, *Glaucosoma hebraicum*, was also plotted, as indicated by the heavy broken line independent of the shading demarcating the parameters used in the theoretical model. To date, St. John and Syers (2005) have made the closest attempt to investigating all of the key parameters involved in CAR mortality in their study on the Westralian jewfish. The curve plotted with their data fell near the middle of the plots generated from the theoretical model, suggesting that the theoretical estimates generated from the model are reasonable (St. John and Syers 2005).

As red snapper are retrieved from deep water via traditional angling gear, the majority of the injuries that will dictate release mortality due to SB overinflation and CDS have already occurred (Figure 5) (Rummer and Bennett 2005). Numerous studies suggest that modifying gear type, slowing retrieval times, venting overinflated SBs, and releasing injured fish in cages results in improved survival rates, but this is only beneficial to some fish over the short-term and does not address the CD injuries that comprise the bulk of the overall detriment experienced by the fish. Realizing the extent of injury that has occurred when a fish undergoes decompression from depth and the potential repercussions of CDS is the first step to clarifying long-term and thus overall CAR mortality (Nichol and Chilton 2006). Retrieval conditions, species and size relationships, handling, and release conditions play a key role in the extent of injury incurred by the fish, and studies should be designed with this comprehensive CAR mortality framework in mind.

Concluding Thoughts

Management strategies are typically designed assuming CAR mortality is below 20% (Muoneke and Childress 1994). Recent field studies suggest this may be possible for red snapper retrieved from depths ranging 20–40 m (Patterson et al. 2001; Burns et al. 2004) but rates may be greater than 70% if fish are retrieved from deeper depths (Burns et al. 2002). Logbook records from commercial vessels suggest rates may range upwards of 72–78% (Poffenberger and McCarthy 2004). In this review, it is evident that current estimates for red snapper CAR mortality are indeed multifarious, which may be the trend for other fish species as well (Nieland et al. 2007, this volume). CAR mortality depends on a multitude of factors, some of which interact with others; however, the underlying cause of CAR mortality, especially in a deep-water physoclistous fish, is directly related to capture depth.

Clearly, the regulations needed in order to ensure CAR mortality remains low would have to be extremely conservative. In toxicology studies, the lethal concentration of a toxicant at which 50% mortality would be predicted (LC50) is commonly reported and used for comparisons between species. Perhaps a similar threshold, a lethal depth at which CAR mortality is 20%, or the LD_{20}, is desired for fish species where CAR is common or required. Because fisheries models are commonly based on CAR mortality of 20% or below, this seems a reasonable starting point. If an LD_{20} was assigned to red snapper based solely on capture depth related mortality, it would be approximately 30 m (data plotted from Rummer and Bennett 2005), which is realistic and a depth where red snapper are fished in some areas of the Gulf of Mexico (Moran 1988; Workman and Foster 1994; Manooch et al. 1998; Dorf 2003; Burns et al. 2004). However, those data only account for capture depth in fish decompressed in a laboratory decompression chamber. If the remaining factors utilized to build the predictive model were considered as confounding this baseline mortality, the predicted LD_{20} for red snapper could be as shallow as 6 m (Figure 5). Again, this estimate dictates that the factors considered exhibit a linear relationship and an additive effect on one another;

multiplicative interactions could result in an even shallower estimate.

For red snapper or any other high profile fishery species, no single investigation considering all of the parameters described in the CAR mortality framework (Figure 3) has yet been executed. It is promising that results from field studies, however, fall within the range of depth related mortality rates calculated from the predictive model. For example, if St. John and Syers' (2005) data for CAR mortality in the Westralian jewfish, *G. hebraicum*, a species with similar depth profile to red snapper, was re-plotted so depth was the independent variable, the deeper end of the LD_{20} range would be close to 21 m. If CAR mortality data for Pacific cod, *Gadus macrocephalus*, a particularly deep-dwelling species, were re-plotted against capture depth, the LD_{20} would be 10 m (data plotted from Nichol and Chilton 2006). The former of the two field studies highlighted used caged-release protocols, and the latter a traditional mark–recapture protocol, making it difficult to make concrete conclusions regarding long-term effects and direct causes of mortality. This information speaks well for the model but poorly for the fate of the fishery. Limiting the red snapper CAR fishery to depths between 6 and 30 m, the most conservative to the most liberal depths from which we can expect 20% CAR mortality, may not be the best course of action. Red snapper occasionally occupy depths deeper than 200 m, and depth and age-class distribution are closely linked, meaning a depth limitation would alter current population structure (Moran 1988; Workman and Foster 1994; Manooch et al. 1998). Furthermore, as seen in Figure 5, as each fishing factor is accounted for, the LD_{20} decreases representing depths where fishing practices probably cannot be sustained economically. This overview illuminates the necessary approach to understanding the root of CAR mortality, starting with capture depth and SB morphology and physiology. This area of research will, undoubtedly be more heavily investigated as stocks continue to decline necessitating modifications to current management strategies, and fits well within the context of conservation physiology, an emerging discipline where physiological responses of organisms to human influences that may contribute to population declines are directly investigated (Wikelski and Cooke 2006).

The most effective way to manage a fishery that succumbs so seriously to CAR mortality is not via size limits, season closures, and bag limits. Countless combinations have been proposed in an effort to maintain status quo while rebuilding the fishery (SEDAR 7 2005). All combinations, however, seem problematic; either the socioeconomics of the red snapper fishery or the potential for population growth and recovery are negatively impacted. Furthermore, sufficient information is not yet available to, with confidence, impose maximum fishing depths, which would be difficult to monitor and may vary too greatly between species. It would seem logical to impose fishing restrictions to discrete areas such that fish populations can be safeguarded from all fishing and CAR activity, therefore protecting age, size, and sex classes and ratios simultaneously. Aquatic protected areas (APAs) and marine protected areas (MPAs) are generally restricted areas, and no-take reserves (NTRs) are extremely restricted and encompass areas where all fishing and extractive activities are banned and human impact is minimal (Bohnsack 1998). Both APA or MPAs and NTRs are modern management strategies with growing acceptance and have been particularly successful along the North American West Coast in protecting long-lived, slow-growing rockfish (*Sebastes* spp.) (Coleman et al. 2000; Soh et al. 2001; Schroeder and Love 2002; Roberts 2003; Berkeley et al. 2004; Bartholomew and Bohnsack 2005; Smith et al. 2006). Average values for fish density, biomass, organism size, and biodiversity increase by almost four-fold, develop quickly, and persist, compared to areas outside reserves (Mosqueira et al. 2000; Halpern and Warner 2002; Ault et al. 2005). Additionally, this strategy protects genetic diversity, ecosystem structure, function and integrity, increases scientific and public knowledge and understanding of aquatic systems, enhances nonconsumptive opportunities, as well as provides fishery benefits (Bohnsack 1998; Coleman et al. 2000). CAR mortality and serial overfishing can be reduced therefore supporting sustainable fisheries without reducing current catch levels (Soh et al. 2001; Roberts 2003). For fish species like red snapper, where overfishing is widespread and CAR mortality is high, or other species where CAR is unclear or a thorough investigation of depth-related CAR mortality has not been performed, strategies based on space (MPAs and NTRs) rather than time or numbers (i.e., season closures, size limits, bag limits, etc.), have the greatest potential for overall conservation and sustainability and should be seriously considered (Coleman et al. 2000).

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