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[Article]

The Differential Response to Decompression in Three Species of Nearshore Pacific Rockfish

ALENA L. PRIBYL* AND CARL B. SCHRECK
Oregon Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Oregon State University, Corvallis, Oregon 97331, USA

MICHAEL L. KENT
Microbiology Department, Oregon State University, Corvallis, Oregon 97331, USA

STEVEN J. PARKER
National Institute of Water and Atmospheric Research, Post Office Box 893, Nelson, New Zealand

Abstract.—The genus *Sebastes* (rockfishes) is an ecologically diverse group of fish, more than 60 species occurring off the Oregon, Washington, and California coasts. As of 2004, seven species of rockfish were classified as overfished by the Pacific Fishery Management Council. Because rockfishes often experience barotrauma to varying degrees when forced up from depth, the management of discard mortality has been difficult. In this study, the macroscopic, morphological, and physiological responses to decompression of black rockfish *S. melanops*, blue rockfish *S. mystinus*, and yellowtail rockfish *S. flavidus*, all nearshore species, were investigated. The rockfish were adjusted to 4.5 atmospheres absolute (ATA; 35 m) over a period of 7–10 d in hyperbaric pressure chambers and when neutrally buoyant were rapidly brought to surface pressure in a simulated ascent. They were then examined for barotrauma injury, and the heart ventricle, head kidney, liver, gill, and pseudobranch were collected for histological analysis. We observed more macroscopic barotrauma indicators in black rockfish and blue rockfish than in yellowtail rockfish. Histological analysis showed emphysema was present in the heart ventricle of more than one-half of the black rockfish, 11% of the blue rockfish, and none of the yellowtail rockfish. No other tissue had observable injury at the histological level that was attributable to barotrauma. The lack of injury at the tissue level for black, blue, and yellowtail rockfishes decompressed from 4.5 ATA is remarkable.

The *Sebastes* genus (rockfishes) is an ecologically diverse group of temperate marine fish as over 60 species occur in the northeast Pacific Ocean (Love et al. 2002). Rockfish are important to both commercial and recreational fishing industries, but since the mid-1980s populations have been in decline (Love et al. 2002). As of 2004, seven species of rockfish in the northeast Pacific Ocean have been designated as overfished by the Pacific Fisheries Management Council (PFMC 2004). Overfished rockfish populations will take many years to recover because rockfish are long-lived and late maturing. Most species will live 40–100 years and will not mature until 5–10 years of age (Love et al. 2002). In addition, rockfish often occur in mixed-species assemblages, making it difficult for fishermen to target only a particular species. As a result, bycatch of nontarget rockfish species is a common occurrence. In the commercial fishery, most rockfish are captured using trawls; longlines and other fixed gears are also used, but to a lesser extent. Rockfish captured as bycatch using these methods are often severely injured by the time they reach the surface due to abrasions from other fish and the long period in the net or on a hook. In the recreational fishery, rockfish are captured using hook and line. Management efforts in the recreational fishery currently include bag limits, size limits, gear restrictions, time–area closures, and discard of species of concern (NMFS 2009). Discard is necessary so overfished species will not be targeted, but often discard mortality of rockfish is high because as rockfish are captured and undergo a forced ascent, the pressure change can cause barotrauma and complications due to barotrauma (excessive buoyancy and or shock) that prevent successful release.

Barotrauma is a condition that results from swim bladder gas expanding as fish are brought up from depth (forced decompression). According to Boyle's Law, as pressure decreases, gas expands exponentially. Many rockfish experience barotrauma because they are physoclists, which means they have a closed swim bladder (unlike physostomes such as salmonids, whose swim bladder is connected to their esophagus via a

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* Corresponding author: alena.pribyl@oregonstate.edu

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duct, allowing uptake–release of gas through the mouth). As a rockfish undergoes forced decompression, the expanding gas inside the swim bladder often leaks into the peritoneal and cranial cavities (Hannah et al. 2008a). The excess swim bladder gas can result in bloating, ruptured swim bladder, crushed organs, eversion of the esophagus, and exopthalmia as well as excessive buoyancy (Gotshall 1964; Rummer and Bennett 2005; Hannah and Matteson 2007; Hannah et al. 2008b; Jarvis and Lowe 2008). Excessive buoyancy makes it difficult for many rockfish species to submerge on their own. Discarded rockfish are often left floating on the surface, where they succumb to predation by birds, thermal shock, or both.

Hannah et al. (2008b) investigated levels of submergence success of nearshore rockfish species when captured from different depths and found some species (blue rockfish *S. mystinus*, canary rockfish *S. pinniger*, and widow rockfish *S. entomelas*) have difficulty submerging when captured at depths exceeding 30 m. Recent research suggests recompression of rockfish using devices such as weighted cages and barbless weighted hooks may increase survival of discarded rockfish because gases recompress, external indicators of barotrauma disappear, and fish are often able to swim away (Hannah and Matteson 2007; Jarvis and Lowe 2008). However, little information on the tissue-level effects of barotrauma in rockfish is available. Parker et al. (2006) investigated acclimation rates to pressure changes and the healing of ruptured swim bladders in black rockfish *S. melanops* decompressed from four atmospheres absolute (ATA; 30 m). Most other studies (Hannah and Matteson 2007; Hannah et al. 2008b; Jarvis and Lowe 2008; Rogers et al. 2008) have focused only on macroscopic observations of decompressed rockfish and not on investigating potential tissue-level injury. In order to gain a better understanding of discard mortality in rockfish, it is important to determine how different species of rockfish respond to decompression both macroscopically and at the tissue level, and how these injuries may relate to mortality.

In this study, we investigated macroscopic and tissue-level responses to decompression from 4.5 ATA (35 m) in three species of nearshore rockfish commonly captured in the recreational fishery: black rockfish, blue rockfish, and yellowtail rockfish *S. flavidus*. Black rockfish are most common at depths less than 55 m, can live up to 50 years, and are often found schooling with other species in the water column (Love et al. 2002). Blue rockfish are most common at depths less than 90 m, can live up to 44 years, and also regularly aggregate throughout the water column with other species (Love et al. 2002). Yellowtail rockfish are found a bit deeper, commonly at depths between 90 and 180 m, and are classified as both a nearshore and deep-shelf species. Yellowtails can live to 64 years and are also usually active in the water column during some part of the day (Love et al. 2002). Both yellowtail rockfish and black rockfish make rapid dives or ascents ranging more than 10 m in the water column (Pearcy 1992; Parker et al. 2008). Although none of these species are currently overfished, they are long-lived and late maturing, which could make them susceptible to more precipitous population declines in the future. By investigating both the macroscopic and tissue-level response of these species to decompression, we can provide fishery managers with more information on the potential for discard mortality of these species if they are discarded.

Methods

Fish collection.—Approximately 19 of each adult black, blue, and yellowtail rockfish were collected off the coast of Newport, Oregon, by hook and line from depths less than 15.2 m. Only rockfishes with no or minimal indicators of barotrauma (swollen abdomen, air in the pharyngo-cleithral membrane) were utilized. We were unable to find large numbers of yellowtail rockfish and blue rockfish at the time of sample collection for these experiments; thus, our sample size was limited to 19 for each species. Black rockfish sizes ranged from 33 to 41 cm in length, blue rockfish ranged from 29 to 41 cm in length, and yellowtail rockfish ranged from 31 to 39 cm in length. Since these lengths fall within the size range for length at first maturity for each species (Love et al. 2002), we classified these fish as adults. Rockfish in these size ranges are commonly captured in the recreational fishery. Upon return to Newport, rockfish were immediately transferred into 2.4-m-diameter flow-through tanks (106,000 L) at the Hatfield Marine Science Center where they were held until they resumed feeding and were neutrally buoyant (minimum 30 d). Cessation of feeding is a common response to stress (physical or perceived), and resumption of feeding can be an indicator that fish have recovered from the stress (Rice 1990). Neutral buoyancy ensures the swim bladder is functioning. Fish were held for a minimum of 30 d as a precaution to ensure recovery from any minor stressors as described in Parker et al. (2006). Other studies (McElderry 1979; Parker et al. 2006) have used this collection and holding technique on hundreds of black rockfish, and no quantifiable effect from capture was seen in control fish in these studies.

Fish density was 10–15 fish per tank, and flow rate was 12–15 L/min. Fish were fed a diet of thawed

TABLE 1.—Numbers of black, blue, and yellowtail rockfish used in decompression experiments. Treatment refers to rapid decompression from 4.5 ATA and control to a controlled ascent to the surface over a 3-day period.

Species	Treatment	Control
Black rockfish	12	7
Blue rockfish	9	4
Yellowtail rockfish	12	7

Atlantic silversides *Menidia menidia*, pink shrimp *Pandalus jordani*, and California market squid *Loligo opalescens* three times a week, and tanks were cleaned by siphoning debris daily. Dissolved oxygen (>80% saturation), salinity (range = 34–37‰), and temperature (range = 9.4–14.4°C) were also monitored daily.

Decompression experiments.—For each decompression experiment, we used a set of three hyperbaric pressure chambers that are described in Parker et al. (2006). Two pressure chambers served as treatment chambers, and the third pressure chamber served as a control chamber. Three to four randomly chosen rockfish (of the same species) were placed in a single pressure chamber. In each experiment, one treatment chamber held one species, and the other treatment chamber held a different species. The pressure chambers were adjusted to 4.5 ATA (approximately 35-m depth) following a standard protocol as described in Parker et al. (2006). Fish were neutrally buoyant within approximately 7–10 d. Once neutrally buoyant, treatment fish were exposed to a simulated capture event by decreasing pressure to 1 ATA over a 90-s period to induce decompression. This translates to a retrieval rate of 0.39 m/s, a rate close to what anglers would typically use. Control fish were slowly brought to surface pressure with a 10% pressure reduction every 2–3 h over a period of 3 d. This controlled rate of ascent was determined by McElderry (1979) as slow enough for black rockfish to adjust with no physical damage. McElderry (1979) determined this rate of ascent by making small adjustments in pressure and observing the length of time it took for rockfish to become neutrally buoyant. We applied the same rate of ascent to blue rockfish and yellowtail rockfish after observing neutral buoyancy in each species prior to each pressure change.

This experiment was replicated three to four times for each species of treatment fish and two to three times for each species of control fish. For adult black rockfish and yellowtail rockfish, a total of 12 treatment fish and seven control fish were sampled. For adult blue rockfish, a total of nine treatment fish and four control fish were sampled (Table 1). There were fewer blue rockfish due to a pump failure during one of the experiments. The pump failure caused a premature return to surface pressure in the chambers for both treatment and control blue rockfish. Because treatment rockfish were not fully acclimated to 4.5 ATA at the time, we were unable to use them for our study. Similarly, because control rockfish were not acclimated to 4.5 ATA and were decompressed too quickly, we could not use them for our study.

Sample collection.—Once at surface pressure, rockfish were immediately removed from the pressure chambers and examined for external barotrauma indicators. External barotrauma indicators were recorded following Hannah et al. (2008b) and included everted esophagus, tight abdomen, exophthalmia, ocular emphysema, and visible bulges or gas within the pharyngo-cleithral membrane (Figure 1). Emphysema refers to the abnormal accumulation of air in

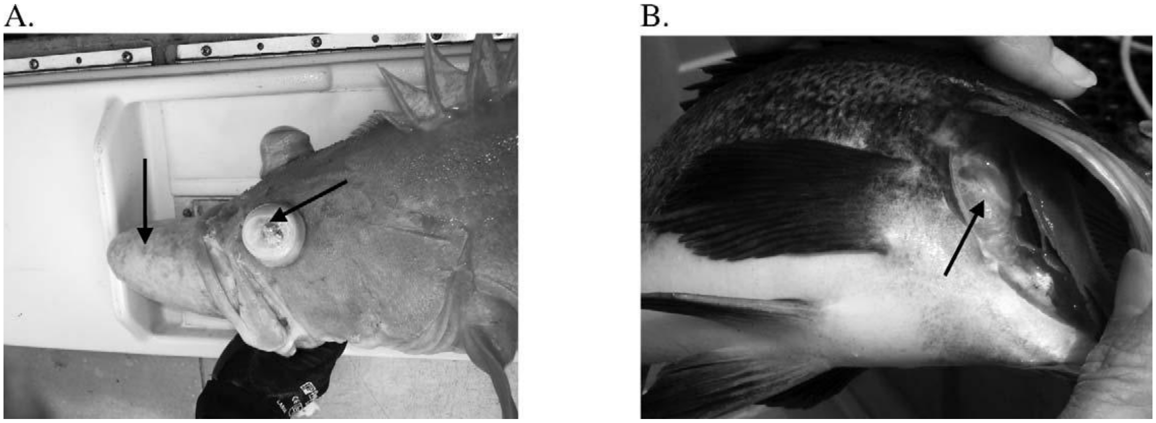

FIGURE 1.—Barotrauma indicators in rockfish. In panel **(A)**, the arrows indicate an everted esophagus, exophthalmia, and ocular emphysema; in panel **(B)**, they indicate an inflated pharyngo-cleithral membrane and air in the pharyngo-cleithral membrane (photo by Polly Rankin, Oregon Department of Fish and Wildlife).

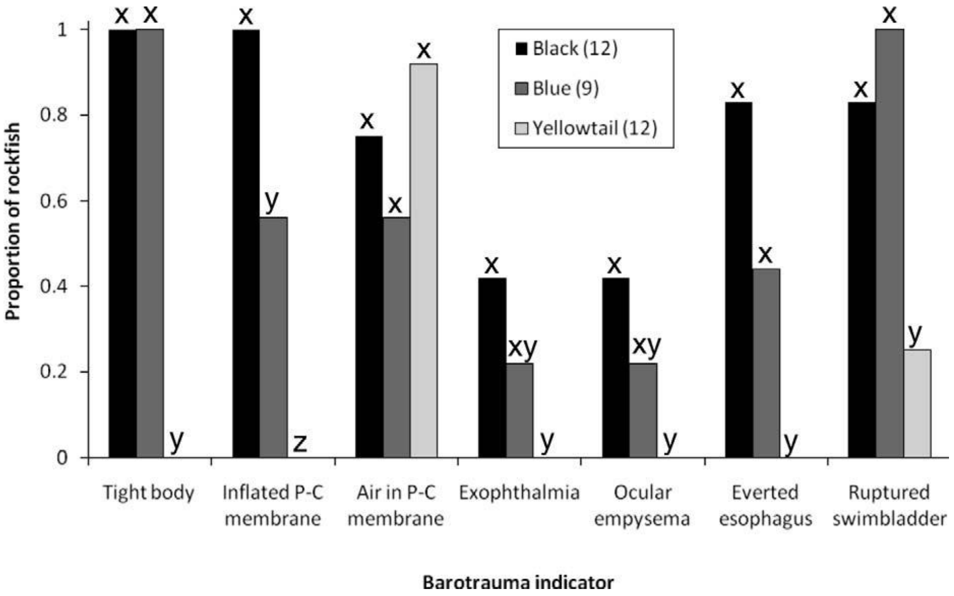

FIGURE 2.—Proportions of black, blue, and yellowtail rockfish with macroscopic barotrauma indicators after decompression from 4.5 ATA. Different letters indicate significant differences at the 0.05 level using Fisher's exact test; P-C stands for pharyngo-cleithral.

tissues (in this case, air bubbles visible in the corneal region of the eye). The pharyngo-cleithral membrane refers to the membrane that is visible posterior to the gill filaments, bridging the area between the pharyngeal arch and the cleithrum (B. Hannah, Oregon Department of Fish and Wildlife [ODFW], personal communication), referred to as the branchiostegal membrane in some studies (Hannah and Matteson 2007; Hannah et al. 2008a, 2008b).

Rockfishes were euthanized in an overdose of tricaine methanesulfonate (MS-222) and then dissected to sample the gill, pseudobranch, liver, head kidney, and heart ventricle. These tissues have been shown to be affected by decompression, gas bubble disease, or both in other fish species (D'Aoust and Smith 1974; Beyer et al. 1976; Feathers and Knable 1983; Longbottom 2000). All fish were dissected within 20 min of euthanatization. Tissue samples were fixed in Davidson's solution (Kent and Poppe 1998) at a ratio of no less than 1:10 (tissue : solution). During dissection, fish were also examined for any macroscopic signs of tissue injury, such as ruptures in the swim bladder, unusual appearance of the liver or kidney, or hemorrhaging.

Sample processing.—Tissues were fixed for a minimum of 30 d and then sectioned to a thickness of 5–7 μm. Slides were stained with hematoxylin and eosin Y. Slides were viewed with a Leica compound light microscope (Model DM LB; Leica Microsystems, Wetzlar, Germany).

Statistical analyses.—In order to compare how different rockfish species respond to barotrauma, all comparisons are among treatment fish only. Due to small sample sizes, Fisher's exact test was used to compare incidences of macroscopic barotrauma indicators both between tanks and between species. Count data were not transformed. Because multiple fish of a single species were included in each tank during a replicate, a preliminary analysis was conducted for "tank effects" (greater variation than expected between tanks–experiments within each species under the binomial assumption). Fisher's exact test was also used to compare histological differences among species. Where differences were found, further Fisher's exact tests were used to compare between species.

Results

Macroscopic Indicators

Control fish did not have any detectable injuries, while all treatment fish had at least minimal injuries. Because only treatment fish had observable injuries, we know injury was due to barotrauma and not due to handling or being held in the pressure chambers. No evidence of tank effects for the three species and seven barotrauma indicators was found ($P > 0.09$ for all 21 tests, and $P > 0.5$ for all but four tests; df = 2 for yellowtail rockfish and blue rockfish, df = 3 for black rockfish). Therefore, between-species comparisons were conducted using the individual fish as the basic unit of analysis (i.e., ignoring tanks).

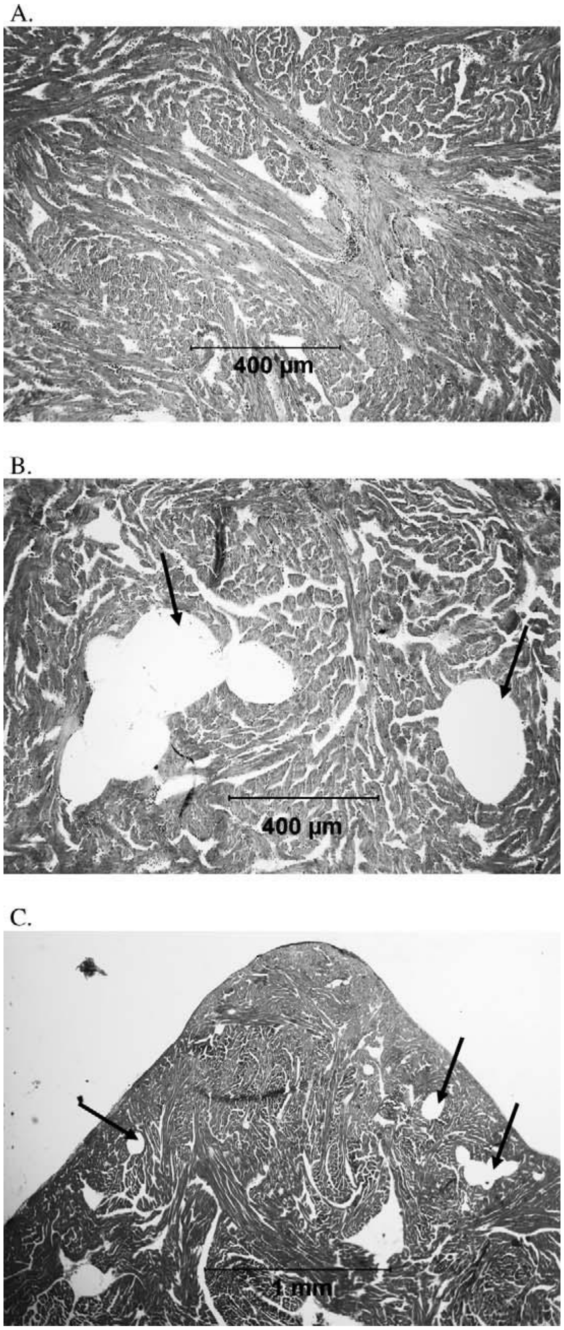

FIGURE 3.—Histology of rockfish heart ventricles. Panel **(A)** shows a normal heart ventricle from a control fish at 100× magnification. Panel **(B)** shows a heart ventricle from a treatment fish with emphysema (gas bubbles in the tissue) at 100× magnification; the arrows indicate individual gas bubbles. Panel **(C)** shows a lower-magnification (25×) view of the tissue section; note that the gas bubbles are located near the periphery.

We only observed macroscopic barotrauma indicators in treatment fish (Figure 2). All barotrauma indicators were present in black rockfish and blue rockfish, while only air bubbles in the pharyngo-cleithral membrane and ruptured swim bladder were present in yellowtail rockfish. Yellowtail rockfish had lower incidences of inflated pharyngo-cleithral membrane, everted esophagus, and ruptured swim bladder compared with black rockfish and blue rockfish ($P < 0.02$; df = 1). Yellowtail rockfish also had lower incidences of exophthalmia and ocular emphysema than black rockfish ($P = 0.0373$; df = 1).

We also observed a large color variation in the liver, in both treatment and control fish, ranging from a uniform creamy-yellow to reddish-orange to green. The reddish-orange and green colors either extended through the liver or were regionalized to the distal portion.

Histology

There was no detectable injury from barotrauma in the liver, head kidney, gill, or pseudobranch in either treatment or control fish. We did observe emphysema in the heart ventricle of treatment black rockfish and blue rockfish (Figure 3), which was characterized by distinct circular spaces representing bubbles in the cardiac muscle. Emphysema was not present in control rockfish and treatment yellowtail rockfish. The proportion of treatment black rockfish with emphysema in their heart ventricle was 0.58 ($n = 12$), and in blue rockfish it was 0.11 ($n = 9$). Black rockfish had higher levels of emphysema in the heart than blue rockfish ($P = 0.0272$; df = 1) or yellowtail rockfish ($P = 0.0007$; df = 1). Approximately 1–19 spherical gas bubbles per tissue section (area of tissue section $\approx$ 16 mm^2) were observed in the compact myocardium for rockfish with emphysema (Figure 3C). Gas bubbles varied in size and, on average, were 0.015 mm^3 ($\pm$0.005). The proportion of gas bubble area to tissue area also varied, ranging from 0.2% to 6.3% of the tissue section.

Discussion

A variety of external barotrauma-related changes occurred in treatment fish, but few internal injuries related to barotrauma were observed.

Yellowtail rockfish that were decompressed from 4.5 ATA did not have any external indication of barotrauma except for gas bubbles under the pharyngo-cleithral membrane. Yellowtail rockfish released gas bubbles from their pharyngo-cleithral membrane during decompression. Pearcy (1992) also made this observation and found the gas to be of the same composition as gas in the swim bladder. Because yellowtail rockfish are able to release excess gas in their swim bladder by way of their pharyngo-cleithral membrane, the trapped gas likely does not build up enough pressure to cause external indicators of barotrauma (such as everted esophagus and exophthalmia; Hannah et al. 2008a). Hannah et al. (2008a) showed that eversion of the esophagus and exophthalmia in rockfish is caused by gas escaping from an unruptured or ruptured swim bladder into the body cavity and moving in an anteriodorsal direction.

All external barotrauma indicators were seen in black rockfish and blue rockfish. Hannah et al. (2008b) found similar proportions of external barotrauma indicators in field-captured black rockfish and blue rockfish when captured from depths between 30 and 39 m. A higher incidence of exophthalmia occurred in black rockfish and blue rockfish in our study, but this could be explained by the fact that the pressure change in our experiment was greater than experienced by fish in Hannah et al. (2008b). Although black rockfish and blue rockfish appear to respond similarly to decompression, studies on their ability to submerge after decompression (Hannah et al. 2008b) and on release behavior after recompression (Hannah and Matteson 2007) indicate they may not share the same ability to recover from decompression. In Hannah et al. (2008b), rockfish were captured from varying depths and tested for their ability to submerge on their own. Black rockfish ($n = 73$) captured from between 30- and 39-m depths were able to submerge 82% of the time, while blue rockfish ($n = 25$) captured from the same depths were only able to submerge 28% of the time. Differences are also evident between black rockfish and blue rockfish after release from a recompression cage (Hannah and Matteson 2007). Black rockfish showed significantly less behavioral impairment from barotrauma when captured between 12- and 39-m depths than blue rockfish.

Internally, the only macroscopic barotrauma injury we observed was swim bladder rupture. This was observed in most black rockfish and blue rockfish, and in a small percentage of yellowtail rockfish. Yellowtail rockfish likely have a low incidence of swim bladder rupture because of their ability to off-gas, as described above. Parker et al. (2006) decompressed and recompressed 90 black rockfish from 4.0 ATA using hyperbaric pressure chambers and observed ruptured swim bladders in 100% of the fish, which is similar to the 83% ruptured swim bladders we found for black rockfish. The same study observed partial healing of the swim bladders by 21 d posttreatment in 77% of the fish. Nichol and Chilton (2006) found Pacific cod *Gadus macrocephalus* with ruptured swim bladders were able to heal their swim bladders enough to hold gas within 24 h, and Bellgraph et al. (2008) found juvenile rainbow trout *Oncorhynchus mykiss* could completely heal ruptured swim bladders after 14 d. This suggests that a ruptured swim bladder may not be an irreversible injury.

Macroscopically, the livers of control and treatment fish showed a variety of colors, ranging from a uniform creamy-yellow to reddish-orange to green. The reddening of the liver was likely due to postmortem congestion, and the green livers were due to bile congestion as a result of starvation (McGavin and Zachary 2007). Rockfish could not be fed for the 14-d duration of the experiments; thus, all had distended gallbladders filled with dark green bile at the time of sampling. Regardless of the cause of color variation in the liver, it is important to note that no histological changes were correlated with these color variations. This emphasizes that caution should be taken when assigning tissue damage to the liver (e.g., hemorrhage) based solely on macroscopic observations.

The only tissue-level injury directly attributable to decompression was emphysema in the heart ventricle of treatment black rockfish and blue rockfish, concentrated in the compact myocardium. Longbottom (2000) also observed lesions in the heart ventricle of the Australasian snapper *Pagrus auratus* after capture from depths ranging between 10 and 35 m, and D'Aoust and Smith (1974) observed histological evidence of gas bubbles in the somatic muscle tissue of fingerling rainbow trout and coho salmon *O. kisutch* after being decompressed from 4.0 ATA. Whereas lesions representing entrapped bubbles have been found in many other organs in fishes with pressure-related diseases (Pauley and Nakatani 1967; D'Aoust and Smith 1974; Beyer et al. 1976; Kulshrestha and Mandal 1982; Smith 1988; Speare 1998), we did not find these outside of the heart in our study. The lack of internal injury in the liver, gill, head kidney, and pseudobranch may be related to the relatively short period of time these internal organs were exposed to high gas pressure. Because gas expands exponentially as pressure decreases, most gas expansion in the swim bladder will occur within the final few meters of the surface. When a fish is brought to the surface, internal organs have been exposed to high gas pressures for just seconds, which is perhaps not enough time for widespread gas-related internal injury to occur. In other pressure-related diseases, such as gas bubble disease, supersaturated water gradually supersaturates the fish over several hours to days. The extended exposure to supersaturating gas in gas bubble disease increases the likelihood of internal injury to tissues (Bouck 1980). Strauss (1979) described tissues as either "fast" or "slow" in their uptake of gas, with well-perfused tissues being "fast" and poorly perfused tissues being "slow." The heart ventricle is a well-perfused tissue and thus may develop emphysema more quickly than other tissues. Alternatively, excess gases are quickly eliminated following decompression (Speare 1998), and in soft tissues evidence of lesions from short-term gas bubbles may disappear.

It is unknown how emphysema in the heart ventricle tissue will affect fish performance in the field. Bouck (1980) suggests tissues with emphysema from gas bubble disease can become necrotic and infected, but this refers to emphysema that has developed from prolonged exposure to supersaturating conditions, not short-term exposure as in our study. Research on injured hearts from zebrafish *Danio rerio* indicate zebrafish have a remarkable capacity for cardiac regeneration (Lepilina et al. 2006) after major injury to the heart ventricle; it is possible this could apply to rockfish as well and should be investigated.

Our study was removed from the natural environment and thus does not address additional issues rockfish face as a result of capture (such as thermal shock, air exposure, and hooking or handling injury). However, this study does provide insight into what happens in rockfish undergoing rapid decompression from a quantifiable depth. Fish that perform vertical migrations, such as yellowtail rockfish and black rockfish, are often not neutrally buoyant at their depth of capture; they often maintain negative buoyancy in order to reduce the effect of gas expansion as they swim higher in the water column (Strand et al. 2005). Thus, it is difficult to quantify depth of capture and relate it to the severity of barotrauma in many species of rockfish without removing the fish to artificial conditions.

Our study is the first to examine barotrauma injury in rockfish from a macroscopic to microscopic level. Macroscopic injuries in black, blue, and yellowtail rockfish were similar to those in other published studies on rockfish (Parker et al. 2006; Hannah and Matteson 2007; Hannah et al. 2008b; Jarvis and Lowe 2008); however, in addition to macroscopic injuries we also found black rockfish and blue rockfish can develop emphysema in the heart ventricle. Surprisingly, no injury was found at the histological level in the head kidney, liver, gill, and pseudobranch, suggesting these tissues may be resilient to short-term exposure of elevated gas pressure when decompressed from 4.5 ATA. Our research also indicates a species-level difference in the response to barotrauma in rockfish and that management of discard mortality in rockfish will depend on understanding the species-specific responses to decompression.

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