Delayed effects of capture-induced barotrauma on physical condition and behavioral competency of recompressed yelloweye rockfish, *Sebastes ruberrimus*

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A B S T R A C T

Rebuilding of some U.S. West Coast rockfish (*Sebastes spp.*) stocks relies heavily on mandatory fishery discard, however the long-term condition of discarded fish experiencing capture-related barotrauma is unknown. We conducted two studies designed to evaluate delayed mortality, physical condition, and behavioral competency of yelloweye rockfish, *Sebastes ruberrimus*, experiencing barotrauma during capture followed by recompression (assisted return to depth of capture). First, we used sea-cage and laboratory holding to evaluate fish condition at 2, 15, and 30 days post-capture from 140 to 150 m depth. All external barotrauma signs resolved following 2 days of recompression, but fish that survived (10/12) had compromised buoyancy regulation, swim bladder injuries, and coelomic and visceral hemorrhages at both 15 and 30 days post-capture. For the second study, we used a video-equipped sea-cage to observe fish behavior for one hour following capture and return to the sea floor. Trials were conducted with 24 fish captured from 54 to 199 m water depth. All fish survived, but 50% of fish from the deepest depth ranges showed impairment in their ability to vertically orient (*P* < 0.01). Most (75%) deep-captured fish did not exhibit “vision-dependent” behavior (*P* < 0.001) and appeared unable to visually discern the difference between an opaque barrier and unobstructed or transparent components of the cage. These studies indicate physical injuries and behavioral impairment may compromise yelloweye rockfish in the hours and weeks following discard, even with recompression. Our results reiterate the importance of avoiding fishery contact with species under stock rebuilding plans, especially in deep water, and that spatially-managed rockfish conservation areas remain closed to fishing.

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1. Introduction

Pacific rockfish (*Sebastes spp.*) constitute a diverse genus of fishes that are well-represented in many marine habitats in the northeast Pacific Ocean. They are generally long-lived and slow to mature, and exhibit a variety of life history traits and niche partitioning strategies, allowing multiple species to occupy the same habitat. Off the U.S. West Coast, rockfish are captured in various mixed-stock fisheries, and some species are subject to harvest restrictions or have been federally declared overfished (PFMC, 2012). While rockfish fishing is prohibited in some areas with relatively high abundances of overfished species (Rockfish Conservation Areas), bycatch within fisheries is still common. In several fisheries, these species must be discarded at sea and their mortality accounted for, to assure stock rebuilding and inform inseason monitoring and management, as well as future stock assessments. Fish show variable responses to the effects of capture which include wounding, stress, temperature changes and time in air (Davis and Ottmar, 2006; Olla et al., 1998; Parker et al., 2003b). Physiologists like rockfish also experience barotrauma, as the gases within their closed swim bladders greatly expand during ascent to the surface, creating a complex suite of severe pressure-related injuries (Hannah et al., 2008b; Jarvis and Lowe, 2008; Pribyl et al., 2011; Rummer and Bennett, 2005). Retained swim bladder gases can also create buoyancy that can prevent discarded rockfish from returning quickly to depth (Hannah et al., 2008a; Hochhalter, 2012). These

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factors make survival and behavioral competency of discarded rockfishes highly uncertain.

To address the question of discard mortality, a number of studies have been conducted to investigate strategies for increasing survival, with mitigation of barotrauma injuries being of primary interest with rockfish. Encouragingly, assisting rockfish with barotrauma back to the bottom (referred to as recompression), where gas volume is decreased, has shown promise in increasing survival (Hochhalter and Reed, 2011; Jarvis and Lowe, 2008). Recompression studies using fish-friendly drum-type cages have quantified 48–72 h survival for a number of rockfish species by depth of capture and provided mortality curves (Hannah et al., 2014, 2012). To facilitate the use of recompression techniques for recreational anglers, fishery managers and private groups have collaborated to provide anglers education materials and training, as well as providing free recompression devices (L. Mattes, ODFW, pers. comm., Theberge and Parker, 2005). Broader acceptance of these methods and strategies has influenced stock assessments resulting in estimates which reflect lower rates of discard mortality (L. Mattes, ODFW, pers. comm.).

Despite this progress, longer-term issues for discarded rockfish remain, as studies show a suite of serious injuries result from the gas expansion; these include: prolapse of the gastrointestinal track, plus cardiac, vascular, swim bladder and optic nerve damage (Hannah et al., 2008b; Pribyl et al., 2011; Rogers et al., 2011; Rogers et al., 2008). Although recompression studies show many fish survive these injuries in the short-term, common sense indicates that fish are not in optimal condition upon release and likely for some time after. For yelloweye rockfish, Sebastes ruberrimus, discard studies show some intriguing complexities. Yelloweye rockfish are extremely long-lived (147 yrs max recorded age), have very specific and geographically limited habitat requirements, exhibit high site-fidelity, territorial behavior and appear to have some complexity of multi-age social structure (O’Connell and Carlile, 1993; Hannah and Rankin, 2011; ODFW, unpublished data; Taylor and Wetzel, 2011; Yamanaka et al., 2006; Yoklavich et al., 1999). Deeper-dwelling yelloweye rockfish with barotrauma retain expanded swim bladder gas at the surface, and as capture depth increases, they become less able to descend on their own (Hannah et al., 2008a; Hochhalter, 2012). But with assistance to the bottom, short-term (24–48 h) survival is excellent at >80% (as tested to 174 m water depth in holding cages), and the probability of survival to 17 days at shallower depths was 99% (as tested to 72 m water depth using weighted hook release) (Hannah et al., 2014; Hochhalter and Reed, 2011). Despite this high survival, behavioral observation studies using video to evaluate very short-term (<5 min) behavior for fish departing from a suspended cage reported increasing behavioral compromise with increasing capture depth (Hannah and Matteson, 2007).

Mark and recapture studies have also provided in-situ evidence of longer-term survival and condition for some fish, but recovery rates of tagged fish were generally low. Studies in Oregon (Coombs, 1979) and Alaska (Hochhalter and Reed, 2011) reported about 20% of tagged yelloweye rockfish were recaptured in the weeks or years following release using recompression at capture depths <72 m. Moreover, recaptured fish in the Alaska study were in good condition; 15 recaptured female yelloweye rockfish were determined to be reproductively viable and 7 sampled for larvae had larval quality equal to females that had not been previously captured (Blaine, 2014).

The use of acoustic tagging and tracking can provide evidence of longer-term survival, fish condition and behavior if fish stay within the range of acoustic reception. In research off Oregon, studies have reported on the movements and high survival rates for a variety of acoustically tagged rockfish species in long-term (4–24 mo) studies (Hannah and Rankin, 2011; Parker et al., 2007; Rankin and Hannah Blume, 2013). Nevertheless, attempts at using acoustic telemetry to investigate movements of tagged yelloweye rockfish have yielded mixed results, a puzzling finding in light of their excellent short-term post-recompression survival (Hannah et al., 2014, 2012; ODFW, unpublished data). Further work indicated the use of multi-day sea-cage holding at depth appeared to increase survival of tagged yelloweye rockfish, and indicated some latent effects of barotrauma were being mitigated (ODFW, unpublished data). We used a baited video lander to observe in-situ (wild) behavior of one of these (48 h cage-held) tagged fish, 7 months post-tagging within a group of yelloweye rockfish and other fish species. This video provided evidence of full recovery, complex intra- and inter-specific social behavior, and natural movements including off-bottom hovering and neutral buoyancy (ODFW, unpublished data). We feel these results, the fish’s natural history, and the overfished status of the stock justify investigation of the short-term behavioral competency and the longer-term effects of capture and barotrauma injury in yelloweye rockfish.

To investigate longer-term mortality and behavioral competency in yelloweye rockfish, we conducted two experiments. The first was a sea cage and laboratory holding experiment designed to establish 15- and 30-day mortality estimates for recompressed yelloweye rockfish captured from 140 to 150 m water depth, a depth zone where yelloweye rockfish are frequently caught by bycatch in the recreational fishery for Pacific halibut (Hippoglossus stenolepis). This experiment also sought to establish the extent and specifics of longer-term barotrauma injuries and to document fish behavior and fish condition over time. The second experiment was designed to investigate the behavior of recompressed yelloweye rockfish after hook and line capture, during a critical time period—the first hour post-recompression. This experiment was designed to be conducted across a variety of depth zones in an attempt to establish the effect of capture depth on post-recompression behavioral competency.

2. Methods

2.1. Delayed mortality and physical condition

We studied the 30-day survival and health of yelloweye rockfish experiencing capture-related barotrauma utilizing a combination of sea-cage and laboratory holding. Condition of surviving fish was evaluated at four time intervals throughout a 30-day period following initial capture. Different groups of five or six fish each were euthanized and evaluated at day 0 (Trial A, to provide baseline data), day 2 (Trial B), day 15 (Trial C) and day 30 (Trial D) post-capture. Fish were examined by either a veterinary pathologist with extensive experience in fish pathology or a Certified Aquatic Veterinarian with extensive training in fish pathology and medicine. Fish were examined at HMSC (Hatfield Marine Science Center) in Newport, OR, or at VDL (Veterinary Diagnostic Laboratory at the College of Veterinary Medicine, Oregon State University in Corvallis, OR). We used predetermined and standardized examination and sampling protocols to minimize the risk of variation between sampler or location. Procedures for evaluating health included complete blood count and blood chemistry panel, necropsy, histopathology and bacterial culture (liver/kidney pool) for each fish.

Yelloweye rockfish were collected on two days, April 13, 2014 for Trial A and B and April 29, 2014 for trials C and D. Fish were captured with hook and line gear, from a depth range of 140–150 m offshore of Newport, OR. For each of four trials, captured fish were evaluated for external signs of barotrauma, measured (cm TL), photographed and PIT-tagged for identification (as per methods in Parker et al., 2003a). To provide baseline data, Trial A fish were sedated with buffered MS222 (tricaine methanesulfonate), sampled for blood, euthanized with buffered MS222, and stored on
ice for postmortem evaluation and tissue sampling conducted at VDL. For the 3 other trials, live fish were captured and immediately recompressed by placing them in individual sea-cages and returned to capture depth for 48 h.

The drum-type sea-cages used had been purpose built for previous studies evaluating post-capture survival, and were designed to minimize abrasion and cage motion, while maintaining adequate water exchange and protection from predators (Hannah et al., 2012). As noted in Hannah et al. (2014, 2012), live rockfish in these studies showed resolution of external signs of barotrauma, with no evidence of expansion of swim bladder gases after 48 h of recompression and retrieval to the surface. In those studies, yelloweye rockfish released from the surface after 48 h in the cage were able to submerge successfully on their own, also indicating minimal gas retention. This lack of gas retention allowed for subsequent transport of these deep-water physiologists, at ambient surface pressure, with no further injury beyond that acquired from their initial capture. Furthermore, 48 h in the sea-cages restricted feeding, so transported fish were in fasted condition for a contained, environmentally-controlled transport, without generation of nutrient waste from digestion or regurgitation.

Cages were brought to the surface after 48 h, fish were photographed and checked for barotrauma and external injuries. Trial B fish were sedated and blood samples were collected. They were then euthanized and transported to VDL for necropsy and tissue sampling. Surviving Trial C and D fish were transported alive to laboratory tanks at the HMSC to be behaviorally evaluated for 15 (Trial C) or 30 (Trial D) days before sampling. Fish were handled by hand or polyethylene bag to eliminate any abrasion or slime coat removal usually incurred by net contact. They were transported in polyethylene bags (6 mm thickness, 56 × 41 × 147 cm) containing aerated, temperature-controlled sea-water, nested in ice within insulated totes. Bags were used to separate individual fish, minimize abrasion and minimize water movement while underway at sea. Totes were hoisted by crane off the vessel and onto trucks for delivery to the laboratory tanks. Fish remained in their aerated transport bags throughout the acclimation to lab tank water for 1–2 h before release into laboratory tanks.

Trial C and D fish were held in six 5000 l insulated tanks, supplied with flow-through (151/min), filtered (25 μm), UV-sterilized, temperature-controlled (8–11 °C) sea water, which is part of a disease-challenge laboratory system designed to minimize the introduction of unwanted pathogens. Each tank contained “habitat” in the form of two grey-colored, weighted, 30-gallon (114 l) plastic trashcans, tipped over onto their sides. Each tank housed two black rockfish (Sebastes melanops) and one or two yelloweye rockfish. Black rockfish were used as controls for tank conditions as they can be collected from shallow (<10 m) depths without barotrauma and are sensitive to water quality conditions. Black rockfish were captured and acclimated to the tanks four weeks prior to the addition of the yelloweye rockfish. Yelloweye rockfish were visually evaluated daily for external injuries and vertical orientation, and twice weekly for return to feeding, neutral buoyancy, ability to avoid an approaching object, response to touch, and general swimming ability. Fish were offered silversides (Menidia menidia) or squid (Loligo spp.) on a thin wire or monofilament line, until they took food freely from the water column. At the end of the holding periods, fish were sedated, blood samples were drawn, and they were photographed and euthanized. Trial C fish were examined and sampled at HMSC. Trial D fish were transported on ice to for examination and sampling at VDL.

Blood samples for all four trials were taken ventrally from the caudal vein using a 21 ga hypodermic needle and syringe. Blood was transferred to two sterile sampling tubes, one with lithium heparin preservative for the blood chemistry panel and one with EDTA as the preservative for the complete blood count. Post-mortem exam included notation of external lesions and eye condition and an internal examination of selected organs and tissues. Histopathology samples included gill, eye, brain, kidney, heart, liver, spleen, pancreas, stomach, gastrointestinal track, swim bladder, gonads, mesentery and connective tissue. Pooled liver/kidney samples from each fish were submitted for bacterial culture.

2.2. Post-recompression behavior

In a separate experiment, we constructed a transparent, aquarium-type video observation cage (125 × 81 × 69 cm) equipped with lights, to observe captured rockfish during and after recompression to their depth of capture (Fig. 1). The cage was designed to minimize fish injury and abrasion, to be large enough to allow a large demersal rockfish to swim and maneuver unimpeded, and to provide some obstacles and stimuli to allow for behavioral assessment. Assessment included observation of the fish’s response to the opening of the cage door, which occurred remotely using a dissolvable link fabricated from a commercial candy bar (Sugar Daddy 1.7 oz pop). All interior surfaces were smooth metal, lexan (polycarbonate) plastic, or pvc (polyvinyl chloride) pipe. Surface and bottom sea water temperature was recorded using two data loggers: Vemco Minilog-II-T and a Wildlife Computers MK9.

For more details on the dimensions, construction and components of the video cage, please see Supplement A.

2.3. Evaluation of behavior

Our evaluation of yelloweye rockfish post-recompression behavior was distributed between two capture-depth zones off Newport, OR, ranging from 54 to 199 m water depth. The “shallow” depth zone was 54–89 m and “deep” was 122–199 m. Fish were captured from a 15 m recreational charter vessel equipped with a crab block which was used to retrieve the observation cage. Fish were captured by hook and line, were measured (cm TL), and a photo was taken. External barotrauma signs were recorded, and each fish was placed into the observation cage on deck. The video camera was turned on and cage door secured with the dissolvable release, then the apparatus was lowered over the side to descend to the seafloor. After one hour, the observation cage was retrieved and video downloaded.

Since all captured wild yelloweye rockfish will typically experience some level of barotrauma during capture and ascent to surface pressure, we sought the use of captive fish as controls for any cage effect on behavior. The Oregon Coast Aquarium (Newport, OR) provided yelloweye rockfish which had been residing off-exhibit in holding tanks. The captive fish did not have barotrauma, but had been treated for topical injuries or an eye wound. All fish were deemed behaviorally competent and able to see as determined by their ability to negotiate structures within a tank and by their ability to find and eat food that was freely distributed throughout the tank. These fish were introduced into their 1,041,000 l home exhibit via the observation cage using the same methods as the experimental fish, with three exceptions: 1) captive fish were not hooked but were moved via stretcher from a holding tank; 2) fish were placed into the partially submerged cage versus being placed into the cage on deck, and 3) cage lights were not used as the home exhibit was fully illuminated.

Inherent in the cage design and operation were a number of stimuli to which fish could respond, allowing us to evaluate their ability to perceive and react to their environment. Video analysis included documenting the behavior and orientation of fish in the cage as well as their response to various stimuli including the motion of the cage on the seafloor. Behaviors assessed included the presence/absence of swimming, upright vertical orientation and vision-dependent movement (Table 1). Vision-dependent behavior
was defined as movements, the execution of which required fish to have some level of ability to see and avoid an opaque barrier. Vision-dependent behavior was scored as present if the fish swam above the sides of the opaque tray and oriented facing outwards from the cage, through a visually unobstructed component (i.e. the transparent polycarbonate or open end of the cage). We evaluated the association between depth of capture and presence/absence of the post-recompression behavior using Fisher’s exact test (one-tailed) (Sokal and Rohlf, 1981).

3. Results

3.1. Delayed mortality and physical condition

Control fish

The twelve black rockfish used as controls in the laboratory holding, remained healthy and vigorous throughout the experimental period, and showed no indication of water quality compromise, nor introduced infection. No wounding nor exophthalmia was observed, fish were neutrally buoyant, fed regularly and activity was normal. Black rockfish were able to maneuver to avoid aggressive behavior (charging and biting) exhibited by their yelloweye rockfish tank mates.

Experimental fish

Twenty four yelloweye rockfish were captured for the four trials. Upon capture, all fish exhibited a suite of barotrauma signs including distended abdomen, eversion of the esophagus into and beyond the mouth, exophthalmia of one or both eyes, and emphysema (abnormal presence of gas) within eye tissues, behind the pharyngocleithral membrane and at the insertion of the fins (dorsal, pelvic, pectoral) (Table 2). Fish lengths ranged from 38 to 60 cm (TL).

Sixteen of 18 fish retrieved from the 48 h sea-cage recompression were alive with no external barotrauma signs and clear eyes. One fish each from Trial C and D was found dead upon cage retrieval, and had hemorrhaged into the coelomic cavity. These fish retained some signs of barotrauma (exophthalmia and everted esophagus). After 48 h in the sea cages, the surviving Trial C and D fish were transported live from offshore waters to HMSC without incident. Transport water temperatures remained within the target range (4–7 °C) and there was no evidence of nitrogenous waste in any of the transport bags. Most fish entered the tanks negatively buoyant and resided on the bottom. Three fish appeared to be slightly positively buoyant as indicated by tail-up swimming behavior, but were residing on the bottom within 24–48 h.

3.1.1. Trial A. condition after initial capture (Table 2)

Physical examinations of fish directly after initial capture, showed all six fish had livers and stomachs everted into the mouth, contained within the everted esophagus. Five of six fish had mild
to moderate bilateral exophthalmia. We noted hemorrhages in the body cavity in three fish: two had scattered blood clots and some hemorrhages of the mesentery and stomach. The third fish (which did not display exophthalmia) had prominent hemorrhages in the coelom, with free blood clots and clots attached to the serosal surfaces of the swim bladder, kidney, spleen and mesentery. All swim bladders appeared to be intact with no visible ruptures. We noted emphysesmas within the connective tissues of the eyes, swim bladder and/or kidney in three fish, although no bubbles were visually observed in the heart. Histopathology showed locally extensive hemorrhaging in four fish; within connective tissue components of the swim bladder (4 fish), stomach (3 fish), and mesentery (1 fish). Two fish had thrombi within the spongy portion of the heart ventricle. Two fish had detached retinas.

3.1.2. Trial B. condition after 48 h sea-cage recompression (Table 2)

Physical examination of six fish after 48-h sea-cage recompression showed they did not retain the everted esophagus, nor exophthalmia, and eyes were clear without emphysema. Externally, all fish were free of any other barotrauma signs. On necropsy, we observed extensive hemorrhage of the gastric serosa and/or within the coelomic cavity. Four of six fish had locally extensive hemorrhages of the swim bladder within the stroma of the dorsal aspect and within the mucosal layer, as well as adherent clots on the serosa. Swim bladders appeared to be intact. Histologically, hemorrhage and thrombi were evident in the swim bladders of four fish, and two fish had blood clots adherent to the spleen.

3.1.3. Trials C and D. behavior 2–15 days post-capture (Table 2)

The 10 surviving fish from Trials C and D were alive until euthanized on either day 15 or 30. Fish initially resided on the bottom next to the tank edge or tucked under the edge of the submerged trashcan habitat. By day 7 post-capture, all 10 fish were still negatively buoyant, but were able to orient vertically for swimming and negotiate the tank and habitat when gently prodded by a ½ in. diameter clear acrylic tube. Fish C5 was unable to orient vertically when at rest, but could do so while swimming. Three fish were observed chasing or biting at black rockfish or a tank mate, during the prodding event. On day 9, one fish (D11) achieved neutral buoyancy and on day 10, the fish was competently swimming, appeared inquisitive, and ate squid and smelt. At day 14, one other fish returned to feeding. All other fish continued to reside motionless on the bottom, were negatively buoyant, and did not eat nor pursue proffered food.

3.1.4. Trial C. condition 15 days post-capture (Table 2)

Physical examination of the five Trial C fish 15 days post-capture showed all eyes were clear (no corneal cloudiness nor emphysema). On necropsy, we observed blood clots or active hemorrhaging in the coelomic cavity (5/5 fish), the esophagus, liver, stomach, spleen, anterior to the head kidney (2 fish), the organ junctures, and tears were observed in the distal lobe of the liver and of the spleen (1 fish). We also recorded hemorrhages in the heart and within the pericardial sac (4 fish), gas on the surface of the atrium, mottled (4 fish) and atypically shaped (rectangular) hearts (1 fish). Gas bubbles were visible within the posterior kidney (1 fish).

Swim bladders were also markedly affected. Four of five swim bladders were at least partially intact, but one fish’s swim bladder was avulsed from the body wall, had ruptured laterally through both walls of the swim bladder, and the posterior chamber was obliterated. Partially intact swim bladders had ruptured tunica externa (2 fish) and extensive hemorrhaging was observed between tunica layers (4/5 fish). We observed gas between the swim bladder and body wall and within the tunica layer (2 fish), and the swim bladder mucosal layers appeared to be inflamed in three fish. Two swim bladders were intact, but we recorded extensive hemorrhage of one swim bladder wall and the presence of swollen grey-brown colored rete in the other. Brown fluid was present in three of five swim bladders.

Histologically four of five swim bladders showed mild to locally extensive stromal and/or luminal hemorrhage. Locally extensive hemorrhages and clots were observed in the gastric tissues of three fish. Multifocal thrombosis was present in the ventricular space of one fish’s heart.

3.1.5. Trial D. behavior 30 days post-capture (Table 2)

By day 23 the remaining five fish had all eaten at least one time, though competency varied with two fish bumping into tank components during the session, their eyes appearing fixed and non-moving. These fish were exhibiting eye movement and were maneuvering effectively at day 28. An additional fish (D9) gained neutral buoyancy on day 23, but by day 29 both neutrally buoyant fish were positively buoyant and were actively swimming head down. The other three of five fish remained negatively buoyant and resided on the bottom through the trial end.

3.1.6. Trial D. condition 30 days post-capture (Table 2)

Physical Examination of fish 30 days post-capture showed all eyes were clear (no corneal cloudiness nor emphysema). We found ventral skin lesions with hemorrhages in two negatively buoyant fish. Gill color for all fish was atypically dark red. On necropsy, we
observed adherent blood clots within the gastric mucosa of one fish and serosal hemorrhage of the ventral aspect of the stomach in another. Swim bladders were intact and partially inflated (3 fish), non-inflated (1 fish), and fully inflated (1 fish). D9 and D11 were two fish that had obtained and lost neutral buoyancy to become positively buoyant. D9’s swim bladder was uninflated and the coelomic cavity contained a large air pocket. D11 had an inflated swim bladder, with serosal and mucosal tissue containing hemorrhages. D10’s swim bladder had two areas containing 2 ml each of brown opaque fluid. Histopathology showed locally extensive stromal hemorrhages in the swim bladder wall of two fish (D8 and D11).

### 3.1.7. Blood values
Average blood values, bacteriology and some discussion are provided in Supplement B.

### 3.2. Post-recirculation behavioral observation

#### Observation cage performance

The observation cage system worked well and fish were readily observed on recorded video. Fish were safely restrained and protected within the cage, but could swim and maneuver freely. We were able to evaluate orientation, reaction to noise and motion stimuli, and assess visual and swimming capability. The transparent polycarbonate walls allowed fish to see out of the cage, and allowed us to view substrate, habitat and other fish outside the cage.

#### Fish Capture
We captured a total of 24 fish using hook and line; 12 “shallow” fish were captured from 54 to 89 m water depth and 12 “deep” fish were captured from 122 to 199 m depth. Four captive yelloweye rockfish acted as pseudo-controls to evaluate cage-effect and were reintroduced into their “home” aquarium exhibit of 7 m water depth after being held in a tank of 1.5 m depth.

All wild-captured fish expressed a suite of barotrauma signs upon capture, including tissue emphysema, but eye conditions were more prevalent in deep-captured fish than shallow-captured, indicating greater expansion of retained swim bladder gas into the cranial area for the deeper dwellers (Hannah et al., 2008b) (Table 3). Exophthalmia and gas within one or both eyes was present in 10/12 and 6/12 deep-captured fish respectively. For shallow-captured fish, 3/12 had exophthalmia, but none had gas in the eye. All visible barotrauma signs appeared to resolve during descent in the video cage, with the exception of gas in the eye for some fish.

Elapsed time from capture until the observation cage reached the seafloor averaged 9 min (range 5–16 min) for shallow-captured fish and 10 min (range 7–16 min) for deep-captured fish. All fish experienced water temperature changes through the process. The temperature differential was 8.2–10.3 °C for deep-captured fish and 3.8 °C for shallow-captured fish.

#### 3.2.1. Fish behavior

##### Control fish

Control fish showed little variability of behavior between fish. All fish swam during the brief cage descent, were oriented upright immediately after the cage landed and remained upright or swim calmly while the cage was on the bottom. All fish exhibited vision-dependent behavior, swim slowly out of the cage before (n = 1) or during (n = 3) cage retrieval, and all were oriented upright upon exiting the cage (Table 3). All fish appeared to be negatively buoyant as was expected by the increased depth of residence.

##### Experimental Fish

**Orientation**

We observed similar patterns of behavior among experimental fish. At the surface and during the first part of the descent, fish had significant barotrauma, so were positively buoyant, upside-down, and immobile except for minimal tail and opercular movements. Later during the descent, after most visible barotrauma signs had diminished, all but three deep-captured fish righted themselves and swim within the cage or sat on the bottom for the rest of the descent. Disoriented fish were either upside down (n = 1) or were lying on their sides (n = 2, Fig. 2). When the cage landed on the bottom, it stopped suddenly and made an audible noise. Most fish showed a startle reaction to this stimulus, but one un-righted, deep-captured fish did not respond at all. At landing and during the next hour, fish orientation was noted (Table 3). All shallow-captured fish were upright in the cage immediately after landing, and remained oriented upright (either swimming or sitting) for the next hour. Three of the deep-captured fish did not orient upright and were laying on their sides upon landing, but within the hour that number increased to 6/12 fish laying on their sides for some duration post-landing, an atypical behavior for yelloweye rockfish (Table 3, Fig. 2). The results of the Fisher’s exact tests showed that orientation at landing was not significantly related to capture depth (P > 0.05), but maintained orientation was significantly negatively related to capture depth (P < 0.01) (Table 3). The one unresponsive fish oriented vertically 49 min post-capture. During the hour, most fish sat on the cage bottom and made short swimming excursions throughout the cage and then returned to sitting on the cage floor. Most fish appeared to be negatively buoyant.

**Vision-dependent movement behavior and exiting the cage**

Vision-dependent movement was prevalent in shallow-captured fish with 12/12 fish orienting vertically while swimming above the opaque tray sides, head directed out of the cage towards the clear polycarbonate or out of the exit area after the cage gate opened (Fig. 3). In contrast, only three deep-captured fish exhibited vision-dependent movement, and two of these found their way out of the cage before any cage retrieval movement was initiated (Table 3). As with the control fish, vision-dependent movement was conducted with slow, non-vigorous swimming. Fish that moved without exhibiting this behavior swam into and made contact with the opaque areas of the cage: the bottom and sides of the tray and the white plate at the camera end of the cage. These fish appeared unable to visually discern the difference between an opaque barrier and an unobstructed area or transparent component of the observation cage. The results of Fisher’s exact test showed that vision-dependent movement behavior was significantly negatively related to depth of capture (P < 0.001) (Table 3).

Most fish did not display any urgency in “escaping” the cage until it moved, as was observed in control fish. Only one shallow-captured and two deep-captured fish exited the cage while the cage was still resting on the bottom. All other exits were initiated when the cage moved during retrieval. Overall, eight shallow-captured fish successfully exited, but four stayed with the cage upon retrieval to the surface, even as barotrauma signs returned. As these fish returned to a state of positive buoyancy, they became agitated and their behavior defaulted to rapid swimming directly down towards the bottom of the tray, versus continuing to swim throughout the cage or out of the open end. This continued until the fish became incapacitated and floated at the top of the cage. Ten deep-captured fish successfully exited the cage, one fish remained within the cage to the surface before being overcome by positive buoyancy, and one fish was unable to exit as the cage door did not release. As cage orientation, water flow, and pressure were inconsistent during cage deployment and retrieval, it is likely this unnatural situation could overwhelm or confuse a fish’s sensory abilities. Accordingly, exit and swimming behavior while the cage was being deployed or retrieved should be interpreted with caution.

**Observations outside the cage**

A number of fish interactions were observed outside the confines of the cage. In one trial there was a single lingcod strike on the
Table 3
Number of specimens in the observation cage experiment exhibiting each barotrauma sign and behavior by depth of capture.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Sample size</th>
<th>Depth (m)</th>
<th>Exophthalmia</th>
<th>Intraocular Emphysema</th>
<th>Swim during cage descent</th>
<th>Vertical orientation at cage landing</th>
<th>Vertical orientation maintained</th>
<th>Vision dependent movement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4</td>
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<td>Shallow</td>
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<td>54-89</td>
<td>4</td>
<td>0</td>
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<tr>
<td>Deep</td>
<td>12</td>
<td>122-199</td>
<td>10</td>
<td>6</td>
<td>9</td>
<td>9(^a)</td>
<td>6(^b)</td>
<td>3(^c)</td>
</tr>
</tbody>
</table>

\(^a\) Depth effect was not statistically significant (P > 0.05).
\(^b\) Depth effect was statistically significant (P < 0.01).
\(^c\) Depth effect was statistically significant (P < 0.001).

Fig. 2. Absence of vertical orientation. Fish is alive and respiring, but laying on its side within the observation cage. Cage is oriented upright.

Fig. 3. Presence of vision-dependent movement. Fish is oriented upright, swimming above the sides of the opaque tray, head oriented towards the transparent barrier.

cage, and another trial received 3 strikes. These strikes were forceful and direct, and resulted in audible sound and a startle response in experimental fish. Schools of canary rockfish (S. pinniger) were visible in the immediate vicinity outside the cage during several trials, as were solitary ratfish (Hydrolagus colliei).

4. Discussion

The findings from these two studies, which reveal severe and lasting injuries, as well as behavioral compromise of recompressed deep-water yelloweye rockfish, reinforce the importance of avoid-
ing fishing contact with deep-dwelling yelloweye rockfish and maintaining spatially-managed rockfish conservation areas closed to fishing.

4.1. Delayed mortality and physical condition

We observed no delayed mortality during the 15 and 30 days of post-barotrauma laboratory holding of 10 yelloweye rockfish. Similarly, we observed a total mortality of only 11%, during the initial 48 h of confinement in a sea cage, consistent with results from Hannah et al. (2014) for this species at similar capture depths. Also as noted in previous work, all external signs of barotrauma in fish that survived, including exophthalmia and ocular emphysema, resolved after 48 h in the cages at depth. Internally, however, fish sustained injuries which were extensive and severe and mostly still evident at day 15 of laboratory holding. Internal hemorrhaging has been previously reported in recompressed rockfish that died of acute (within 48 h) barotrauma-related causes, but the prevalence and duration of hemorrhages in surviving fish and the protracted nature of healing from these vascular injuries, are noteworthy findings (Hannah et al., 2014; Parker et al., 2006). Another significant finding was that swim bladder function was markedly compromised for all 10 lab-held fish.

Although displaced swim bladder gas is recompressed at depth, it remains within the tissues to which it was displaced (like the eye), until the physiological process of resorption takes place (in a live fish). The barotrauma signs still evident upon retrieval of the two fish that died during recompression, indicate that fish did not survive long enough for the body to resorb the displaced gas. The continued presence of the everted esophagus indicates the fish’s condition was such that it may have been unable to “swallow” the everted esophagus, as is often observed in less compromised rockfish during recompression.

The two fish that ultimately (day 9 and day 23) regained buoyancy control during holding, exhibited responses to external stimuli that were indistinguishable from those of wild yelloweye rockfish observed with a stationary video lander (ODFW, unpublished data); they were suspended off bottom, approached a novel object, and appeared generally curious. However, both of these fish regressed behaviorally as swim bladder function became impaired; swim bladder gas was being produced but could not be contained, or could not be regulated for the inhabited depth. All of the other fish remained negatively buoyant. The ability of surviving discarded yelloweye rockfish to ultimately regain normal swim bladder function and buoyancy regulation remains a central question regarding their long-term behavioral competency in the wild. Holding studies lasting longer than 30 days will be needed to determine how frequently normal buoyancy regulation is regained, and how long this may take, for yelloweye rockfish experiencing severe capture-related barotrauma.

Compromised buoyancy control and compromised trim from extraneous gas within the body cavity has high energetic costs, even for fish known to be bottom-oriented (Pelster, 1997; Strand et al., 2005). Hovering suspended off bottom, acquisition of prey, interactions with conspecifics and general movement patterns are all affected. Additionally, labored or atypical swimming postures and erratic movements, can cue predators and stimulate predation. Contact lesions were another noted side effect in negatively buoyant fish: two fish had developed open lesions at the bases of the ventral fins at the points of contact with the tank bottom, a serious health effect which can lead to systemic infection. These delayed effects reflect the severity and complexity of injuries from capture-related barotrauma, and the complications that may arise throughout the process of healing and repair, including failure to regenerate, fibrosis (thickening and scarring of connective tissue), unattached and/or displaced organs, and the potential onset of infection.

The high standard of laboratory water quality along with the excellent condition of the control black rockfish indicated that laboratory holding conditions were generally very good. Pathogens can still be introduced by the fish themselves, but in a flow-through (non-recirculating) system, disease-causing organisms are not concentrated as they can be by a recirculating system. All fish used the structure we provided as refuge, which can reduce stress in captivity. Despite these mitigating factors, stress in captive fish is well-documented and can influence healing (Davis, 2010). Conversely, captive holding can provide unnatural protection for injured fish. Pathogens, parasites, predators and predatory amphipods (Family Lysianassidae) common in Pacific Northwest waters can infect or consume an injured fish in the wild, suggesting that our reported high latent survival could be better than for fish being released back into the ocean.

There is little known about blood values for rockfish, and acquiring “normal” reference values for deep-dwelling physiologists is particularly problematic. Blood values are reported with some discussion in Supplement B for reference, however results were variable and we recommend they be interpreted with caution.

4.2. Post-recompression behavior

The use of the field-deployed, stationary video platform provided difficult-to-obtain behavior data about the recovery of these fish throughout a critical time period in the fishery discard process—the hour post-capture and recompression. Encouragingly, many shallow-captured fish were sufficiently capable, behaviorally and visually, to orient, explore and exit the cage upon sensing the physical instability of their environment (the cage) after one hour. Unfortunately, 50–75% of fish captured from deeper depth zones exhibited increasingly diminished behavioral competency for very basic reflex (orientation) and/or sensory (visual) function. At a minimum, our results show that a significant proportion of yelloweye rockfish captured from deeper waters are physically and behaviorally compromised for some time period following capture and release, potentially affecting their ability to avoid predation and seek refuge.

Compromised visual ability and disorientation with increasing capture depth can be explained by the exponential expansion of swim bladder gas upon ascent, causing increasingly profound tissue and vascular damage, blood loss and shock if the fish survives. Our results and previous work showed 10–20% of yelloweye rockfish captured from >100 m water depth and recompressed in holding cages, die within 48 h, so one would expect some behavioral indication in similar percentages (Hannah et al., 2014). But the increase of orientation loss over time to 50% of deep-captured fish indicates that many fish are undergoing the delayed effects of shock and decreasing consciousness during this time interval. Maintaining orientation is an innate reflex behavior in many fish and the loss of equilibrium is used as a behavioral measure of decreasing consciousness in fish under anesthesia and in fish being evaluated for behavioral impairment after exposure to a stressor (Davis and Parker, 2004; Summerfelt and Smith, 1990). In studies evaluating the lethal effects of capture stress in fish, the presence or absence of the orientation reflex is one of several behaviors which may be used to predict mortality (Davis, 2010).

The use of behavioral evaluation in addition to evaluation of a fish’s injury, such as wounding, has proven to be an effective tool for predicting mortality, as demonstrated by Davis and Ottmar (2006) in pivotal studies utilizing scoring criteria called RAMP for Reflex Action Mortality Predictor (Davis, 2007; Davis and Ottmar, 2006). These techniques establish and quantify innate reflex behaviors that drop out or become “completely inhibited” as a fish becomes...
increasingly physically compromised. For example, some scoring criteria include noting the presence or absence of a response to stimulation of the fish’s body, operculum, mouth and eye as well as orientation and startle response. Unfortunately, using RAMP to assess fish with barotrauma at surface pressures can be challenging as they may be rendered immobile or unresponsive, due to expanded retained swim bladder gas. However, observing fish after recompression provides an opportunity to evaluate reflex behaviors without the artifacts of expanded gas and associated movement limitations and could feasibly be used to establish RAMP criteria to predict mortality in recompressed rockfish.

4.3. Barotrauma effects on vision

The apparent compromise of visual function we observed in yelloweye rockfish in both laboratory holding and video-cage observation can be the result of several eye effects. The occurrence of exophthalmia and ocular emphysema indicates gas retained in the body cavity has expanded forward into the cranium area (Hannah et al., 2008b). Gas emboli in the eye may directly block or alter the visual field, but emphysema also stretches optic nerves and the muscles of the eye, and may be responsible for the detached retinas we observed in necropsies (Rogers et al., 2008; Smiley et al., 2012). In yelloweye rockfish, all external signs of barotrauma resolve immediately with recompression to the depth of capture, except intraocular emphysema, which resolves sometime within 48 h at depth (Hannah et al., 2014, 2012; current study). The lag time associated with the resolution of acute onset intraocular emphysema may contribute to visual compromise and disorientation for some time after recompression and appeared to be a factor in the apparent visual compromise exhibited during feeding of lab-held fish several weeks post-recompression, although eyes appeared to be clear and free of gas. Rogers et al. (2011) used an optokinetic reflex test in recompressed rosy rockfish (S. roscaceus) which had experienced exophthalmia and intraocular gas, and reported functional vision four days post-recompression and improved vision at one month, as indicated by eye movement rates. These results and the improved ability of our lab-held fish to visually locate food, indicate healing and some recovery of visual function for fish over multiple days and up to at least several weeks post-recompression.

4.4. Light and temperature effects

At the time of this writing, yelloweye rockfish are primarily captured incidentally in fisheries conducted during the daytime (L. Mattes, ODFW, pers. comm.), so would be exposed to the same full daylight and temperature changes as our experimental fish. Temperature change is unavoidably confounded with depth in the study area, so even without barotrauma injuries, deeper fish may well be affected by the greater temperature change, a variable known to have detrimental effects on lab-tested fish undergoing simulated capture (Davis and Olla, 2002; Olla et al., 1998).

The effect of bright sunlight on vision and orientation must also be considered for fish captured from waters receiving less ambient light (Brill et al., 2008). Although deep-captured fish were undoubtedly in very dark waters, ambient light is not solely depth-related in Oregon waters, as upwelling conditions and the resulting productivity can cause spatially variable light penetration. In the offshore study area, deep-captured fish likely experienced greater change in ambient light conditions throughout the process than our shallow-captured fish. The possibility also exists that exposure to the cage’s artificial light at depth could affect vision and orientation. The close proximity of numerous other fish, including canary rockfish, lingcod, and ratfish indicated the artificial light was not generally inhibitive. One event provided compelling evidence of the dominance of the vestibular system for these fish: in one shallow trial, the cage landed on a large rock structure, slid off end first, then gently landed upside-down. From the fish’s perspective, the cage light would have been shining up from the bottom, a stimulus which can, for some fish, be very disorienting (P. Rankin personal observation). The cage later returned to an upright orientation. The study fish managed to achieve and maintain upright orientation throughout the event, apparently relying on vestibular cues and overriding the visual disorientation of bottom-up lighting.

5. Conclusion

Recompression is a valuable treatment for discarded rockfish that would otherwise be too buoyant to return to depth without assistance. However, the loss of reflex actions as basic as vertical orientation, along with the evidence we found of visual compromise in deep-dwelling recompressed yelloweye rockfish, is concerning, as are the long-lasting physical injuries and lack of neutral buoyancy observed in the weeks after capture and recompression. At a minimum, these effects indicate limits to a rockfish’s ability to move effectively, find refuge, and avoid predators upon release. Beyond this most basic initial evaluation, we must consider the ramifications in light of a longer temporal period and of this species’ more complete natural history. It remains an open question; what proportion of these deeper-dwelling, behaviorally complex fish can find refuge or “home” and reestablish their position within a social structure, after sustaining injuries that compromise such basic senses as orientation and vision? Can these fish move and interact effectively with compromised swim bladder function, blood loss and cardiac injuries which persist for at least several weeks post-capture and recompression? Coleman et al. (2000) strongly advocate the use of ecologically relevant data including longevity, site-fidelity, and social behavior, in the management of the heavily impacted, reef-dwelling grouper-snapper complex in the southeastern United States, many elements of which resemble yelloweye rockfish ecology. The authors conclude in a policy statement that spatial management is the tool of greatest promise, with complete avoidance of take in key areas, imperative. For yelloweye rockfish this is of particular importance in light of minimizing serious injuries for at least some populations of large, healthy, breeding yelloweye rockfish, which may contribute a disproportionately high number of robust larvae to the recruiting population (Berkeley et al., 2004).

Alaska studies have shed some light on yelloweye rockfish discard behavior in capture depths of 18–72 m, within our study’s “shallow” range. Hochhalter (2012) reported some yelloweye rockfish (22%) are able to descend upon release, but show that survival of discarded yelloweye rockfish would be increased by 4.5 times if fish were released at depth within 2 min of capture. In Hochhalter and Reeds’s (2012) model of 17-day rockfish discard survival probability, fish length was positively correlated with survival up to a length of 400 mm, which they note may be due to increased predation or susceptibility to thermal stress in smaller fish post-recompression. Our results, and that of Blaine (2014) showing reproductive capability and good larval quality of recompressed female yelloweye rockfish reinforce the benefits of recompression for yelloweye rockfish captured from <72 m of water. Fortunately, a large amount of the recreational fishery discard of yelloweye rockfish takes place at these shallower capture depths. For example, in 2013 and 2014, Oregon recreational fisheries operating in less than 91 m of water depth accounted for 87–92% of recreational yelloweye rockfish bycatch, and fishers reported 57–62% of yelloweye rockfish were released using recompression devices (L. Mattes, ODFW, pers. comm.).
Low submergence success and high survival of recompressed deep-captured yelloweye rockfish indicates these tough fish benefit significantly from recompression post-capture, despite significant injury, behavioral effects and delayed healing. Best practices for handling discarded yelloweye rockfish continue to point to the use of recompression devices as a valuable strategy for increasing survival of fish that are otherwise unable to descend and would experience the worsening effects of gas expansion, along with exposure to air and predatory birds. The longer-term effects of capture, barotrauma and recompression must still be considered, however, in light of the yelloweye rockfish’s more complete natural history. Our results reiterate the importance of avoiding fishing contact with species under stock rebuilding plans, especially in deep water, and of maintaining spatially-managed rockfish conservation areas close to fishing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishes.2016.09.004.

References
