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Fisheries Research

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## Recovery of visual performance in rosy rockfish (*Sebastes rosaceus*) following exophthalmia resulting from barotrauma

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### ARTICLE INFO

#### Article history:

Received 29 May 2011

Received in revised form 1 August 2011

Accepted 2 August 2011

#### Keywords:

Optokinetic

Rockfish

*Sebastes*

Catch-and-release

Barotrauma

Exophthalmia

### ABSTRACT

Rapid ascent during fishing capture can cause exophthalmia ('pop eye') in physoclastic fishes, resulting in stretching of the optic nerves and extraocular muscles, but it is not known whether exophthalmia affects vision temporarily or permanently. We used the optokinetic reflex test to assess changes in visual performance of rosy rockfish (*Sebastes rosaceus*) that had experienced exophthalmia. Vision was functional 4 days after recompression and was improved after 1 month of recovery evidenced by individuals being able to track both smaller and faster-moving gratings. Our results suggest that, after recompression, rosy rockfish recover from exophthalmia fairly rapidly and perhaps fast enough to minimize significant adverse impacts on survival. This measured recovery from exophthalmia, in addition to evidence of high short-term, post-release survivorship, shows that recompression of unwanted rosy rockfish may be a viable management technique, and may be appropriate for other rockfish species, some of which are at low population densities due to high fishing pressure.

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### 1. Introduction

Rockfishes experience barotrauma when brought rapidly to the surface during fishing (Hannah et al., 2008a; Parker et al., 2006). The most commonly observed eye injury is exophthalmia, a physical displacement of the eye (Rogers et al., 2008) caused by escaping gas from the swim bladder that makes its way into the ocular region (Hannah et al., 2008b). While many of the physical external signs of barotrauma, including exophthalmia, have been shown to be reversible when captured fish are recompressed to their depths of capture (Hannah and Matteson, 2007; Jarvis and Lowe, 2008), little is known about its intermediate- and long-term effects on visual performance. This information can be valuable for estimating the utility of catch-and-release practices on the long-term post-release survival of rockfishes because a number of rockfish populations have showed decline as a result of fishing pressure, habitat loss, and high by-catch mortality (Davis, 2002; Dotson and Charter, 2003).

Exophthalmia may induce long-term visual impairment and potentially reduce prey capture success, response to light cues, location of micro-habitats, and predator avoidance (Hannah et al., 2008a; Jarvis and Lowe, 2008; Longbottom, 2000; Parker et al.,

2006). A study on the short-term effects of catch and release of 17 species of rockfishes recompressed to depth in holding cages showed an average of 75% 2-day post-release survival (Jarvis and Lowe, 2008). However, it was unclear whether these individuals were visually impaired as the result of initial trauma. Hannah and Matteson (2007) found that rockfishes brought to the surface, assessed, and then recompressed showed signs of behavioral disorientation potentially associated with visual impairment. The fundamental questions remain as to the functional extent and duration of visual impairment following barotrauma. We assessed the visual function in rosy rockfish (*Sebastes rosaceus*) following exophthalmia resulting from barotrauma using the optokinetic reflex (OKR). During the OKR, eyes track moving stimuli to keep an image stationary on the retina (Carvalho and Tillitt, 2004; Douglas and Hawryschyn, 1990). Eye movement rate was used as a measure of visual performance (Roeser and Baier, 2003), specifically the functional characteristics of the ocular muscles and optic nerve.

For the OKR test, we manipulated the spatial frequency and the speed of stimuli at two different times (4 days after fish experienced exophthalmia and 1 month later). We hypothesized that exophthalmia would cause overstretching of the optic nerves and extraocular muscles (see Rogers et al., 2008), which would translate into nerve damage, decreased mobility of the eyes, and consequently decreased visual performance. Studies on guinea pigs and mice have shown that nerve damage results after extensive optic nerve stretch (Bain et al., 2001; Saatman et al., 2003), and that eye tracking ability is reduced after extensive extraocular muscle stretch (Kaminski et al., 2002).

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**Fig. 1.** Head-on view of a rosy rockfish (*S. rosaceus*) with exophthalmia (eye displacement) and corneal gas bubbles.

We hypothesized that eye movement rate would increase after 1 month due to ocular tissue repair, and that eye movement rate would increase more at smaller grating widths (Bilotta, 2000; Northmore et al., 2007) and faster stimulus speeds (Carvalho et al., 2002) over time, potentially as a result of restored corneal clarity, nerve repair, or muscle repair (Tan et al., 2009; Ubels and Edelhauser, 1983). Finally, we hypothesized that individual fish with greater degrees of exophthalmia would show lower visual performance during assessments.

## 2. Materials and methods

### 2.1. Subjects

Rosy rockfish (*S. rosaceus*) were chosen as a model species because they have a body shape typical of most benthic rockfishes (Love et al., 2002), and show a high incidence of barotrauma-induced exophthalmia (83% of the time) (Jarvis and Lowe, 2008). All animal handling procedures were approved by the California State University Long Beach IACUC (protocol #250). Rosy rockfish (17–24 cm TL) were captured in waters between 63 and 110 m using hook-and-line in Monterey Bay, California during April and June 2009. We retained individuals with signs of exophthalmia and/or corneal gas bubbles ( $n = 12$ ) (Fig. 1). Fish visual performance was measured at two time periods: 4 days and 1 month after trauma. Fish caught at depth were brought to the surface using standard fishing practices. The experimental design used was meant to follow standard catch and release conditions: (a) capture that induced rapid decompression and resulted in exophthalmia, (b) forced-recompression treatment using hyperbaric chambers to simulate release at depth, and (c) slow controlled decompression in chambers to surface pressure, preventing a second barotrauma or exophthalmia event, and allowing fish to be tested outside of the pressurized chamber. Steps (b) and (c) took place in the laboratory (see below). After 1 month in the lab at surface pressure, we re-measured visual performance of all individuals to quantify potential recovery.

At the time of capture, we recorded total length (TL) and photographed each fish. Pit tags with unique electronic identification codes were inserted in the right dorsal musculature. Because eye displacement can predict the severity of optic nerve injury in other taxa (Bain et al., 2001; Saatman et al., 2003), we quantified

the degree of exophthalmia in rockfish by measuring eye distension (mm) from the mid-cranial line to the anterior corneal edge using digital calipers on live individuals, or measured it from the photographs using ImageJ. Measurements on live animals were not significantly different from measurements made from digital images ( $t_9 = 1.1$ ,  $p = 0.290$ ). After fish were removed from the chambers, normal eye position was measured from the mid-cranial line to the corneal edge, which could then later be compared to eye displacement resulting from exophthalmia for estimating percent eye displacement.

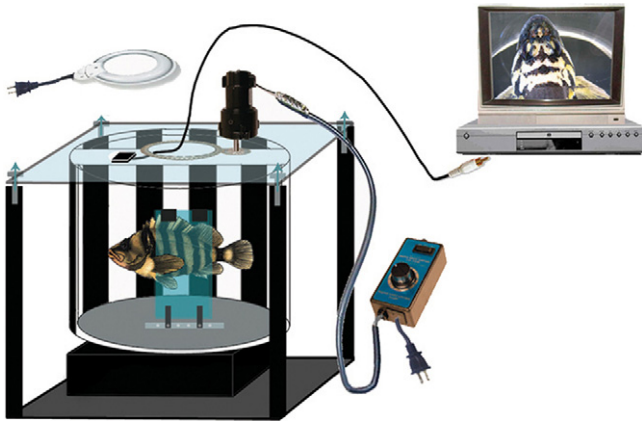
### 2.2. Controlled chamber recompression and slow-decompression

After capture, individuals spent 5–10 min in a live well on the vessel before being placed inside a portable hyperbaric pressure chamber. Water pressure inside the chamber was increased to 5.2–5.7 atm (equivalent to depth of 32–38 m or 60–70 psi), thereby alleviating external signs of exophthalmia by recompressing gases inside the fish (see also Parker et al., 2006; Smiley and Drawbridge, 2007; Wilson and Burns, 1996). A staging tube attached to the side of the hyperbaric chamber was pressurized to match the inside chamber pressure, so that new fish could be added to the chamber without reducing the pressure on fish that were already inside. Chambers were then transported to the lab and attached to a flow-through seawater system. To bring fish to surface pressure, water pressure inside the chamber was slowly decreased over 96 h in a stepwise fashion at roughly 6-h intervals [5.7, 5.0, 4.0, 3.0, 2.3, 2.0, 1.68, 1.54, 1.40, 1.27, and 1.20 atm] until reaching 0 psi or about 1 atm of pressure inside the chamber, or at intervals slow enough to prevent positive buoyancy (Parker et al., 2006). Once fish reached 1 atm (surface pressure), they were removed from the chambers and eye position was re-measured with calipers. Rockfish were then light-adapted for at least 30 min before first visual assessment (4 days after initial capture/trauma). Because all of the fish could not be tested simultaneously, some fish were light-adapted for up to 4 h while waiting for visual assessment measurements.

### 2.3. Optokinetic reflex (OKR)

The optokinetic reflex (OKR) in many vertebrates, including most fish, consists of a compensatory eye response to motion (Krauss and Neumeier, 2003): eyes follow a moving stimulus that is progressing past the visual field of the animal and then the eyes reset naturally to a known position by snapping back in the opposite direction of the stimulus. We built an OKR chamber that consisted of a transparent cylindrical acrylic aquarium (33.3 cm inner diameter, 0.6 cm thickness, and 35.6 cm height) filled with seawater ( $15 \pm 1^\circ\text{C}$ ; Fig. 2). An outer water-resistant paper cylinder open on its top and bottom rotated around the outside of the stationary aquarium by a variable-speed DC motor (Bodine Electric Company; 8.41 kg cm torque), horizontally covering  $360^\circ$  around the fish and about  $96^\circ$  vertically.

An individual fish was restrained in the middle of the OKR chamber using a foam V-shaped cradle with Velcro straps (Davis, 2002; Fig. 2) to isolate the measurement of eye movements from any confounding optomotor response. The cradle restrained the mid-section of the fish's body, just behind the operculum, allowing full opercular pumping movements for gill ventilation, but preventing it from swimming. Seawater inside the aquarium was replaced between trials and water temperature remained between  $13$  and  $16^\circ\text{C}$ . A color video camera was positioned above the OKR device, providing a dorsal view of the fish for real-time viewing and backup recordings of eye movements on a Sony DVD recorder (RDR-GX360). Individual trials in the OKR device lasted on average ( $\pm\text{SE}$ ) between  $35 \pm 0.8$  min. Fish with over-inflated abdomens and



**Fig. 2.** Optokinetic device used to assess eye movement rates. Fish were restrained in an aquarium filled with seawater, and an external cylinder drum was rotated around the drum by a motor. The drum could be interchanged for other drums with narrower grating widths. A light illuminated the gratings and a small video camera was positioned above the eyes of the fish and displayed on a monitor. A DVD recorder was used as a backup for logging eye movements.

physically constricted eyes from exophthalmia were not tested mainly due to ethical considerations. Because mortality rates are high for fish that are not recompressed within 10 min after capture (Jarvis and Lowe, 2008), fish would likely not have been able to endure the physical restraint associated with the OKR test.

Six paper cylinders were constructed for displaying a series of equal black and white vertical gratings (created in Adobe Photoshop, 600 dpi, laminated) and the following individual grating sizes were determined based on the circumference of the aquarium for each of the six grating patterns: 5.08, 2.54, 1.27, 0.76, 0.48, and 0.33 cm (or 0.012, 0.024, 0.048, 0.080, 0.127, and 0.185 cyc/deg, respectively). In a preliminary test with black-and-yellow rockfish, *Sebastes chrysomelas* (not used in the experiment), we established the approximate range of gratings that fish could detect. We used this species because they could be captured in shallow water (<10 m) without inducing exophthalmia and they also exhibit a typical benthic body shape of many rockfishes. The average reactive distance (RD, distance between the center of the eye and the visual stimulus grating; Breck and Gitter, 1983) in our experiment was 7 cm.

Surface illumination was provided by overhead fluorescent room lighting and a warm 40W fluorescent ring light (General Electric) shown through a diffusion shield above the OKR device, emitting an average of 50 lx onto the gratings directly in front of the fish. We used a reflectance light level of 50 lx to ensure visibility of the gratings for fish. Rockfish at the 100 m depth of capture would encounter lower usable light levels of likely much less than 1% surface levels (for 400–500 nm wavelengths; Garrison, 2002). The contrast of bars were measured and calculated at 90% using a Pentax Spotmeter and contrast equation  $C = (L_1 - L_2) / (L_1 + L_2)$  (Land and Nilsson, 2002).

Each fish was tested using three stimulus speeds chosen from preliminary trials: slow (26.1°/s), medium (41.8°/s), and fast (57.9°/s). Fish were always presented speeds in order from fast to slow to ensure that the sudden onset of the drum at the fast speed would elicit an observable positive response at the beginning of each trial. Stimuli were presented in the same order across trials for maximizing testing time efficiency and reducing the time fish were restrained. Additionally, each fish was tested with the drum rotating in both directions (clockwise and counter-clockwise) to validate eye tracking responses. Based on a delayed response from fish in preliminary trials, we started recording 3 s after the onset

of drum rotation. Eye movements were recorded for 30 s at each combination of grating, stimulus speed, and direction for a total of 36 recordings per individual fish.

We recorded eye tracking movements, which consisted of a slow pursuit eye movement that followed gratings in the direction of movement, and a fast reset eye movement in the opposite direction where the eyes quickly snapped into default medial position. The rate of these eye movements (number of eye movements in 30 s) was our measure of visual performance (Carvalho et al., 2002).

After the first visual performance assessment, rockfish were held in 1890- and 3780-L tanks with chilled seawater ( $\sim 15 \pm 1^\circ\text{C}$ ), sand filtration, aeration, 12 h:12 h light/dark cycle, under ambient light conditions for 1 month. Fish were fed a diet of shrimp, anchovy, and squid *ad libitum* every 3 days. They were provided semi-natural habitat and shading from direct laboratory lighting. We conducted the second visual performance test on the same individuals about  $30 \pm 2.3$  (mean  $\pm$  SE) days after the first assessment by following the same procedures described above.

During our recordings at the narrowest grating (0.33 cm), we observed eye movements that did not precisely follow the gratings of the moving drum. We assumed this could be a result of residual eye momentum or normal difficulty tracking gratings and did not use data from the 0.33 cm grating since such eye tracking responses did not fit the defined OKR response. We corrected for this change by subtracting the same number of eye movement values in a standardized fashion across data for each individual fish. This change did not affect the pattern of data. Ultimately, we only used the five widest levels of grating widths (5.08, 2.54, 1.27, 0.76, and 0.48 cm) for our analyses. Eye movement rates were averaged for each individual fish, but only clock-wise responses were used since drum direction was not a significant factor affecting eye movement rates ( $F_{1,17} = 1.7, p = 0.20$ ).

#### 2.4. Statistical analyses

Although the occurrence of exophthalmia was obvious for individuals experiencing barotrauma, we ran a repeated measures general linear model to show that the degree of exophthalmia (eye displacement) was statistically different from the normal eye position as measured after recompression treatment. Eye position (displaced and normal) was used as a categorical variable in the model and the relationship between percent eye displacement against total body length was quantified to determine whether larger fish displayed a greater degree of exophthalmia, which could potentially lead to more serious eye injury and reduced eye tracking behavior. We used body length because eye size is proportional to body length in fish due to continuous growth (Zygar et al., 1999). Only right eye morphometrics were used since there was no significant difference in eye displacement of right and left eyes in an individual ( $t_{20} = 0.9, p = 0.34$ ).

We used a general linear mixed model to assess variations in eye movement rates. Independent variables included grating width (5.08, 2.54, 1.27, 0.76, and 0.48 cm), stimulus speed (slow, medium, and fast), assessment time (4 days after capture and 1 month after capture), and percent exophthalmia (% eye displacement from normal). We also included two interaction effects: grating width and time, and stimulus speed and time. Because the same individuals were measured at the two assessment times, we included individual as the within-subject identity in a repeated measures design. Planned pair-wise comparisons were used to test for differences between levels of a factor using t statistics (SAS 9.1.3, SAS Institute Inc.). We report means  $\pm$  SE throughout.

3. Results

3.1. General

All fish strongly tracked gratings in the direction of drum rotation, and exhibited coupled eyes movements, except for movements at the most narrow grating which were not as tightly linked to grating rotation. Over both sampling times and across all factor combinations, mean (±SD) rate was 14.8 ± 0.5 eye movements per 30 s (range = 0–45; median = 13.2). This is equal to about 0.4 ± 0.01 eye movements per second.

3.2. Degree exophthalmia

Upon capture, all fish showed extreme exophthalmia and corneal gas bubbles with a mean percent eye displacement of 60.9 ± 5.1%, normalized to body length. The absolute degree of right eye displacement (23.7 ± 1.1 mm) was significantly greater than the normal eye position (14.7 ± 0.3 mm;  $F_{1,2} = 854.5, p = 0.001$ ). There was a significant positive linear relationship between normal eye position and body length ( $F_{1,10} = 38.7, p < 0.001, R^2 = 79.5$ ). There was no significant interaction between absolute degree of right eye displacement and total length of fish ( $F_{2,9} = 12.0, p = 0.08$ ), with fish total length ranging from 16.9 to 24.8 cm; mean = 21.5 cm. Similarly, there was no significant relationship between the percent eye displacement (right eye only) and total length of fish ( $F_{5,12} = 0.88, p = 0.37$ ). Therefore, the degree of exophthalmia was not significantly associated with fish length.

3.3. Visual performance

Overall visual performance was significantly affected by the time of assessment and OKR parameters. Eye movement rates of rosy rockfish were significantly higher at assessment 1 month after capture (18.2 ± 0.7 eye movements/30 s) compared to 4 days after capture (11.5 ± 0.5 eye movements/30 s; Table 1). Percent eye displacement caused by exophthalmia did not significantly affect eye movement rate (Table 1). Eye movement rates (eye movements/30 s) differed significantly across the five grating sizes (Table 1) (grating 5.08: 17.7 ± 0.9; grating 2.54: 19.5 ± 1.0; grating 1.27: 18.0 ± 1.1; grating 0.76: 12.7 ± 1.1; and grating 0.48: 6.0 ± 0.5; Table 2), with significantly higher eye movement rates at wide gratings 5.08, 2.54, and 1.27 than those at narrow gratings 0.76 and 0.48 (Table 3). Eye movement rates were also significantly affected by stimulus speed (Table 1), with a decrease towards the high speed (slow = 15.9 ± 0.6; medium = 15.8 ± 1.0; and fast = 12.7 ± 0.8) (Table 2). Eye movement rates were significantly higher at slow than at fast stimulus speeds ( $t_{22} = 3.88, p < 0.001$ ), medium than at fast velocities ( $t_{22} = 3.8, p = 0.001$ ), but did not

**Table 1**  
Results from a general linear model where eye movement rate (events per 30 s) of rosy rockfish in relation to the percent eye displacement, grating width (5.08, 2.54, 1.27, 0.76 and 0.48 cm), stimulus speed (slow, medium and fast), time since exophthalmia (4 days after capture in chamber recovery and 1 month after capture in the lab), and the interactions between grating width and time, and stimulus speed and time.

Effect	F	d.f.	p
Percent eye displacement	12.95	1, 10	0.2132
Grating	53.94	4, 44	0.0001*
Stimulus speed	9.83	2, 22	0.0009*
Time	98.31	1, 1	<0.0001*
Grating × time	2.77	4, 44	0.0387*
Stimulus speed × time	4.14	2, 22	0.0298*

\* Indicates that those values were statistically significant, following statistical convention.

**Table 2**  
Means ± SE of eye movement rates for all rosy rockfish at each grating width (cm) and each stimulus speed since exophthalmia (4 days after capture in chamber recovery and 1 month after capture in the lab).

Grating width (cm)	Mean ± SE
5.08	17.7 ± 0.9
2.54	19.5 ± 1.0
1.27	18.0 ± 1.1
0.76	12.7 ± 1.1
0.48	6.0 ± 0.5
Stimulus speed	Mean ± SE
Slow	15.9 ± 0.6
Medium	15.9 ± 1.0
Fast	12.7 ± 0.8

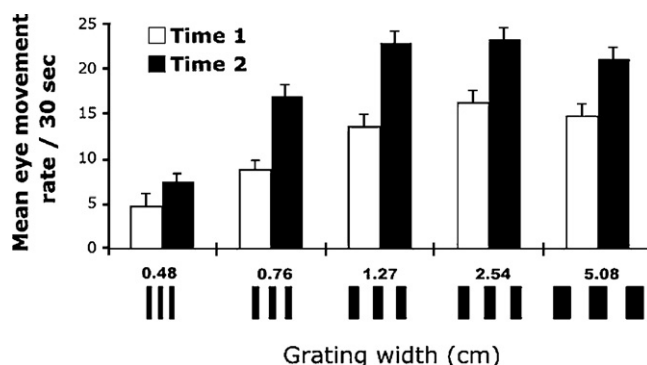
**Table 3**  
Planned pair-wise comparisons between five grating widths that rosy rockfish were exposed to in an optokinetic test. The subscript number represents the degrees of freedom.

Grating width	$t_{44}$	p
2.54 and 0.48 cm	12.68	<0.0001*
2.54 and 0.76 cm	6.36	<0.0001*
2.54 and 1.27 cm	1.41	0.17
2.54 and 5.08 cm	1.73	0.09
0.48 and 0.76 cm	-6.32	<0.0001*
0.48 and 1.27 cm	-11.27	<0.0001*
0.48 and 5.08 cm	-10.96	<0.0001*
1.27 and 0.76 cm	4.96	<0.0001*
1.27 and 5.08 cm	0.32	0.75
0.76 and 5.08 cm	-4.64	<0.0001*

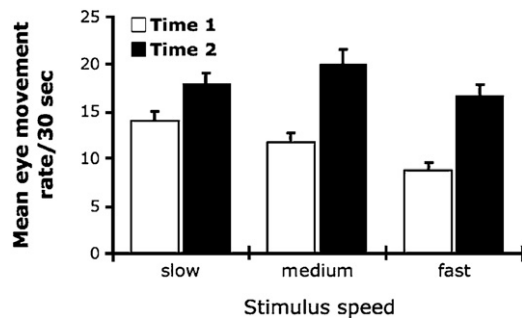
\* Indicates that those values were statistically significant, following statistical convention.

vary significantly between slow and medium velocities ( $t_{22} = 0.08, p = 0.937$ ).

There was a significant interaction between grating width and time (Table 1) that resulted from a peak in eye movement rate at the second widest grating (2.54 cm) at 4 days after capture, but a shift in the peak eye movement rate 1 month after capture toward the next narrowest grating (1.27 cm; Fig. 3). There was also a significant interaction between stimulus speed and time (Table 1), which resulted from an increase in eye movement rate at faster velocities over time (Fig. 4). At 4 days after capture, eye movement rate was the highest at slow velocities, but 1 month after capture, eye movement rate was highest at medium velocities (Fig. 4). Patterns of eye movement rates in response to different stimulus speeds were similar in both assessment times for grating width 5.08; e.g., peaking at the medium stimulus speed (Fig. 4). For grating widths 2.54, 1.27,



**Fig. 3.** Interaction effect between grating width and time for mean eye movement rates of rosy rockfish. Time 1 represents visual performance 4 days after capture and post-chamber-recompression, and time 2 represents visual performance 1 month after time 1.



**Fig. 4.** Interaction effect between stimulus speed and time for mean eye movement rates of rosy rockfish. Time 1 represents visual performance 4 days after capture and post-chamber-recompression, and time 2 represents visual performance 1 month after time 1.

and 0.76 eye movement rates declined with faster stimulus speeds in the assessment 4 days after capture, but peaked at intermediate stimulus speeds at the second assessment 1 month after capture (Fig. 4). For grating width 0.48, eye movement rates declined with faster stimulus speeds in the assessment 4 days after capture, but peaked at the slow and high stimulus speeds at the assessment 1 month after capture (Fig. 4).

#### 4. Discussion

We found that rosy rockfish recovering from exophthalmia after recompression treatment could visually track gratings across a range of parameters, and exhibited improved visual performance. These findings suggest that the effects of exophthalmia in rosy rockfish are reduced over time, following immediate recompression, and do not indicate irreversible damage to vision within 1 month of the barotrauma event. This assumes that the original barotrauma event decreased the visual performance (e.g., eye movement rate) of the fish in our study. We did not measure visual performance immediately following barotrauma for ethical considerations, since fish are compromised and under considerable physical stress from an over-inflated abdomen and extended eyes. Therefore, our main goal was to measure the visual performance of fish *after* recompression treatment.

The effects of time on visual performance were particularly pronounced in relation to grating width and stimulus speed. We found a significant interaction between grating width and time, and between stimulus speed and time, showing that individuals were capable of tracking smaller and faster-moving gratings over time. At least three possible explanations could account for these positive interaction effects. First, visual performance at 4 days after capture may have been hindered by handling stress or chamber stress. For example, rockfishes have been shown to exhibit elevated cortisol hormone levels in response to barotrauma (Pribyl, 2010; Gliniak et al., 2006), which could potentially affect behavior or physiological condition.

Second, because higher light levels usually allow better image resolution (Land and Nilsson, 2002), it is possible that the higher eye movement rate 1 month after capture resulted from adaptation to brighter lighting conditions while in captivity. Nevertheless, short-term retinomotor adaptation from rod- to cone-based vision is known to occur in teleosts over a couple of hours or less (Burnside et al., 1983). Furthermore, it is likely that individuals were similarly adapted to experimental lighting conditions during both assessment times and that any long-term light adaptation effects would be unlikely to occur within 1 month. Although it is unclear whether increased light levels negatively affected retinal function, Brill et al. (2008) found that the retinal cell potentials of black rockfish (*Sebastes melanops*) exposed to barotrauma did not show

significant differences from baseline cell potentials. As a result, it is more likely that rosy rockfish exhibited visual improvement more due to recovery from ocular trauma rather than from retinal cell adaptation due to changes in light conditions.

Third, enhanced visual performance with smaller grating widths and faster speeds over time is likely related to recovery from physical tissue damage (optic nerve stretch and/or extraocular muscle stretch; Rogers et al., 2008). Cellular regeneration within the visual system has been documented in fishes (Maggs and Scholes, 1990; Shayne-Emile and Hitchcock, 1998), and multiple studies have observed an improvement in optokinetic response after other types of ocular traumas. For example, visual performance of rainbow trout (*Oncorhynchus mykiss*) and goldfish (*Carassius auratus*) assessed after toxin injection revealed a significant improvement in optokinetic tracking ability (Carvalho and Tillitt, 2004; Lindsay and Powers, 2007), while bluegill sunfish (*Lepomis macrochirus*) showed an improvement in optomotor responses after optic nerve crush injury (Northmore et al., 2007). Furthermore, acute stretching of muscle tissue has been shown to reduce muscle stiffness and create a lag in muscle twitch reflex (Kubo et al., 2001), and such damage to extraocular muscle nerves has been shown to produce blurred and double vision in humans (Kaminski et al., 2002). Because the extraocular muscles are essential for maintaining proper alignment of visual axes (Collins and Dore-Mazars, 2009), we speculate that stretched eye muscles may have reduced eye movement rates in rosy rockfish. Such a physical limitation would be expected to constrain visual function and reduce the ability of scanning surroundings with the area of the retina with the highest visual acuity, regardless of whether any other tissues are compromised. However, strong eye tracking ability, both 4 days and 1 month following capture and recompression treatment, suggests fairly rapid tissue repair.

An equally plausible explanation could be that optic nerve damage reduced the ability to appropriately match stimulus speeds. The 1-month interval between assessments could have allowed restoration of muscle integrity and function, although not necessarily to the normal levels. Because we could not logistically measure optokinetic responses on the same individuals that were also *not* exposed to ocular trauma, we were not able to obtain baseline levels of normal visual performance, and cannot confirm that recovery levels are equivalent to an individual's normal levels. However, we used a range of grating widths that overlap with those of another optokinetic study on adult African cichlid fishes (grating widths range = 2.02–0.06 cm; total length = 6–8.7 cm) (Dobberfuhr et al., 2005), indicating that other fish are capable of detecting comparable grating widths. Furthermore, the rosy rockfish we tested were able to track rapidly moving gratings, which are well below the size of small common prey items such as copepods, even prior to the 1-month recovery period.

We found that rosy rockfish exhibited a peak in visual performance at a relative intermediate grating width, and lower performance on either side of the peak, as commonly observed in other optokinetic studies (e.g., Beck et al., 2004; Harmening et al., 2009; Rinner et al., 2005). This response can be explained as a function of both photoreceptor density, which determines the ability to resolve the grating detail, and neural tuning, which determines the ability of different types of neurons to respond to a stimulus (McFarland and Loew, 1983). Visual neurons use neural tuning to track moving stimuli and are highly sensitive and efficient at responding to stimuli of biological relevance (Ibbotson et al., 1994). Rosy rockfish responded best to medium-range grating widths, which may indicate the most biologically relevant tuning for this species that allows rosy rockfish to detect and recognize prey, mates or predators. Therefore, the positive increase in eye movement responses over time, presumably due to neural repair, was also most noticeable over these more sensitive medium ranges.

As expected, the fastest stimulus speed resulted in the lowest eye movement rates of rosy rockfish because faster-moving objects have less time to illuminate and activate photoreceptors, making objects more difficult to track (Land and Nilsson, 2002). Rosy rockfish responded with higher eye movement rates to the slow and medium velocities, which could again be related to stimuli velocities relevant to this particular species. For instance, small copepod prey (e.g., *Acartia hudsonica*) have an average potential escape velocity of  $25.7 \text{ mm s}^{-1}$  (Sullivan et al., 1997), which is much less than the slow OKR stimulus speed of  $26.1^\circ/\text{s}$  ( $95.5 \text{ mm s}^{-1}$ ) in our study. This suggests that at least faster than average copepod motion could conceivably be detected by recompressed rockfish, provided the necessary levels of other image components such as size and contrast are also adequately present.

We did not find a significant effect of the degree of eye displacement resulting from exophthalmia on eye movement rate. Fish tested were similar in length and all exhibited a similar degree of eye displacement, so it is possible that a greater observable graded effect could be seen from either fish with a broader range in body lengths or other species of rockfish that may be more likely to show increased variation in original eye injury.

While exophthalmia has the potential to disrupt visual performance, our results suggest that quickly alleviating symptoms of exophthalmia by recompression allow fish to recover visual capabilities. This is a relevant finding because recompression in rockfish has practical applications for fisheries management. In the past, establishing standard harvest control measures, such as minimum size limits, has been limited because rockfish were thought to suffer high mortality when captured as a result of visible barotrauma injury and their inability to swim down due to overinflation. However, recent evidence from barotrauma studies shows that not only do rockfish exhibit high survival rates following recompression despite the extent of barotrauma (Jarvis and Lowe, 2008; Lowe et al., 2009; Hannah and Matteson, 2007), but there is now compelling evidence that some rockfish species do not suffer long-term visual impairment resulting from exophthalmia (Brill et al., 2008, this study). Therefore, our results provide additional support for the use of catch-and-release practices that utilize recompression techniques to assist rockfish in recovery. Implementation of minimum size limits for rockfishes, along with education and outreach for fishers on the benefits of forced-recompression techniques (Theberge and Parker, 2005), may be an effective management tool for reducing rockfish release mortality.

## Acknowledgements

We thank Joe Welsh for his extensive help with the capture of rockfishes and use of chambers, and the Monterey Bay Aquarium for their support on this project. Funding for this work was provided by CSULB Graduate Research Fellowship, CSULB Summer Stipend award, SCTC Marine Biology Foundation, Donald R. Reish Grant, USC Sea Grant, Mineral Management Service, and the AAUS Kevin Gurr Scholarship.

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