

Abstract—Demersal fishes hauled up from depth experience rapid decompression. In physoclists, this can cause overexpansion of the swim bladder and resultant injuries to multiple organs (barotrauma), including severe exophthalmia (“pop-eye”). Before release, fishes can also be subjected to asphyxia and exposure to direct sunlight. Little is known, however, about possible sensory deficits resulting from the events accompanying capture. To address this issue, electroretinography was used to measure the changes in retinal light sensitivity, flicker fusion frequency, and spectral sensitivity in black rockfish (*Sebastes melanops*) subjected to rapid decompression (from 4 atmospheres absolute [ATA] to 1 ATA) and Pacific halibut (*Hippoglossus stenolepis*) exposed to 15 minutes of simulated sunlight. Rapid decompression had no measurable influence on retinal function in black rockfish. In contrast, exposure to bright light significantly reduced retinal light sensitivity of Pacific halibut, predominately by affecting the photopigment which absorbs the green wavelengths of light (≈520–580 nm) most strongly. This detriment is likely to have severe consequences for postrelease foraging success in green-wavelength-dominated coastal waters. The visual system of Pacific halibut has characteristics typical of species adapted to low light environments, and these characteristics may underlie their vulnerability to injury from exposure to bright light.

Manuscript submitted 28 February 2008.
Manuscript accepted 23 June 2008.
Fish. Bull. 106:427–437 (2008).

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Effects of rapid decompression and exposure to bright light on visual function in black rockfish (*Sebastes melanops*) and Pacific halibut (*Hippoglossus stenolepis*)

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The effects of events during capture and release on postrelease mortality have been characterized in a range of demersal fish species (e.g., Davis, 2002; Parker et al., 2003; Davis and Parker, 2004; Davis and Schreck, 2005; St John and Syers, 2005; Davis and Ottmar, 2006; Davis, 2007; Hannah and Matteson, 2007; Rummer, 2007), but their impacts on sensory systems have not been addressed. Demersal fishes are commonly subjected to rapid decompression during capture in both commercial and recreational fisheries. The resultant overexpansion of the swim bladder in physoclists causes injuries to multiple organs (barotrauma) including exophthalmia (“pop-eye”) (Parrish and Moffitt, 1993; Rummer and Bennett, 2005). Fishes are also commonly held out of the water while being unhooked, released from nets or traps, or sorted from a trawl (Davis and Olla, 2001). During this period they can experience severely impaired oxygen exchange (asphyxia), as well as temperature and light levels above those in their

depth range. One or more of the following could, therefore, significantly impair visual function: 1) mechanical damage to the optic nerve or retina resulting from rapid decompression-induced exophthalmia (Rogers et al., 2008); 2) physiological damage to the retinal cells resulting from multiple embolisms, low blood oxygen levels in the choroid rete, avascularity of the retina, and the need of a continuous supply of oxygen in the retinal cells (Fonner et al., 1973; Berenbrink et al., 2005); 3) permanent bleaching of retinal cell photopigments or retinal cell apoptosis (cell death) due to exposure to bright light (Loew, 1976; Wu et al., 2006); and 4) clouding of the cornea or lens (cataract formation) (Midtlyng et al., 1999). Reduced visual function could subsequently result in increased mortality due to predation (Mesa et al., 1994) or the diminished ability to capture prey (Stoner, 2003).

Black rockfish (*Sebastes melanops*) and Pacific halibut (*Hippoglossus stenolepis*) are good representative species for testing the consequences

of events during capture on sensory function. They are commercially and recreationally important demersal species caught by hook-and-line and trawl gear along the west coast of North America. Because of stringent fisheries regulations, both are frequently discarded (Pacific Fishery Management Council, 2004; Hannah et al., 2008). Black rockfish are a deep dwelling physoclist species (Parker et al., 2008) and experience significant barotrauma when brought to the surface, including severe exophthalmia (Hannah and Matteson, 2007; Hannah et al., 2008). Pacific halibut lack a swim bladder and do not suffer apparent injuries associated with rapid decompression. Pacific halibut are, however, often kept on deck for 30–60 min during sorting operations on commercial trawl vessels before being discarded (Davis and Olla, 2001). This time onboard results in prolonged exposure to air and direct sunlight. Exposure to bright light causes photoreceptor damage in both vertebrates and invertebrates (Meyer-Rochow, 1994; Wu et al., 2006); and fishes that normally live in dim light environments are predicted to be especially prone to light-induced damage (Loew, 1976).

Our objective was to examine changes in visual function in black rockfish subjected to rapid decompression and in Pacific halibut exposed to simulated sunlight with electroretinography. The electroretinogram (ERG) represents the summed potentials of various cell types within the retina, not just those of the photoreceptor cells. Nevertheless, the ERG is considered a useful technique for addressing questions about visual function, including the identification of gross visual deficits (Brown, 1968).

Materials and methods

Black rockfish (37.6–46.3 cm total length [TL]) were captured by hook-and-line in waters off shore of Newport, OR (44°33'N, 124°6'W). Efforts were made to collect fish from as shallow a depth as possible (<25 m), and only individuals showing minimal signs of barotrauma (as defined in Hannah and Matteson, 2007) were retained. Fish were transported to the Hatfield Marine Science Center (Newport, OR). During transport, excess swim bladder gases were reduced by inserting a sterile hypodermic needle through the body wall into the swim bladder in any fish that were positively buoyant or that showed an inability to maintain vertical orientation. In order to be able to identify individuals, all fish were tagged with 12 mm × 2.1 mm Destron-Fearing ISO FDX-B 134.2-kHz passive integrated transponder (PIT) tags (Destron-Fearing, St. Paul, MN). Tags were placed in the hypaxial musculature (ventral to the cleithrum at a depth of 0.5–1.0 cm) by using a 12-gauge stainless steel veterinary needle and a modified syringe as described by Parker and Rankin (2003).

Fish were held for six months in a fiberglass tank (3.1 m diameter, 1.0 m depth) before use in experiments. The holding tank was supplied with seawater (flow rate: 20 L/min, temperature: 10–12°C, salinity:

30–32‰) and maintained under dim fluorescent light (0.01 μmol photons/m²/s) with a 12-hour photoperiod. Fish were fed *ad libitum* three times per week with a mixture of chopped frozen clams (*Spisula solidissima*), squid (*Loligo opalescens*), capelin (*Mallotus villosus*), and silversides (*Menidia menidia*).

Age-0 Pacific halibut (31.8–40.2 cm TL) were captured with a beam trawl from Chiniak Bay, Kodiak Island, AK (57°40'N, 152°30'W) and shipped to the Hatfield Marine Science Center. They were subsequently reared for two years before use in experiments in fiberglass tanks (3.1 m diameter, 1.0 m depth) supplied with seawater (flow rate: 20 L/min, temperature: 8–10°C, salinity: 30–32‰). The tanks were maintained under dim fluorescent light (0.01 μmol photons/m²/s) with a 12-hour photoperiod. Fish were fed *ad libitum* three times per week during the first year and twice per week during the second year with a gel food consisting of squid, Pacific herring (*Clupea pallasii*), pelleted food, krill (*Euphausia superba*), amino acid supplements, vitamins, and gelatin.

Rapid decompression experiments with black rockfish

The rapid pressure change (of 3 atmospheres absolute [ATA]) to which black rockfish were subjected was chosen to mimic the changes in depth that fish encounter during capture by both commercial and recreational fisheries, and which have been shown to cause significant barotrauma (Parker et al., 2006, 2008). Pressure changes were achieved using a large flow-through hyperbaric aquarium system capable of maintaining two groups of fish separately at up to 4.25 ATA. This system (described by Parker et al. [2006]) produces the same signs of barotrauma in captive fish as those observed in wild fish subjected to equivalent pressure changes when being brought up from depth. Two experimental trials were performed. For each trial, three control and four treatment fish were placed in the hyperbaric chambers and acclimated to 4.0 ATA over a period of seven days (Fig. 1). Treatment fish were subjected to a simulated capture scenario consisting of a 3.0-ATA pressure drop over 90 seconds. Individuals were removed from the hyperbaric chamber with a dip net, identified, assigned a score to quantify the external signs of barotrauma, and then immediately placed back in the chamber for repressurization. These procedures resulted in a simulated surface interval (i.e., at 1 ATA pressure) of 10 min, but only a brief period (<1 min) out of the water. Treatment fish were then repressurized to 4.0 ATA over 30 seconds simulating the return to depth after release. Fish were held at 4.0 ATA for an additional 20 hours after the rapid decompression event, then gradually brought to 1.0 ATA according to the decompression schedule (Fig. 1) developed by Parker et al. (2006). To account for any effects of the chamber not associated with rapid pressure change, control fish were subjected to an identical schedule of gradual pressure changes, but not the rapid decompression event. After completion of all pressure changes, fish were removed from the chambers with a

dip net and placed in circular polyethylene tanks (2.0 m diameter, 0.8 m depth) for up to three days before evaluation of visual function. These holding tanks were supplied with seawater (flow rate: 8 L/min, temperature 10–12°C, salinity: 30–32‰) and maintained under dim fluorescent light (0.01 $\mu\text{mol photons/m}^2/\text{s}$) for a 12-hour photoperiod. Fish were not fed during this period.

Bright light exposure experiments with Pacific halibut

Individual Pacific halibut were removed with a dip net from their holding tank and held in a seawater bath (12°C). A high intensity xenon lamp (CVI Laser Spectral Products, Albuquerque, NM) was used to produce simulated sunlight. The spectral range of the lamp ($\approx 320\text{--}700\text{ nm}$) approximated the visible (400–700 nm) plus UV range of sunlight at sea level when the sun is directly overhead (Lalli and Parsons, 1997). Light, conducted by fiber optic guide, was aimed at one eye of the fish for 15 minutes. Light intensity at the exit of the fiber optic light guide was 2000 $\mu\text{mol photons/m}^2/\text{s}$ (measured over the visible spectral range of 400–700 nm) and matched the intensity of sunlight (2010 $\mu\text{mol photons/m}^2/\text{s}$) measured at Newport, OR, under a clear sky at 12:00 noon PST on 5 October 2007. The 15-minute period of exposure to simulated sunlight was chosen to mimic the minimum time that fish would be left on deck during sorting operations on commercial trawl vessels (Davis and Olla, 2001; Davis and Schreck, 2005). Control fish were treated in the same manner except that the light source was not turned on.

Evaluation of visual function

Fish were maintained under dim light conditions during transport, weighing, and drug injection procedures. They were anesthetized with ketamine hydrochloride (Ketaset, Butler Animal Health, Middletown, PA, dose $\approx 30\text{ mg/kg}$) injected intramuscularly and paralyzed with the neuro-muscular blocking drug gallamine triethiodide (Flaxedil, Sigma Chemical Co., St. Louis, MO, dose $\approx 20\text{ mg/kg}$) injected directly into the caudal vein. Additional doses of the drugs were administered during the course of an experiment. Fish were euthanized at the conclusion of the experiment with a massive overdose ($>300\text{ mg/kg}$) of sodium pentobarbital (Beuthanasia-D, Schering-Plough Animal Health Corp., Union, NJ) injected intramuscularly.

After drug injections, individual fish were moved into a light-tight enclosure and placed on a perforated rubber sling stretched across an acrylic box. The majority of the body was submerged; only a small portion of the head and the eye receiving the light stimulus remained

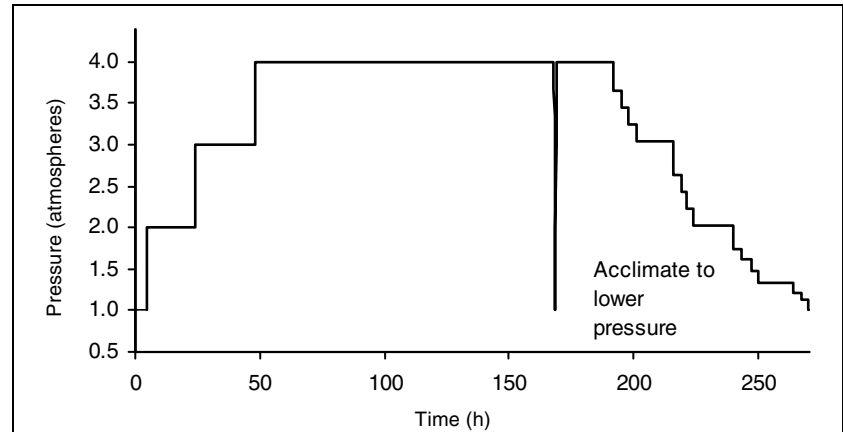


Figure 1

A schematic graph of the time course of pressure changes to which black rockfish (*Sebastes melanops*) were subjected in flow-through hyperbaric aquaria. Control and experimental fish received the same treatments, with the exception that control fish were not subjected to the rapid decompression and recompression shown at approximately 160 h (simulating capture and subsequent return to depth). Time zero indicates the point at which the fish were initially placed in the chamber.

above the water. The box was supplied with running seawater (12°C) and a small submersible pump continuously circulated water over the gills of the fish. Fish were allowed to acclimate to the dark for at least one hour before any measurements were taken.

Silver-silver chloride electrodes, constructed from teflon-coated silver wire, were used for recording the ERGs. The active electrode was lightly placed on the corneal surface and the reference electrode either in one of the nares or on the skin over the head. (Electrodes were positioned under dim red light [peak wavelength 660 nm] produced by light-emitting diodes [LEDs].) The recording system was grounded to the seawater through a stainless steel plate. ERG signals were amplified by using a 10,000 \times gain with 1 Hz high pass and 1 kHz low pass filter settings (amplifier model DAM 50, World Precision Instruments, Sarasota, FL). The resultant signal was further filtered with a Humbug[®] active electronic filter to remove 60 Hz noise (Quest Scientific, North Vancouver, BC, Canada), and digitized at 1 kHz sampling frequency with a multifunction data-acquisition card (model 6024E, National Instruments, Austin, TX). Data recording and stimulus presentations were controlled by a custom-designed software developed by Eric Warrant (University of Lund, Lund, Sweden) using the LabVIEW graphical programming system for measurement and automation (National Instruments, Austin, TX). In order to account for any influence of circadian rhythms on visual responses (Mangel, 2001), experiments were conducted during the hours the fish holding tanks were lit (herein referred to as “day”), and then repeated on the same individual during the hours the fish holding tanks were in darkness (herein referred to as “night”). As a result, the night experi-

ments on Pacific halibut were conducted approximately 10–12 hours after exposure to bright light.

Three separate procedures were conducted to test for treatment effects on visual function: responses to increasing light intensities (V-log I response curves), flicker fusion frequency, and spectral sensitivity. For the first two procedures, light stimuli were produced by a circular (3.8 cm diameter) light source (model SL2420, Advanced Illumination, Rochester, VT) comprising 20 white LEDs. The LEDs were mounted behind a thin diffuser and collimating lens to produce an even ($\pm 10\%$ edge to edge) illumination field. Light output was controlled by an intensity controller (model CS410, Advanced Illumination, Rochester, VT), which in turn was controlled the analog output of the data acquisition card. A series of neutral density filters (Kodak Optical Products, Rochester, NY) were used to extend the range of light levels as needed.

For the determination of spectral sensitivity, the output of a xenon fiberoptic light source (model Y1603, CVI Laser Spectral Products, Albuquerque, NM) was controlled with a monochromator (model CM110, CVI Laser Spectral Products, Albuquerque, NM), two filter wheel assemblies (model AB301, CVI Laser Spectral Products, Albuquerque, NM) containing quartz neutral density filters, and an electronic shutter (model LS6, Uniblitz, Vincent Associates, Rochester, NY). The monochromator produced single wavelength light (with an 8 nm 50% bandwidth) between 300 and 700 nm. The filter wheel assemblies allowed the attenuation of light from 0 to 5 log units in 0.2 log-unit steps. The monochromator and filter wheel assemblies were controlled by using serial (RS232) interfaces, and the shutter was controlled by the digital output of the data acquisition card. Light from the xenon light source was conducted through the monochromator \rightarrow filter wheel \rightarrow shutter assembly, and from there directed at the eye through 3-mm light guides. The LED light source and exit point of the light guide were placed approximately 5 cm from the corneal surface. The outputs of the LED and xenon light sources (the latter measured at exit of the light guide after passage through the monochromator \rightarrow filter wheel \rightarrow shutter assembly) were calibrated with a research radiometer (model IL 1700, International Light, Inc., Newburyport, MA).

To construct V-log I response curves, light intensities were increased in 0.2 log-unit steps from levels that produced no measurable responses, to those that produced maximal responses. Stimuli consisted of a train of five 200-ms duration light flashes 200 ms apart. The trains of stimuli at each light intensity were presented every five seconds and repeated five times. The ERG responses to the final flash of each train were recorded and averaged. The data were subsequently normalized by expressing the average response to an intensity step as a fraction of the maximum observed average response. Normalized ERG responses versus log light intensities (candela/meter²) were plotted to construct V-log I response curves. Mean V-log I curves for each

species were constructed by averaging the normalized curves of all individuals within a treatment group recorded during the day or during the night.

Flicker fusion frequencies were determined by using five-second sinusoidal light stimulus trains, followed by five seconds of darkness. The maximum light intensity of the sinusoidal stimulus was that required to produce a response that was 50% of the maximal response. This value was determined by eye during experiments from the individual V-log I response curves. Stimulus trains were repeated five times at each frequency and the responses averaged. Stimulus frequencies were increased from 1 Hz (0 log units) to 63.1 Hz (1.8 log units) in 0.2 log-unit steps. The flicker fusion frequency was determined by comparing the power spectrum of the averaged response at each stimulus frequency (signal) to the power spectrum of a neighboring frequency (noise) and was defined as the frequency at which the power of the signal fell below the power of the noise.

Spectral response curves were determined using monochromatic light flashes produced by a xenon light source and monochromator \rightarrow filter wheel \rightarrow shutter assembly. Approximately isoquantal light stimuli from 300 to 650 nm, regulated by the monochromator and neutral density filters, were presented to subjects in 10-nm wavelength steps. Five stimuli of 40 ms duration were presented at each wavelength, and five seconds were allowed between each light flash. The responses to the five flashes were averaged and mean amplitudes recorded.

Spectral sensitivity curves were subsequently calculated from the spectral response curves as follows. First, spectral response data were corrected for differences in lamp output at specific wavelengths, as well as for differences in neutral density filter values from their nominal values, through the application of correction factors. The correction factors were based on the calibration curves developed with the research radiometer described above. Second, responses to exactly isoquantal intensities were predicted by adjusting the response amplitude at each wavelength by using spectral V-log I response curves generally following the methods described in Coates et al. (2006). The only exception was that a fourth-order polynomial was fitted to the individual spectral V-log I response data. Spectral V-log I response curves were recorded immediately after measurement of the spectral response curves by using a series of increasingly intense flashes at the wavelength which generated the largest response. Five flashes (200 ms duration, five seconds apart) were delivered at each intensity step and the response amplitudes averaged. Intensities increased in 0.2 log-unit steps and ranged from those producing no response, to those producing a maximal response.

Individual spectral sensitivity curves were normalized by using the maximal response at each wavelength. Mean spectral sensitivity curves were constructed by averaging the spectral sensitivity curves of all individuals within a treatment group recorded during the day or during the night

Table 1

Mean (and 95% confidence bands) intensities (log candela/meter²) of broad spectrum white light required to produce electroretinogram (ERG) responses 50% of the maximal observed responses in black rockfish (*Sebastes melanops*) and Pacific halibut (*Hippoglossus stenolepis*). The 50% response points were calculated to explore day-night differences, species-specific light sensitivities, and treatment effects. The mean 50% response point in control Pacific halibut was more than an order of magnitude lower than that of black rockfish, indicating the significantly greater light sensitivity of the former. There was no effect of rapid decompression on the 50% response point of black rockfish, whereas 15 minutes of exposure to simulated sunlight increased the 50% response points of Pacific halibut, clearly indicating a diminished light sensitivity in the retina.

	Day	Night
Black rockfish, control	2.1 (2.1–2.2), n=7	2.0 (1.8–2.1), n=7
Black rockfish, rapid decompression	2.3 (2.2–2.3), n=6	1.9 (1.8–2.0), n=6
Pacific halibut, control	0.09 (0.01–0.19), n=6	–0.07 (–0.16 –0.05), n=5
Pacific halibut, light exposed	0.56 (0.47–0.63), n=5	0.78 (0.61–0.91), n=5

Statistical procedures

To explore species differences and treatment effects on retinal light sensitivity, the Weibull four-parameter sigmoid function contained within SigmaPlot for Windows version 10 (Systat Software, San Jose, CA) were fitted to the mean V-log I response data. This function was chosen because ERG responses generally exhibit a sigmoid response to increasing light intensities (Kobayashi, 1962). Light intensities required to produce responses that were 50% of that needed to produce a maximal response (and their 95% confidence bands) were taken from the predicted values produced by the curve-fitting program.

Differences in the mean flicker fusion frequency data collected during the day and night were tested with paired-*t* tests (SigmaStat 3.1, Systat Software, San Jose, CA) because they represented “before-and-after” trials on the same animal. In those instances where no differences were found, day and night data were combined. Differences in the flicker fusion frequency between control animals and those subjected to rapid decompression (black rockfish) or simulated sunlight (Pacific halibut), were likewise treated with *t*-tests. In instances where no treatment effects were present, data were combined. The Mann-Whitney rank sum test was used to test for species differences because the combined data sets were not normally distributed. In all instances $P < 0.05$ was taken to indicate significant differences.

To explore the specific effects of bright light exposure on retinal function in Pacific halibut, the vitamin A1 rhodopsin absorbance templates developed by Stavenga et al. (1993) were fitted to the normalized spectral sensitivity data assuming the presence of two visual photopigments. Unknown model parameters (photopigment absorption maxima and their weighting proportions) were estimated by using maximum likelihood within the software package *R* (vers. 2.7.0, R Foundation for Statistical Computing, Vienna, Austria).

Results

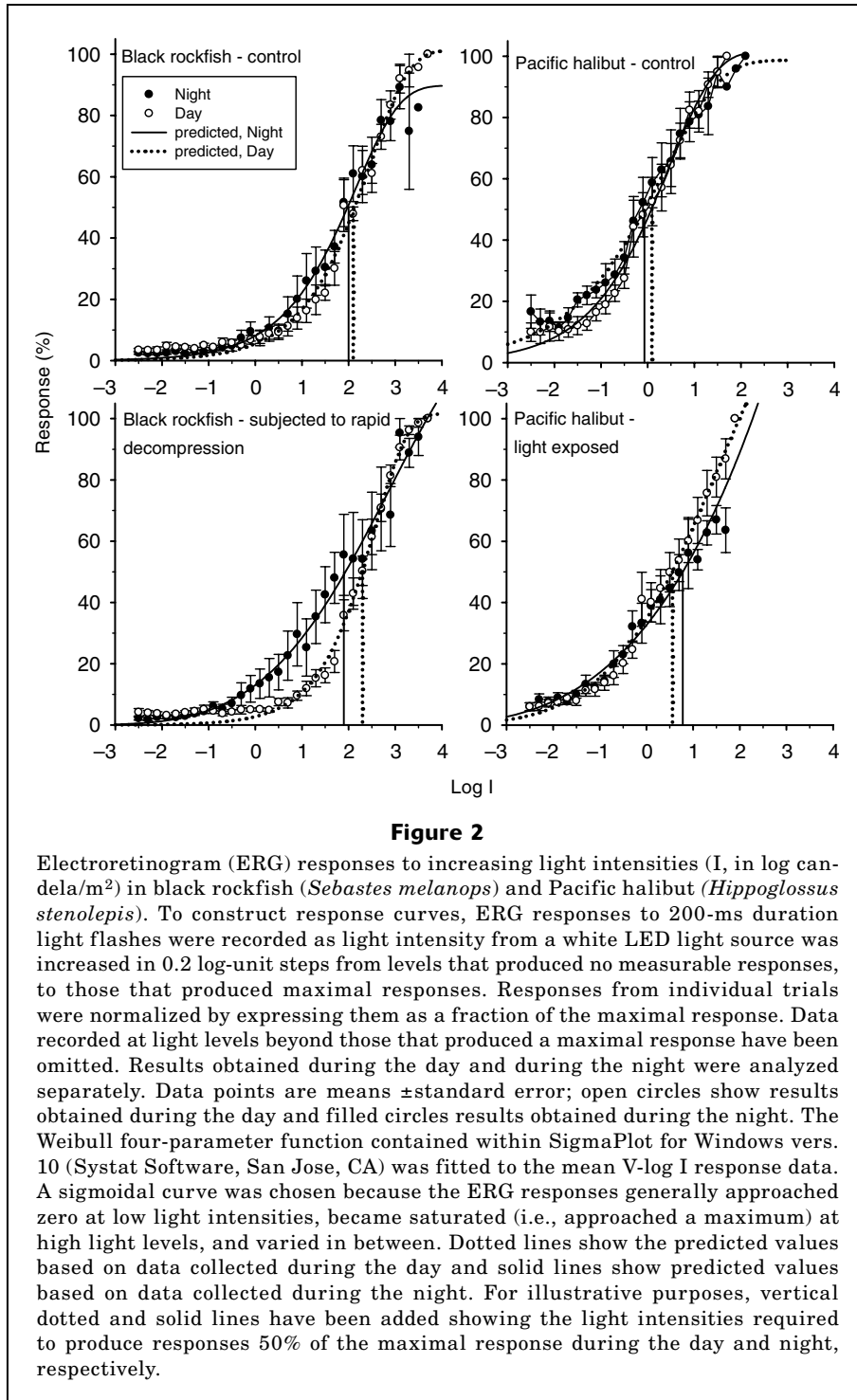
Effects of rapid decompression

Five of eight black rockfish exposed to simulated capture showed severe exophthalmia immediately after rapid decompression, and one fish in this condition also displayed corneal emphysemas. All eight fish showed other external signs of barotraumas, such as gas bubbles under the branchiostegal membrane, and seven of the eight showed esophageal eversion. None showed any gas bubbles within the vitreous humor. Exophthalmia and other signs of barotrauma disappeared in all fish immediately after recompression. There were no obvious external anatomical abnormalities or evidence of disease in any of the fish at the time they were used in an experiment.

Responses to increasing light intensities

The amplitude of ERG responses of both black rockfish and Pacific halibut increased with increasing light intensities (Fig. 2) and produced the expected sigmoid V-log I response curves (Kobayashi, 1962). Based on the overlap of mean 50% response points and the 95% confidence bands (Table 1), there were no significant day-night differences in the light sensitivity of either species within treatments with the possible exception of black rockfish exposed to rapid decompression. The mean 50% response points in the control Pacific halibut were more than an order of magnitude lower than those of the black rockfish (Table 1), indicating a significantly greater light sensitivity in the former.

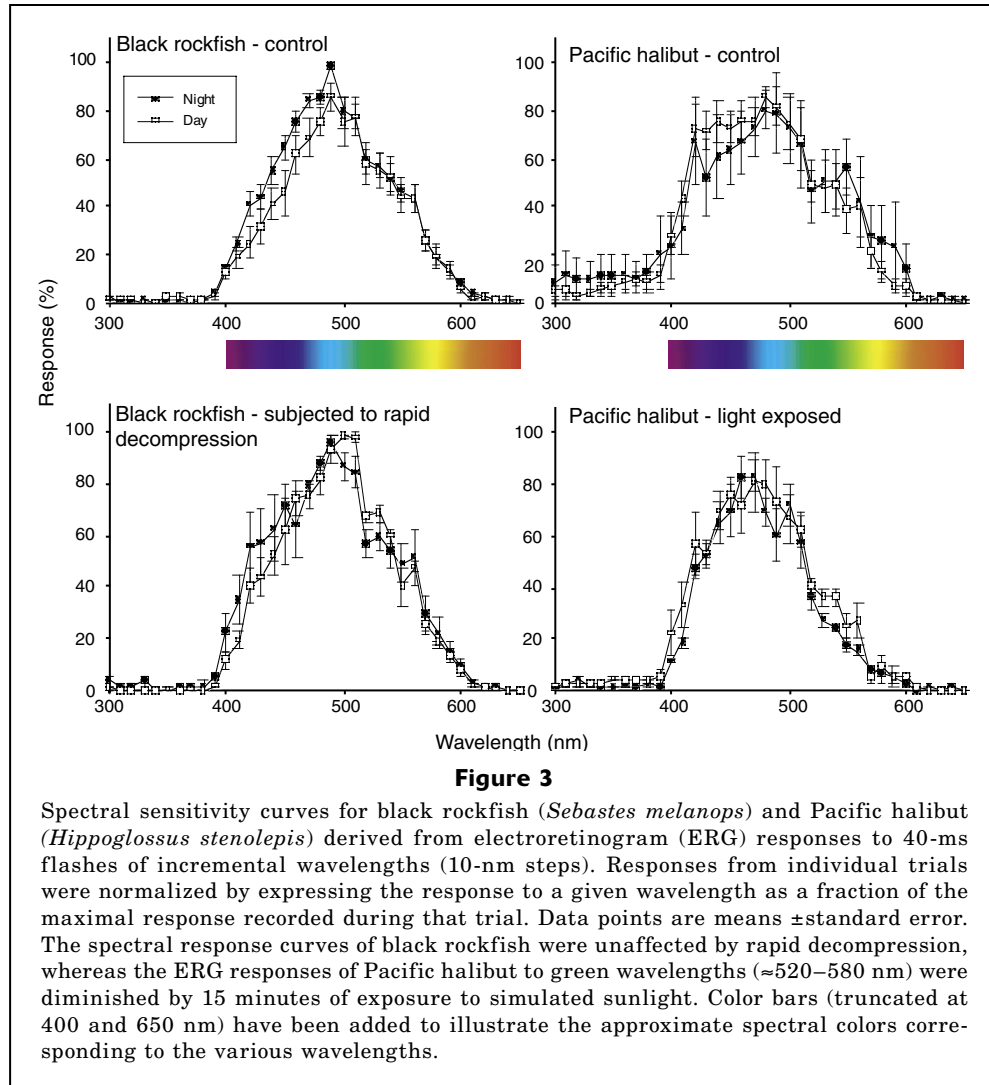
There was no effect of rapid decompression on the 50% response point for black rockfish. In contrast, the responsiveness of Pacific halibut retinas was significantly diminished by exposure to bright light. During both day and night recordings, the V-log I response curves for Pacific halibut exposed to simulated sunlight were clearly right-shifted compared to controls (Fig. 2). The mean 50% response points for treated



fish were approximately 0.5 to 0.8 log units higher than the mean values for control fish (Table 1). In other words, the light levels required to reach the 50% response points in Pacific halibut exposed to simulated sunlight were three to seven times higher than the light levels required to reach the 50% response points in control fish.

Flicker fusion frequency

There were no day-night differences in the flicker fusion frequencies for either black rockfish or Pacific halibut. There was also no detectable influence of rapid decompression on flicker fusion frequency for black rockfish, nor an apparent effect of exposure to bright light on



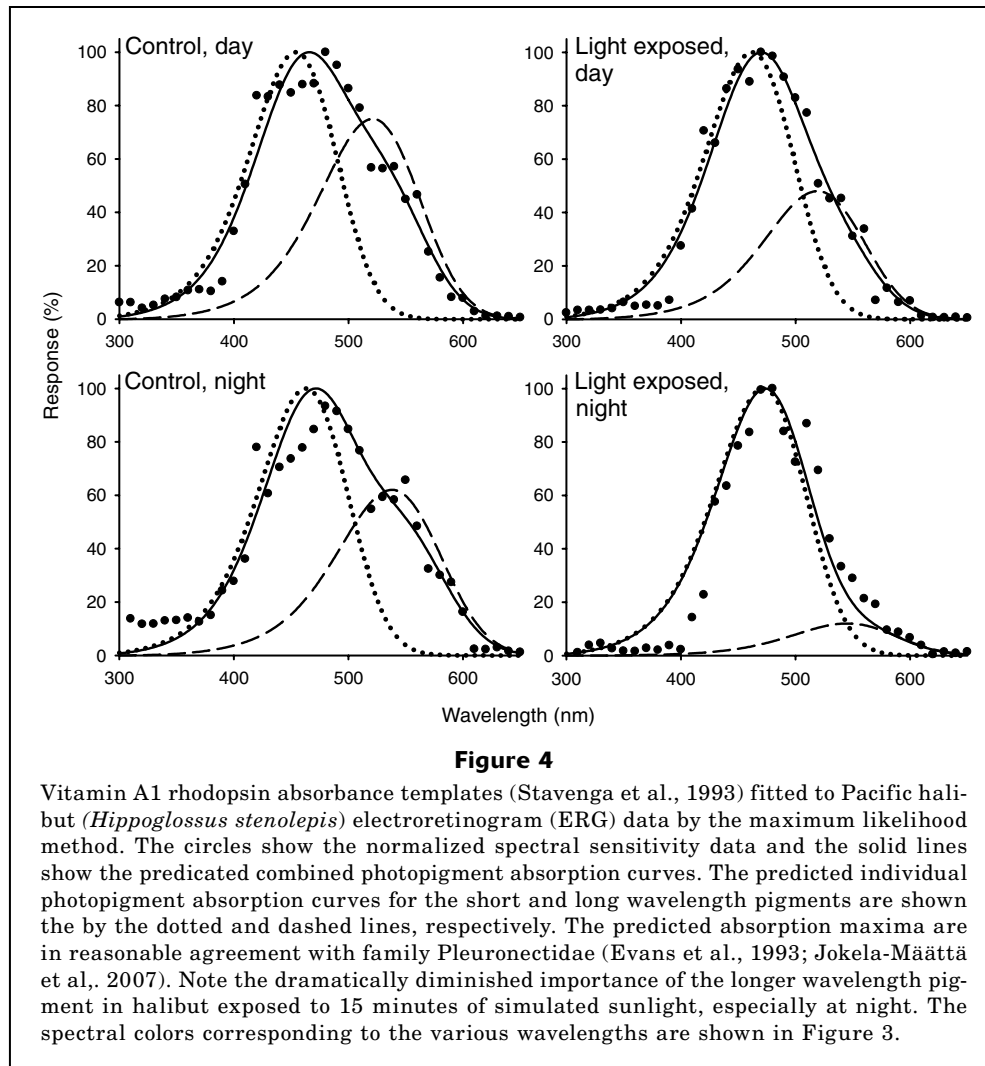
the flicker fusion frequency of Pacific halibut. Within-species data were therefore combined to test for cross-species differences. The median flicker fusion frequency for Pacific halibut (30 Hz) was significantly lower than that of black rockfish (49 Hz) ($P < 0.001$, Mann-Whitney rank sum Test).

Spectral curves

The spectral sensitivity curves of black rockfish and Pacific halibut were very similar (Fig. 3). Both species showed strong sensitivity to blue-green wavelengths (480–590 nm), and a range of responses from 380 nm (violet) to 610 nm (orange). There was no appreciable sensitivity to the shorter (UV-A, 350–380 nm) nor longer (red, >620 nm) wavelengths in either species.

There was no indication that the spectral sensitivity of black rockfish was affected by rapid decompression (Fig. 3), whereas the spectral sensitivity of Pacific halibut was clearly influenced by exposure to

simulated sunlight (Fig. 3). Vitamin A1 rhodopsin absorbance templates developed by Stavenga et al. (1993) were, therefore, used to further assess these changes. In all cases, the templates provided reasonable fits to the observed ERG data (Fig. 4). The parameters showing the largest effects of bright light exposure were clearly the ratios of the long wavelength to short wavelength photopigment weighting factors that are indicative of the relative value of the two photopigments to the composite curve. In control Pacific halibut, this ratio ranged from 0.75 during the day to 0.62 during the night, indicating only a slight predominance of the shorter wavelength photopigment (Fig. 4). In contrast, in Pacific halibut exposed to simulated sunlight these ratios were 0.48 and 0.12 during the day and night, respectively. These results indicate a much reduced functional importance of the longer wavelength photopigment, especially during the night (i.e., approximately 12 hours after exposure to simulated sunlight).



Discussion

Our observations with black rockfish do not support our original contention that exophthalmia and other internal events associated with rapid decompression compromise retinal function. We found no differences in light sensitivity (V-log I response curves), flicker fusion frequency, or spectral sensitivity between control and experimental fish. Our procedures would not, however, detect damage to the optic nerve or other parts of the central nervous system associated with vision. Experiments involving visually evoked potentials (Bullock et al., 1991), predator- and prey-sighting distance, the optomotor response, or other behavioral procedures (Douglas and Hawryshyn, 1990; Vogel and Beauchamp, 1999; Herbert and Wells, 2002) are needed to confirm the lack of detrimental effects of barotrauma on visual function in black rockfish. Rockfish simply discarded on the surface after being subjected to rapid decompression during capture frequently float. They are than subjected to high rates of avian predation. Returning rockfish to

depth (repressurization) reverses the external signs of barotrauma (Parker et al., 2006). Our observations confirm that releasing rockfish at depth is an effective procedure for minimizing postrelease mortality, except for fish with severe hook injuries (St. John and Syers, 2005).

In contrast to the apparent lack of effects of barotrauma on vision in black rockfish, there are multiple lines of evidence that 15 minutes of exposure to simulated sunlight dramatically affects the visual function of Pacific halibut. First, exposure to bright light causes a large reduction in sensitivity (Table 1) indicated by the approximate 3 to 7× increase in amount of light required to achieve an ERG response to broad spectrum white light that is 50% of the maximal response (Table 1). We strongly suspect that low-light vision was also affected. Measuring low-light sensitivity (i.e., minimal detectable ERG response) requires a specific set of procedures different from the ones we employed (Reilly and Thompson, 2007) and we did not have sufficient support for this project to allow us to

conduct the requisite experiments. Pacific halibut are less able to detect baits in near total darkness than at brighter light levels (Stoner, 2003). By extension, we conclude that individuals whose visual function has been compromised by exposure to bright light will be less able to feed and avoid predators than normal animals. Behavioral tests quantifying the effects of bright light exposure on the ability of Pacific halibut to locate and capture prey or detect predators are clearly warranted.

To the best of our knowledge, there are no published descriptions of retinal anatomy in Pacific halibut. The retinas of Atlantic halibut (*Hippoglossus hippoglossus*) contain both rods and cones (Kvenseth et al., 1996), and we strongly suspect that the retinas of Pacific halibut do also. Likewise, we know of no microspectrophotometry studies detailing the absorbance maxima of photopigments in juvenile or adult Pacific halibut retinas. Microspectrophotometry studies of other members of the family Pleuronectidae (*Platichthys flesus* [flounder] and *Pseudopleuronectes americanus* [winter flounder]) show that the peak absorbance of the photopigment in rod cells is ≈ 510 nm, that in single cones is ≈ 450 nm, and that in double cones is ≈ 530 or 550 nm (Evans et al., 1993; Jokela-Määttä et al., 2007). From these lines of evidence, and the results obtained by fitting rhodopsin absorbance templates to the ERG data by the maximum likelihood method (Fig. 4), we concluded that Pacific halibut retinas contain two photopigments with absorbance maxima similar to other members of the family Pleuronectidae. Our conclusion is also in general agreement with the maximum spectral sensitivities of a range of coastal and continental shelf species (Levine and MacNichol, 1979; Bowmaker, 1990).

The change in spectral sensitivity curves of Pacific halibut (Fig. 3) caused by exposure to bright light and the results of photopigment template fitting (Fig. 4) imply that it is the functional properties of a single class of cells (those containing the longer wavelength ≈ 520 to 540 nm photopigment) which are predominately disrupted by exposure to bright light. The retinas of larval Atlantic halibut and adults of the related species—winter flounder—are dominated by the so-called “green cones” (Evans et al., 1993; Helvik et al., 2001). If this is also the case in Pacific halibut, our results indicate disruption of the photoreceptor cells which normally provide maximal quantal absorption in the green-light dominated coastal waters (Levine and MacNichol, 1979; Lythgoe, 1975, 1980; Crescitelli, 1991). This detriment to vision is likely to have severe consequences for postrelease predator avoidance and foraging success. Moreover, the results from photopigment template fitting indicate that the specific functional deficit persists for at least 10 to 12 hours after the exposure to bright light and worsens with time (Fig. 4). If this diminished functionality is due to apoptosis induced by photic injury (Wu et al., 2006), it is likely that it will continue to worsen progressively and be permanent.

Hook-and-line caught Pacific halibut can be discarded quickly and are not subject to significant time periods out of the water (Kaimmer and Trumble, 1998). Because they would not be exposed to direct sunlight for prolonged periods, minimal or no reduction in visual function would be expected. In contrast, trawl-caught Pacific halibut can be exposed to bright light during prolonged sorting operations (Davis and Olla, 2001). Increased mortality has been demonstrated in Pacific halibut that remain on deck for 20–40 min (Trumble et al., 1995). Although the exact causes are unknown, our results clearly imply that these fish could have had significant visual impairment when discarded. Development of procedures to improve survival of Pacific halibut may therefore require not only reducing sorting time (and therefore reducing exposure to air and extreme temperatures), but also sheltering the fish from bright light.

The low flicker fusion frequency and high light sensitivity of Pacific halibut are characteristics of a visual system adapted to function at low light levels (Warrant, 1999). We hypothesize that these features make Pacific halibut, and other demersal fishes with similarly structured visual systems, more susceptible to damage by exposure to direct sunlight than species normally inhabiting brightly lit environments. Should this be the case, there would be significant implications for fishery management, although obviously many significant questions remain. For example, we do not know how long individuals have to be exposed to direct sunlight to incur deficits in visual acuity, nor do we know the threshold of light intensity that causes retinal damage. Research is also warranted on exactly which of the various cell types within the retina are being damaged, the effect(s) of light-induced visual deficits on predator-avoidance and prey-finding behaviors, the resultant changes in rates of mortality, and possible effects at the population level.

Acknowledgments

This project was funded by Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration. All procedures described herein were approved by the Oregon State University Institutional Animal Care and Use Committee (ACUP 3577), and comply with all applicable U.S. laws and regulations. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. The authors gratefully acknowledge the hospitality of the staff of the Hatfield Marine Science Center (Newport, Oregon), and A. Horodysky for his efforts to initiate this project, his comments on earlier drafts of this manuscript, and his help with the photopigment template fitting procedures. R. Latour developed the R-code required for photopigment template fitting. This is contribution 2938 from the Virginia Institute of Marine Science.

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