The Response to Forced Decompression in Six Species of Pacific Rockfish

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ARTICLE

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Abstract

Pacific rockfish experience high discard mortality when captured owing to a condition called barotrauma, which is caused by the change in pressure during capture. This condition appears to be species specific at the macroscopic level; however, little is known about the microscopic tissue-level effects of barotrauma. Determining whether tissue-level injuries are also species specific or influenced by factors such as life history and phylogenetic relatedness can improve our management of discard mortality. We evaluated the responses of six species of Pacific rockfish (black rockfish *Sebastes melanops*, blue rockfish *S. mystinus*, yellowtail rockfish *S. flavidus*, quillback rockfish *S. maliger*, canary rockfish *S. pinniger*, and yelloweye rockfish *S. ruberrimus*) captured from varying depths to forced decompression at the histological level (heart ventricle, rete mirabile, head kidney, liver, gill, and eye) as well as the macroscopic level. At the macroscopic level we focused on injuries caused by barotrauma, namely, everted esophaguses, exophthalmia, ocular emphysema, and ruptured swim bladders. Yellowtail and quillback rockfish experienced the fewest macroscopic injuries. Depth of capture influenced the presence of exophthalmia in quillback rockfish and ocular emphysema in quillback and yelloweye rockfish. Tissue injuries as a result of forced decompression included emphysema in the heart ventricle, emboli in the vessels of the rete mirabile, and emboli in the vessels of the head kidney. No injuries were observed at the histological level in the liver, gill, or eye owing to barotrauma. We could not detect a difference in the tissue-level response to barotrauma among the six species, suggesting that all species are susceptible to high internal gas pressure during forced decompression.

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The rockfish (genus *Sebastes*) is very diverse and has over 65 species that occur off the West Coast of North America from Baja California to Alaska (Love et al. 2002). Rockfish species inhabit areas from nearshore to the continental slope and have both benthic and semipelagic life histories. Most rockfish species have an average lifespan of 40–100 years and reach reproductive age between 5 and 15 years of age (Love et al. 2002).

Rockfish are physoclists, which means they have a swim bladder that is not connected to the esophagus. When rockfish are captured, gas inside the swim bladder expands as the rockfish is brought to the surface. This gas can leak into the visceral and cranial cavities through ruptures or small tears in the swim bladder and cause the condition known as barotrauma (Hannah et al. 2008b). Barotrauma injuries can include bloating, ruptured swim bladder, crushed organs, eversion of the esophagus, exophthalmia, and emphysema in the heart tissue, as well as excessive buoyancy (Gotshall 1964; Rummer and Bennett 2005; Hannah and Matteson 2007; Hannah et al. 2008b; Jarvis and Lowe 2008; Pribyl et al. 2009). Excessive buoyancy can make it difficult for many rockfish species to submerge once released. Discarded rockfish from fishery activity are often left floating on the surface where they can succumb to thermal shock or predation. Understanding how barotrauma affects different species of rockfish is important to properly manage discard mortality.

Research has identified the external effects of barotrauma in different species of rockfish (Hannah and Matteson 2007; Hannah et al. 2008b; Jarvis and Lowe 2008) and their ability to submerge after capture (Hannah et al. 2008a); however, little work has been done to systematically evaluate the internal effects of decompression on organs or tissues in rockfishes. Research on black rockfish *Sebastes melanops*, blue rockfish *S. mystinus*, and yellowtail rockfish *S. flavidus* decompressed from 4.5 atmospheres absolute (ATA; 35-m depth) found emphysema (gas bubbles) in the heart ventricle (Pribyl et al. 2009), but no injury in the liver, head kidney, gill, or pseudobranch. More research is needed to evaluate the tissue-level effects of barotrauma on a greater variety of rockfish species to determine whether tissue injuries are species specific or related to life history or phylogenetic differences.

We investigated the macroscopic and tissue-level responses to forced decompression in six species of Pacific rockfish captured from a variety of depths to determine whether barotrauma injuries are species specific at the tissue level as well as at the macroscopic level or whether life history or phylogeny affect tissue response. We also investigated whether internal tissue injuries could be predicted from external macroscopic barotrauma injuries. Rockfish species included black rockfish, blue rockfish, yellowtail rockfish, canary rockfish *S. pinniger*, quillback rockfish *S. maliger*, and yelloweye rockfish *S. ruberrimus*. Black rockfish and blue rockfish are common at depths less than 90 m and regularly aggregate throughout the water column. Yellowtail rockfish are common at depths between 90 and 180 m and are also active in the water column. Black, blue, and yellowtail

rockfishes are known to school together along with other species of midwater rockfish. Canary rockfish are common between 80 and 200 m depths and are usually found near the bottom. Canary rockfish often associate with yellowtail rockfish and other deep-shelf (100–200 m) rockfish species. Quillback rockfish are also bottom dwellers and can occur from the subtidal zone to 274 m. Although primarily bottom feeders, quillback rockfish may consume fish at depths up to 12 m above the bottom. Yelloweye rockfish are most common between depths of 91–180 m and are primarily found on or near the ocean bottom (Love et al. 2002). Based on these life history patterns, the rockfish species in this study could be divided into two groups: one group (black, blue, and yellowtail rockfishes) that is more active in the water column, and one group (quillback, canary, and yelloweye rockfishes) that is primarily benthic.

Phylogenetically, yellowtail rockfish and black rockfish are the most closely related, having separated only about 1.3 million years ago (MYA; Hyde and Vetter 2007). Blue rockfish are the next closest species, having separated from black rockfish and yellowtail rockfish about 4.2 MYA. Black, yellowtail, and blue rockfishes are part of the Sebastosomas clade. Contrary to the closely related Sebastosomas clade species though, quillback, canary, and yelloweye rockfishes are not closely related. The quillback rockfish node, canary rockfish node, and the Sebastosomas clade node separated over 6 MYA and the yelloweye rockfish node separated over 7 MYA (Hyde and Vetter 2007). Based on phylogeny, we would expect black, blue, and yellowtail rockfishes to group together in their response to barotrauma.

All six species of rockfish investigated are commonly captured in recreational and commercial fisheries, and both canary rockfish and yelloweye rockfish are currently listed as depleted (PFMC 2008). Based on the life histories and phylogeny of the rockfish species we investigated, we expected to find different responses to forced decompression between rockfish species that are primarily benthic (quillback, canary, and yelloweye rockfishes) and those that are known to spend some time in the water column (black, blue, and yellowtail rockfishes).

METHODS

Sample collection.—Rockfish were sampled immediately after capture by hook and line on chartered fishing vessels out of Newport and Depoe Bay, Oregon. Rockfish sampling took place in June through September during 2005 to 2007. From each species 15 to 17 fish were sampled (Table 1). Minimum lengths of each species were within the size range for length at first maturity for each species (Love et al. 2002) and depths of capture ranged from 20 to 194 m. Immediately upon capture, rockfish were examined for external barotrauma indicators and measured for total length. The following external barotrauma indicators were recorded as described by Hannah et al. (2008a) and Pribyl et al. (2009): everted esophagus, swollen abdomen, inflated pharyngo-cleithral membrane, air bubbles in the pharyngo-cleithral membrane, exophthalmia, and ocular

TABLE 1.   Number of fish sampled in the field (*N*), average total length, average depth of capture (DOC), and sex ratio of the six rockfish species used in the study. Values in parentheses are ranges.

Rockfish species	*N*	Total length (cm)	DOC (m)	Sex ratio[a]
Black	16	41.5 (39–47)	37.1 (26–46)	1.29
Blue	16	35.2 (34–42)	36.1 (20–48)	All female
Yellowtail	15	39.0 (33–52)	56.0 (31–145)	2.75
Quillback	16	39.5 (35–46)	45.5 (29–77)	1.00
Canary	17	38.1 (30–56)	62.2 (24–146)	3.25
Yelloweye	17	51.6 (31–62)	116.7 (37–194)	0.70

[a]Number of females/number of males.

emphysema. Exophthalmia refers to the bulging of the eye from the socket, in this case because of high gas pressure. Emphysema refers to the abnormal presence of gas in tissues (in this case, gas bubbles visible in the corneal region of the eye). After blood sampling, rockfish were killed immediately with a blow to the head and subsequent severing of the spinal column. Rockfish were then dissected and portions of the heart ventricle, liver, head kidney, rete mirabile, and gill were removed within 20 min of capture and fixed in Davidson's solution at a ratio of no less than 1:10 (tissue : fixative). We also collected a subsample of eyes from rockfish that exhibited exophthalmia and ocular emphysema. During the first year of sampling, not all tissues were collected, thus sample numbers by tissue vary. Recorded sample information included capture depth, length, sex, external barotrauma indicators, and internal signs of injury such as ruptured swim bladder and hemorrhaging.

Tissues were fixed for a minimum of 30 d, processed for embedding into paraffin blocks, and then sectioned at a thickness of 5–7 μm and mounted onto microscope slides. Eyes were sectioned at Oregon State University's Veterinary Diagnostic laboratory, to provide a vertical cross section that showed the entire circumference of the eye including the cornea, iris, lens, retina, choroid, and sclera. Slides were stained with hematoxylin and eosin Y and viewed with a Leica compound light microscope (model DM LB; Leica Microsystems, Wetzlar, Germany) at magnifications between 100 and 400×. All images were obtained with SPOT Advanced imaging software (Diagnostic Instruments, Inc, Starling Heights, Michigan).

Statistical analyses.—For macroscopic barotrauma indicators, we focused on four presence–absence indicators associated with more severe barotrauma: everted esophagus, exophthalmia, ocular emphysema, and ruptured swim bladder. We used Fisher's exact test to compare counts of macroscopic barotrauma and histologic barotrauma injuries among species. When there were differences among species, we used further Fisher's exact tests with a correction for false discovery rates (Waite and Campbell 2009) to determine the source of the differences. We calculated 95% confidence intervals by means of Wilson's method (Wilson 1927), which works well with small sample

sizes (Agresti and Coull 1998). We used Mann–Whitney *U*-tests for each species to determine whether depth of capture was different between fish with and without each barotrauma injury. We used Fisher's exact test to compare counts of each barotrauma injury by sex. We did not test for differences due to length because length varied linearly with depth of capture. All analyses were conducted with the statistical package SPSS version 17.0.

RESULTS

Macroscopic Indicators

Analysis of macroscopic barotrauma indicators showed many species-specific differences, including a tendency for yelloweye rockfish and canary rockfish to have a similar response to barotrauma and yellowtail rockfish and quillback rockfish to have a similar response (Table 2). Yellowtail rockfish and quillback rockfish were less affected by macroscopic barotrauma indicators than were black, blue, canary, and yelloweye rockfishes (Figure 1; Table 2), while canary rockfish and yelloweye rockfish had the highest proportions of exophthalmia and ocular emphysema. Mann–Whitney *U*-tests comparing the depth of capture between the presence–absence of barotrauma indicators within each species showed exophthalmia was associated with greater depths of capture in quillback rockfish, ocular emphysema was associated with greater depths of capture in quillback and yelloweye rockfishes, and ruptured swim bladder was associated with lesser depths of capture in black rockfish (Table 3). Sex did not appear to affect the response to barotrauma (Fisher's exact test: *P* > 0.20 for all tests).

Histology

We observed emphysema (gas bubbles) in the heart ventricle (Figure 2B), emboli in the rete mirabile (Figure 2D), and emboli in the vessels of the head kidney (Figure 2F) as a result of
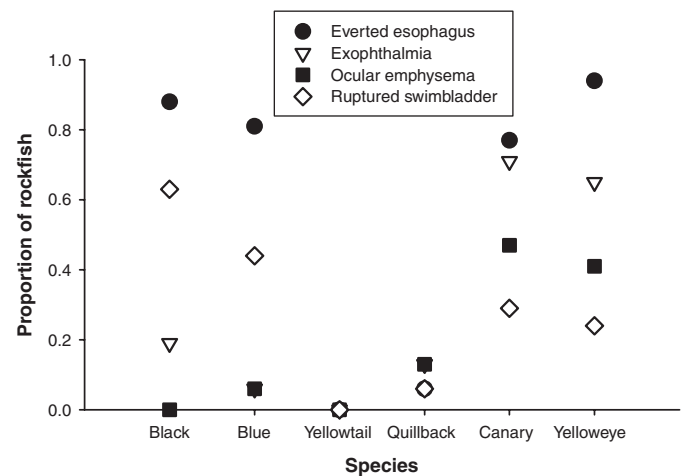

FIGURE 1.   Proportions of rockfish with selected macroscopic barotrauma indicators. The species names along the *x*-axis are in order of their average depth of capture in this study.

TABLE 2. Proportions of macroscopic barotrauma indicators in the six species of rockfish. The 95% confidence intervals (CIs) were calculated by Wilson's method. Different lowercase letters represent significant differences between species (Fisher's exact test: df = 1, $\alpha = 0.05$, $P < 0.02$ with false discovery rate correction).

Indicator	Rockfish species	N	Proportion	95% CI
Everted esophagus	Black	16	0.88 z	0.64–0.97
	Blue	16	0.81 z	0.57–0.93
	Yellowtail	15	0.00 y	0.00–0.20
	Quillback	16	0.06 y	0.01–0.28
	Canary	17	0.77 z	0.53–0.91
	Yelloweye	17	0.94 z	0.73–0.99
Exopthalmia	Black	16	0.19 y	0.07–0.43
	Blue	16	0.06 y	0.01–0.28
	Yellowtail	15	0.00 y	0.00–0.20
	Quillback	16	0.13 y	0.04–0.36
	Canary	17	0.71 z	0.47–0.87
	Yelloweye	17	0.65 z	0.41–0.83
Ocular emphysema	Black	16	0.00 x	0.00–0.19
	Blue	16	0.06 yx	0.01–0.28
	Yellowtail	15	0.00 x	0.00–0.20
	Quillback	16	0.13 zyx	0.04–0.36
	Canary	17	0.47 z	0.26–0.69
	Yelloweye	17	0.41 zy	0.22–0.64
Ruptured swim bladder	Black	16	0.63 z	0.39–0.82
	Blue	16	0.44 zy	0.23–0.67
	Yellowtail	15	0.00 yx	0.00–0.20
	Quillback	16	0.06 y	0.01–0.28
	Canary	17	0.29 zyx	0.13–0.53
	Yelloweye	17	0.24 zyx	0.10–0.47

barotrauma. No injury from barotrauma was observed in the liver, gill, or eye.

We observed emphysema in the compact myocardium of the heart ventricle in all rockfish species except for yellowtail rockfish (Figure 3; Table 4). We failed to detect a difference among species for proportions of emphysema in the heart ventricle (Fisher's exact test: df = 1, $P > 0.01$ for all 15 tests; for $\alpha = 0.05$, $P < 0.001$ with false discovery rate correction). Mann–Whitney U-tests comparing the depth of capture between the presence–absence of emphysema in the heart ventricle also failed to detect a difference in any of the species (Mann–Whitney U-test: $P > 0.1$ for all six tests). There was also no evidence that the four macroscopic barotrauma indicators or sex affected the presence or absence of emphysema in the heart ventricle within each species (Fisher's exact test: df = 1, $P > 0.07$ for all tests). When we combined data from all species, however, we did find that the presence of emphysema in the heart ventricle was related to the presence of an everted esophagus (Table 5).

We observed emboli in the rete mirabile in all species of rockfish (Figure 3; Table 4). Emboli were isolated and, on average, we found one to five emboli per cross section when emboli were present. We failed to detect a difference among

species (Fisher's exact test: df = 1, $P > 0.05$ for all 15 tests; for $\alpha = 0.05$, $P < 0.001$ with false discovery rate correction). Mann–Whitney U-tests comparing the depth of capture between the presence–absence of emboli in the rete mirabile also failed to detect a difference in any of the species (Mann–Whitney U-test: $P > 0.3$ for all six tests). There was no evidence that the four macroscopic barotrauma indicators or sex affected the presence or absence of emboli in the rete mirabile within each species (Fisher's exact test: df = 1, $P > 0.1$ for all tests) or when data from all species were combined (Table 5).

Emboli were also present in a few fish in the blood vessels of the head kidney in all species (Figure 3; Table 4). Again, emboli were isolated and, on average, we only found one or two emboli per cross section when emboli were present. We failed to detect a difference among species for the proportion of fish with emboli in the head kidney (Fisher's exact test: df = 1, $P > 0.08$ for all 15 tests; for $\alpha = 0.05$, $P < 0.001$ with false discovery rate correction). Mann–Whitney U-tests comparing the depth of capture between the presence–absence of emboli in the head kidney also failed to detect a difference in any of the species (Mann–Whitney U-test: $P > 0.2$ for all six tests). There was no evidence that the four macroscopic barotrauma indicators

TABLE 3. Summary of Mann–Whitney test results to determine whether the depth of capture was related to the presence or absence of macroscopic barotrauma indicators. Asterisks denote significant relationships ($P < 0.05$). Abbreviations are as follows: U = the Mann–Whitney U-statistic; Z = the Z-statistic from the normal distribution.

Indicator	Rockfish species	U	Z	df	P
Everted esophagus	Black	8.0	−0.971	1	0.332
	Blue	11.5	−1.095	1	0.274
	Quillback	3.0	−0.987	1	0.324
	Canary	20.5	−6.250	1	0.532
	Yelloweye	4.0	−0.818	1	0.413
Exophthalmia	Black	17.0	−0.343	1	0.732
	Blue	1.5	−1.324	1	0.185
	Quillback*	1.0	−2.087	1	0.037
	Canary	19.5	−1.110	1	0.267
	Yelloweye	20.5	−1.259	1	0.208
Ocular emphysema	Blue	1.5	−1.324	1	0.185
	Quillback*	1.0	−2.087	1	0.037
	Canary	16.0	−1.930	1	0.054
	Yelloweye*	9.0	−2.542	1	0.011
Ruptured swim bladder	Black*	11.0	−2.100	1	0.036
	Blue	19.5	−1.292	1	0.196
	Quillback	5.0	−0.548	1	0.583
	Canary	17.0	−1.375	1	0.169
	Yelloweye	12.0	−1.588	1	0.112

or sex affected the presence or absence of emboli in the head kidney within each species (Fisher's exact test: df = 1, $P > 0.08$ for all tests) or when data from all species were combined (Table 5).

We also observed chronic inflammation in the rete mirabile, although this injury was not related to barotrauma. Development of this advanced stage of inflammation takes days to weeks (Roberts 2001) and could not occur in the few

TABLE 4. Proportions of histologic barotrauma indicators in the six species of rockfish. There were no differences among species for any indicator. See Table 2 for additional details.

| Indicator	Rockfish species	N	Proportion	95% CI
Heart ventricle emphysema	Black	16	0.13	0.04–0.36
	Blue	16	0.19	0.07–0.43
	Yellowtail	15	0.00	0.00–0.20
	Quillback	16	0.13	0.04–0.36
	Canary	17	0.06	0.01–0.27
	Yelloweye	13	0.39	0.18–0.65
Rete mirabile emboli	Black	15	0.67	0.42–0.85
	Blue	12	0.67	0.39–0.86
	Yellowtail	14	0.57	0.33–0.79
	Quillback	12	0.33	0.14–0.61
	Canary	12	0.33	0.14–0.61
	Yelloweye	12	0.25	0.09–0.53
Head kidney emboli	Black	16	0.13	0.04–0.36
	Blue	15	0.07	0.01–0.30
	Yellowtail	15	0.33	0.15–0.58
	Quillback	16	0.39	0.19–0.61
	Canary	17	0.29	0.13–0.53
	Yelloweye	12	0.25	0.09–0.53
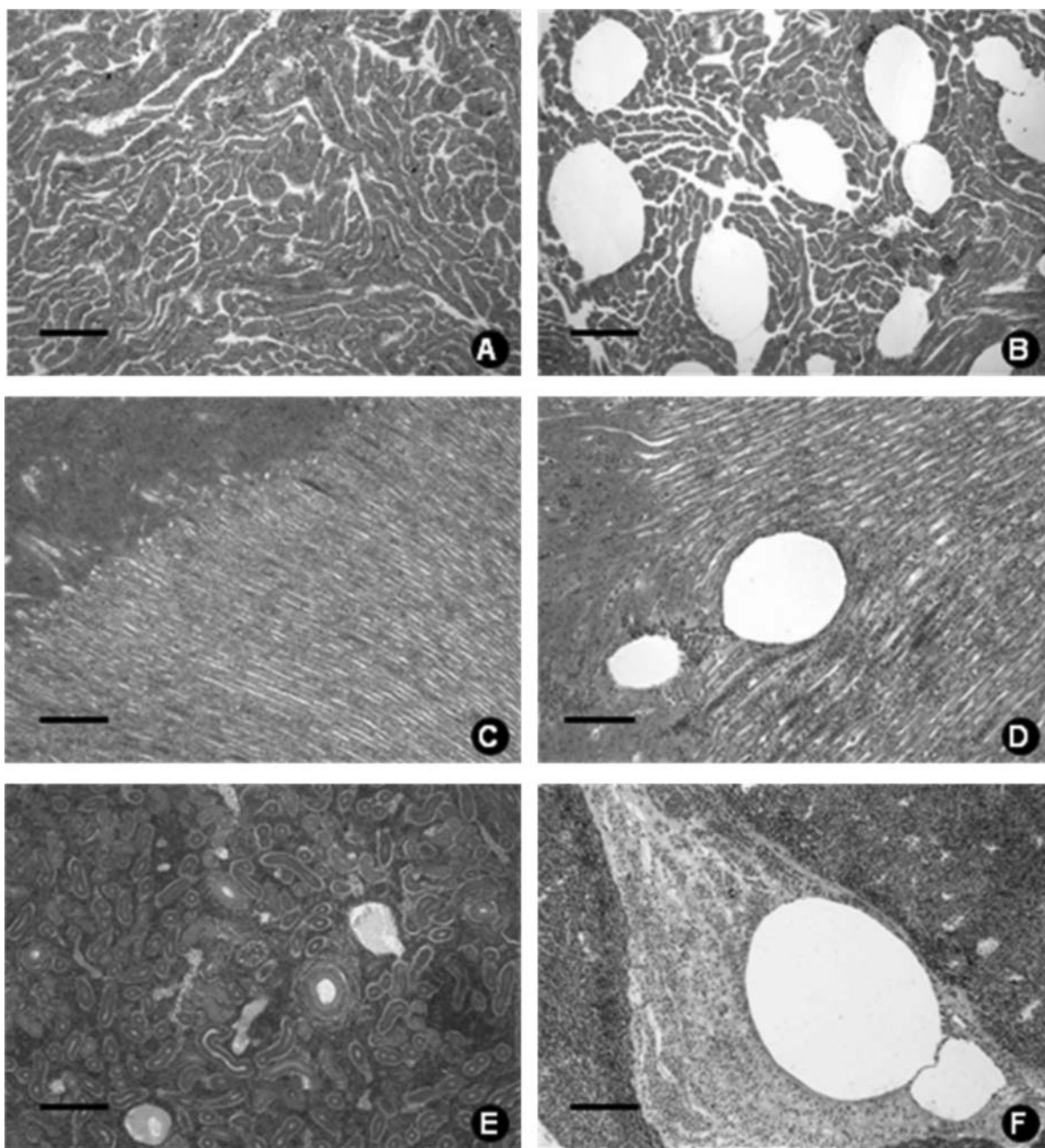
FIGURE 2. Micrograph showing barotrauma injuries in the heart, rete mirabile, and head kidney of rockfish. The individual panels are as follows: **(A)** black rockfish, normal heart ventricle (bar = 200 μm); **(B)** yelloweye rockfish, tissue emphysema in the heart ventricle (bar = 200 μm); **(C)** canary rockfish, normal rete mirabile (bar = 200 μm); **(D)** blue rockfish, emboli in the rete mirabile (bar = 100 μm); **(E)** canary rockfish, normal head kidney vessel (bar = 200 μm); and **(F)** canary rockfish, emboli in a vessel of the head kidney (bar = 100 μm).

minutes between capture and dissection. Chronic inflammation in the rete mirabile was characterized by large aggregations of macrophages and lymphocytes throughout the tissue, often obliterating capillaries (Figure 4A). Inflammation was primarily located in the capillary portion of the rete mirabile, although in a couple cases it was also present in the gas gland. Yellowtail rockfish had higher proportions of rete mirabile inflammation than any other species (Fisher's exact test: df = 1, $P < 0.03$ for all five tests; for $\alpha = 0.05$, $P < 0.03$ with false discovery rate correction), and black rockfish had the next highest proportions of inflammation (Fisher's exact test: df = 1, $P < 0.03$ for all five tests; for $\alpha = 0.05$, $P < 0.03$ with false discovery rate correction). Blue, quillback, canary, and yelloweye rockfishes had no or very low proportions of inflammation.
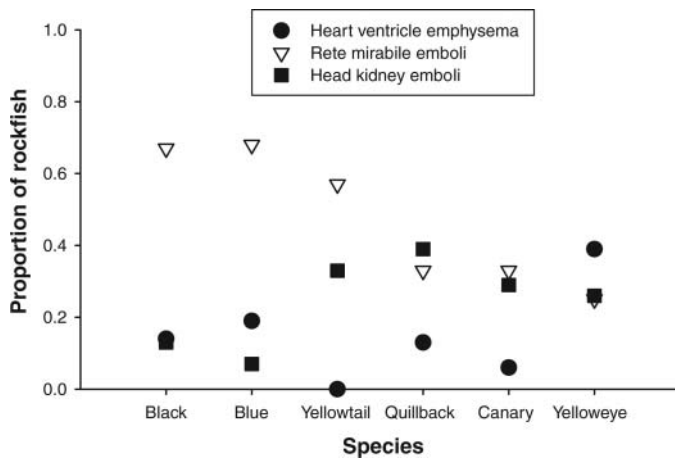
FIGURE 3.   Proportions of rockfish with histologic barotrauma indicators.

DISCUSSION

Macroscopic barotrauma injuries among the six species of rockfish investigated tended to be species specific, as has been found with several other studies (Hannah and Matteson 2007; Hannah et al. 2008a; Jarvis and Lowe 2008; Pribyl et al. 2009). The tendency for both yellowtail rockfish and quill-back rockfish to show minimal macroscopic injury from forced decompression is supported by earlier findings that quill-back rockfish, in addition to yellowtail rockfish, have few, if any, macroscopic barotrauma indicators (Hannah and Matte-son 2007; Jarvis and Lowe 2008; Pribyl et al. 2009). The likely reason for this is that both yellowtail rockfish and quillback rockfish are able to release excess gas by way of their pharyngo-cleithral membrane (Pearcy 1992; Hannah et al. 2008a; Pribyl et al. 2009). Other than an ability to release excess gas, these two species have little in common; quill-back rockfish are thought to be primarily benthic bottom feed-ers and not very active in the water column, while yellow-
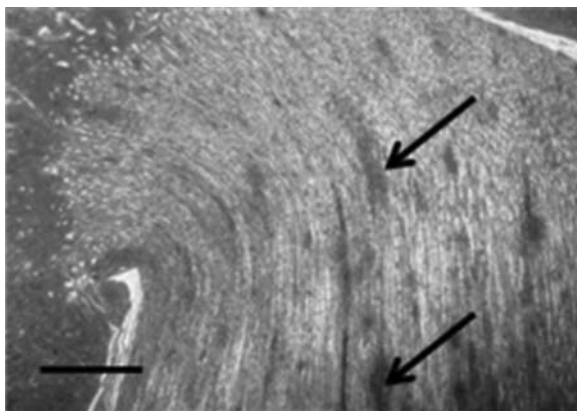

FIGURE 4.   Micrograph showing areas of inflammation in the rete mirabile of yellowtail rockfish (arrows); bar = 500 μm.

tail rockfish feed mostly in the water column and are of-ten observed off the seafloor. These two species are also not closely related at a phylogenetic level (Hyde and Vetter 2007). These findings suggest that life history or phylogenetic relat-edness cannot always be used to predict rockfish response to barotrauma.

Depth of capture played an important role in determining the presence or absence of a macroscopic barotrauma indicator for several species. This appeared to especially be true for eye injuries. The two rockfish species we captured from the great-est depths, yelloweye rockfish and canary rockfish, also had the highest incidences of macroscopic eye injuries. Jarvis and Lowe (2008) also found increasing depths of capture significantly af-fected the number of barotrauma indicators in rockfish. Hannah and Matteson (2007) showed that as depths of capture increased so did behavioral impairment in black, blue and yelloweye rock-fishes when they were released from a cage after recompression. Decompression studies in other fish species, such as red snap-per *Lutjanus campechanus* (Gitschlag and Renaud 1994; Rum-mer and Bennett 2005), largemouth bass *Micropterus salmoides* (Feathers and Knable 1983), and West Australian dhufish *Glau-cosoma hebraicum* (St John and Syers 2005), have shown an increase in the effects of barotrauma with increasing depths of capture as well. These studies along with our results suggest that depth of capture may play an important role in the ability of rockfish to survive decompression.

Besides depth of capture, the temperature differential rock-fish experience when brought to the surface from depth may also affect the severity of barotrauma conditions. Not only does a decrease in pressure cause gas to expand, an increase in tem-perature will also cause gas to expand. Depending on the thermal stratification at the time of capture, this could increase the sever-ity of barotrauma in rockfish, especially in rockfish captured from greater depths. We were unable to measure temperature at depth of capture for the rockfish in this study, so we do not know the extent to which a temperature differential may have affected our results. Off the Oregon coast, we typically do not have a strong thermocline in summer due to upwelling; thus, it is possible the temperature differential in our study was not too great. In areas with greater thermal stratification, it is possible barotrauma injuries could be more severe.

We did not find that species-specific differences at the macro-scopic level translated to species-specific differences at the tis-sue level, although this may have been due to our small sample sizes. We did observe the same tissue injuries in all species of rockfish though (with the exception of heart emphysema in yel-lowtail rockfish), which suggests that despite differences in how excess gas travels internally through different rockfish species, internal tissues can still be exposed to gas pressures high enough to cause injury, regardless of species. Emphysema forming in the heart ventricle, previously observed by Pribyl et al. (2009), is probably a result of high gas pressure in the visceral and peri-cardial cavities as a result of ruptured or leaking swim bladders (Hannah et al. 2008b). The presence of emphysema in most

TABLE 5. Summary of Fisher's exact tests to determine whether macroscopic barotrauma indicators were related to the presence of histologic barotrauma indicators. Data from all six species of rockfish were combined for these analyses; df = 1. The asterisk denotes the only significant relationship between the two types of indicators.

Histologic indicator	Proportion with histologic indicator	Macroscopic indicator	Present?	N	P
Heart emphysema	0.21	Everted esophagus	Yes	53	
	0.05		No	40	0.036*
	0.19	Exophthalmia	Yes	26	
	0.12		No	67	0.505
	0.19	Ocular emphysema	Yes	16	
	0.13		No	77	0.691
	0.19	Ruptured swim bladder	Yes	27	
	0.12		No	66	0.512
Rete mirabile emboli	0.54	Everted esophagus	Yes	41	
	0.44		No	34	0.489
	0.38	Exophthalmia	Yes	21	
	0.54		No	54	0.305
	0.29	Ocular emphysema	Yes	14	
	0.54		No	61	0.137
	0.50	Ruptured swim bladder	Yes	22	
	0.49		No	53	1.000
Head kidney emboli	0.18	Everted esophagus	Yes	51	
	0.33		No	40	0.139
	0.24	Exophthalmia	Yes	25	
	0.24		No	66	1.000
	0.25	Ocular emphysema	Yes	16	
	0.24		No	75	1.000
	0.19	Ruptured swim bladder	Yes	27	
	0.27		No	64	0.593

rockfish species suggests the heart ventricle, being a highly perfused organ, is more sensitive to excessive gas exposure than other less well-perfused organs (Speare 1998; Pribyl et al. 2009).

The presence of emboli in the head kidney and in the rete mirabile of all six species of rockfish is a novel finding. The rete mirabile is a gas-concentrating organ inside the swim bladder consisting of venous and arterial capillaries side by side. Because it is the gas in the swim bladder that expands as a fish is brought to the surface, gas pressure in the swim bladder increases dramatically, exposing the rete mirabile to high gas pressure as well. Thus, it is not surprising we found emboli forming in the rete mirabile. The presence of emboli in the rete mirabile and head kidney could block blood flow or coalesce to block blood flow in progressively larger vessels (Bouck 1980) if left untreated. Emboli have been observed histologically in the heart (Smith 1988; Edsall and Smith 1991), gill (Smith 1988; Edsall and Smith 1991; Speare 1998), and eye (Smith 1988; Speare 1998) of fish suffering from gas bubble disease; however, in gas bubble disease fish are exposed to supersaturating concentrations of gas in the water over long periods of time, not from acute high gas concentrations originating from within the fish. Because emboli from decompression are formed rapidly,

in rockfish that are recompressed quickly after capture so that gases can recompress, emboli should disappear and not cause serious injury. Jarvis and Lowe (2008) found that time on deck was a significant factor affecting a rockfish's ability to survive forced decompression (if recompressed); emboli forming in vessels may be one of the reasons rockfish held on deck for longer periods of time had lower rates of survival.

Unlike the tissue injuries we observed as a result of barotrauma, the presence of chronic inflammation in the rete mirabile may be attributable to differing life histories or phylogenetic relatedness in rockfish. Chronic inflammation is a condition that develops over several days to weeks when inflammatory stimuli are not eliminated from an acute inflammatory response (Roberts 2001); thus, this condition could not be caused by forced decompression from capture. Chronic inflammation can be triggered by a wide range of factors including diet or infection with bacteria, fungi, or parasites (Secombes 1996). We did not find any evidence of bacterial, fungal, or parasitic infection in the rete mirabile, leading us to believe some other mechanism was responsible for the inflammation. One such mechanism could be frequent changes in swim bladder gas pressure. The two species of rockfish with the greatest proportion of inflammation in the

rete mirabile, black rockfish and yellowtail rockfish, are also known to make rapid dives or ascents ranging more than 10 m in the water column (Pearcy 1992; Parker et al. 2008). This behavior has not been documented in the other four species of rockfish we investigated. Interestingly, black rockfish and yellowtail rockfish are also very closely related at a phylogenetic level (Hyde and Vetter 2007), suggesting the possibility that the dive behavior may have a genetic basis. Although not tested, the chronic inflammation in the rete mirabile could be associated with frequent gas pressure changes in the swim bladder from rapid dives.

It is noteworthy that we found no injury due to barotrauma in the liver and gill in all species of rockfish examined, as well as in the subset of eyes from rockfish with exophthalmia and ocular emphysema. It appears that barotrauma may not affect these organs in rockfish, and perhaps this is due to the short period of time these organs are exposed to high gas pressure. Research on eye function in black rockfish supports our findings; Brill et al. (2008) showed that there was no indication that rapid decompression and associated exophthalmia had any effect on rockfish retinal function. However, research on the optic nerve in rockfish showed severe exophthalmia caused extreme stretching of the optic nerves and gas build-up in an orbital space behind the eye (Rogers et al. 2008). This could indicate that although we found no injury to the eye at the histological level, there could still be vision problems in rockfish associated with the optic nerve.

In this study we investigated how different species of rockfish respond to barotrauma at both a macroscopic and microscopic level. We found species-specific differences in the response to barotrauma at the macroscopic level that were not related to life history or phylogeny. We did not find species-specific differences at the microscopic level in tissues, suggesting gas pressure from decompression can build up to high internal levels regardless of species. This study reinforces the need to examine rockfish responses to barotrauma on an individual species level, as opposed to attempting to combine species based on life history patterns or phylogenetic relatedness.

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