

This article was downloaded by: [Oregon State University]

On: 06 September 2011, At: 13:25

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Buoyancy Regulation and Barotrauma in Two Species of Nearshore Rockfish

Steven J. Parker^a, Howard I. McElderry^b, Polly S. Rankin^a & Robert W. Hannah^a

^a Oregon Department of Fish and Wildlife, Marine Resources Program, Hatfield Marine Science Center, Newport, Oregon, 97365, USA

^b Archipelago Marine Research, Limited, 525 Head Street, Number 200, Victoria, British Columbia, V9A 5S1, Canada

Available online: 09 Jan 2011

To cite this article: Steven J. Parker, Howard I. McElderry, Polly S. Rankin & Robert W. Hannah (2006): Buoyancy Regulation and Barotrauma in Two Species of Nearshore Rockfish, Transactions of the American Fisheries Society, 135:5, 1213-1223

To link to this article: <http://dx.doi.org/10.1577/T06-014.1>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan, sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Buoyancy Regulation and Barotrauma in Two Species of Nearshore Rockfish

STEVEN J. PARKER*

Oregon Department of Fish and Wildlife, Marine Resources Program, Hatfield Marine Science Center,
Newport, Oregon 97365, USA

HOWARD I. McELDERRY

Archipelago Marine Research, Limited,
525 Head Street, Number 200, Victoria, British Columbia V9A 5S1, Canada

POLLY S. RANKIN AND ROBERT W. HANNAH

Oregon Department of Fish and Wildlife, Marine Resources Program, Hatfield Marine Science Center,
Newport, Oregon 97365, USA

Abstract.—Fishes with closed swim bladders regulate buoyancy during depth changes by secreting and resorbing swim bladder gases. Forced ascent during fishery capture results in barotrauma caused by rapid expansion and exsolution of gases from body fluids. Pressure changes in hyperbaric chambers were used to examine changes in swim bladder integrity and acclimation rates in two ecologically different, yet congeneric, species: black rockfish *Sebastes melanops* and China rockfish *S. nebulosus*. We also conducted simulated-capture experiments to investigate the relationship between capture in a fishery, barotrauma from pressure change, and survival after release. Black rockfish acclimated faster than China rockfish to both increases and decreases in pressure, but both species were much slower to acclimate than other physoclists, such as Atlantic cod *Gadus morhua*. Black rockfish required up to 48 h to acclimate from 4 atmospheres absolute (ATA; depth equivalent of 30 m) to surface pressure and required up to 168 h to become neutrally buoyant at 4 ATA after starting from surface pressure. In contrast, China rockfish required over 250 h to become neutrally buoyant at 4 ATA after starting from surface pressure. All black rockfish exposed to a 3-ATA decrease in pressure during simulated capture had ruptured swim bladders. However, mortality from simulated capture and subsequent recompression was low; only $3.3 \pm 1.7\%$ (mean \pm SE) mortality was observed after 21 d. In experiments with black rockfish, rapid recompression reversed visible barotrauma, suggesting that a quick return to depth could be used to minimize mortality of discarded black rockfish in nearshore fisheries.

Many rockfishes *Sebastes* spp. on the U.S. West Coast are the targets of both commercial and recreational fisheries throughout a wide range of depths (Parker et al. 2000; PFMC 2004). Rockfishes occur in mixed-species assemblages and often have similar feeding habits, so targeting a single species in hook-and-line fisheries is difficult and bycatch is a common problem. Currently, several rockfishes are classified as overfished and must be discarded if captured (PFMC 2004). A concern with this management strategy is that many rockfishes are believed to have high discard mortality rates due to (1) pressure-related injuries incurred during capture and (2) the inability to return to depth because of exhaustion and excessive buoyancy. However, the effects of barotrauma and discard mortality rates in rockfishes are poorly understood.

There are over 50 rockfish species in the northeast Pacific (Love et al. 2002) that occupy a wide depth range and a myriad of habitats. Many are demersal, occupying reef crevices; some are found suspended in the water column near structure; and others school semipelagically and undergo more extensive vertical movements (Brodeur and Pearcy 1984; Love et al. 2002). We studied two nearshore rockfish species that are important to both recreational and commercial fisheries on the West Coast. They also represent different ecological groups; black rockfish *S. melanops* are semipelagic, whereas China rockfish *S. nebulosus* are more demersal (Love et al. 2002). Black rockfish are also known to make more extensive vertical movements than China rockfish (McElderry 1979). Comparing the pressure-related ecology and physiology of these two species will aid in our understanding of the effects of barotrauma in nearshore fishes and assist in evaluating discard as a management tool for nearshore rockfishes.

Rockfishes have a physoclastic swim bladder configuration and use the swim bladder as a hydrostatic

* Corresponding author: steve.parker@oregonstate.edu

Received January 18, 2006; accepted March 24, 2006
Published online September 7, 2006

organ and, in some species, for sound production (Hallacher 1974). Physoclists secrete gas from the blood into the swim bladder through a specialized vascular plexus, the rete mirabile, and remove gas via the resorption chamber (Alexander 1966). This design allows gas to be secreted against large pressure gradients. Gas removal is regulated through neural and muscular control of exposure of swim bladder gas to a capillary bed in the posterior chamber (Ross 1979). Removal of gas is dependent on passive diffusion of gas into the blood and then into the water via the gills. Accordingly, the rate is dependent on the rate of blood flow (Harden Jones and Scholes 1985). Interestingly, rockfishes inhabiting nearshore areas (<50 m) are more prone to barotrauma caused by expanding swim bladder gases during ascent than rockfishes in deeper water. Following Boyle's Law, the change in swim bladder volume from a short ascent in shallow water is substantially greater than the change in volume that occurs when making the same absolute change in depth but starting in deeper water. This aspect of swim bladder function creates a relatively narrow zone of neutral buoyancy in shallow waters and results in (1) constraints on natural vertical movements and (2) injuries associated with forced ascent during fishing. Depending on the degree of pressure change, barotrauma can involve bloating, swim bladder rupture, compression injuries to organs, eversion of the esophagus or stomach, exophthalmia, and embolism in almost any body tissue, such as capillaries of the gills, heart, and liver (Longbottom 2000). Little work has been done to systematically evaluate tissue or organ barotrauma resulting from forced ascent of rockfishes during capture.

Our goal in this study was to learn about the acclimation abilities of two ecologically different rockfish species relative to pressure changes encountered during recreational fishery capture in waters up to 40 m deep. The objectives of these experiments were to compare black rockfish and China rockfish in terms of their swim bladder integrity and injuries due to barotrauma and to document and compare rates of acclimation to changes in pressure. In addition, for black rockfish, our objective was to estimate the mortality rate from a simulated-capture event and subsequent recompression. We report on earlier comparative experiments, conducted at the Bamfield Marine Station (Vancouver Island, British Columbia), which examined swim bladder morphology, fish body density, red blood cell density, and pressure acclimation in black rockfish and China rockfish in small, single-fish hyperbaric chambers. We also report on more recent experiments that used larger hyperbaric chambers with groups of black rockfish at the Hatfield

Marine Science Center (Newport, Oregon) to study acclimation rates and mortality due to barotrauma caused by forced ascent.

Methods

Comparative Morphology of Black Rockfish and China Rockfish

Black rockfish and China rockfish specimens were obtained by gill net or by diving with hook and line in shallow water (<20 m) off Bamfield, British Columbia. Before dissection, fish were euthanized with quinaldine.

Rete mirabile morphology.—For black rockfish (75–410 mm standard length [SL]) and China rockfish (85–300 mm SL), the ventral surface of the swim bladder was excised to describe the morphology of the rete mirabile for each species. For each fish, the tunica internus was laid flat and photographed. Surface area of the rete mirabile from specimens of various sizes of each species was measured on photographs with a zero-compensating polar planimeter. Differences in rete mirabile area for each species, standardized by weight, were compared with a Student's *t*-test.

Fish density.—We compared the tissue densities between the two species to determine whether swim bladder volumes should be similar for similarly sized individuals. Recently euthanized fish were blot dried and weighed. Each fish was then dissected, the swim bladder was punctured, and all the gas was removed by immersion in seawater. Fish weights in air and in water were determined with an analytical balance by suspending the fish in air or water. Densities were compared between species by use of a Student's *t*-test.

Blood analysis.—Hematocrit samples were taken from field-fresh, recently dead specimens. Blood samples were drawn into heparinized hematocrit tubes and spun at $13,460 \times$ gravity (*g*) for 3 min in a hematocrit centrifuge to determine the proportion of red blood cells in the plasma. Hematocrit comparison between species was measured with a Student's *t*-test.

Acclimation Rates

Individual hyperbaric chambers.—Specimens used for hyperbaric experiments were collected in shallow reef areas near the Bamfield Marine Station. Black rockfish were taken by hook and line at capture depths of less than 10 m to avoid barotrauma. China rockfish were collected (usually at depths from 10 to 15 m) by divers equipped with fishing poles. Before ascent, China rockfish swim bladders were drained with a sterile, 12-gauge hypodermic needle. The different methodology between the two species was reflective of the much higher incidence of macroscopic barotrauma in China rockfish. Specimens were then held in

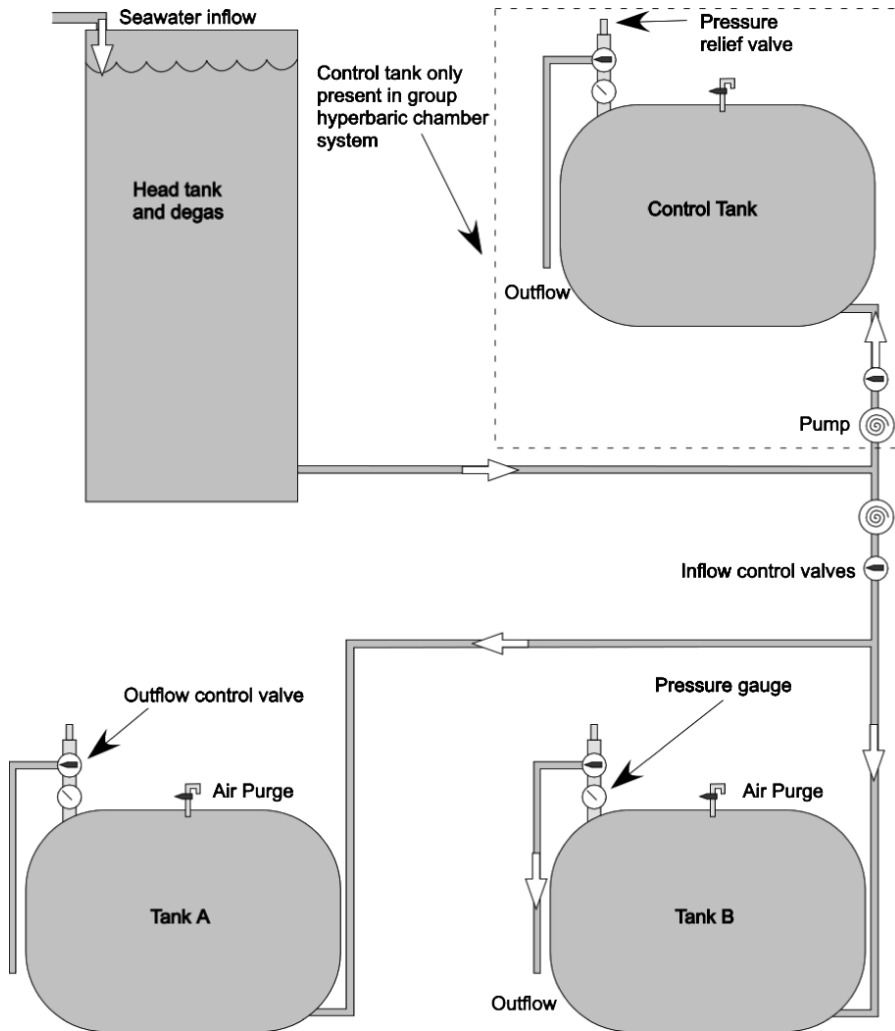


FIGURE 1.—General schematic of hyperbaric chamber design and flow regulation used to examine swim bladder integrity and effects of barotrauma in black and China rockfishes.

laboratory aquaria for approximately 3 d to allow buoyancy to become neutral and to recover from any minor effects from the process of draining swim bladder gases. Individuals appeared to have recovered from their needle wounds and were regulating their buoyancy normally by that time.

To compare acclimation rates of black rockfish and China rockfish, we constructed two small hyperbaric chambers from acrylic cylinders (85 L) that were large enough to hold a single fish. Flow-through seawater (1.8–3.4 L/m) was supplied to each tank. Pressure and flow were regulated by a valve at the outflow (Figure 1). Water flow rates varied with pressure level so that total water exchange occurred at a minimum of 45 min.

Individual fish were placed in the hyperbaric

chamber and held for a period of 24 h at 1 atmosphere absolute (ATA); pressure was then increased at a rate of 1 ATA/min to the test pressure (Figure 2). The time of acclimation to increased pressure was examined for pressure changes of 1, 2, and 3 ATA for black rockfish and for a 2-ATA change for China rockfish. During acclimation, periodic checks were made to determine the neutral buoyancy depth by observing the tendency for motionless fish to rise, sink, or hover in the tank while small adjustments to pressure were made.

Once fish had established neutral buoyancy at the elevated test pressure, the hyperbaric chamber pressure was lowered in a stepwise fashion that allowed the fish to acclimate to each pressure level before the next pressure reduction was made. The increment of

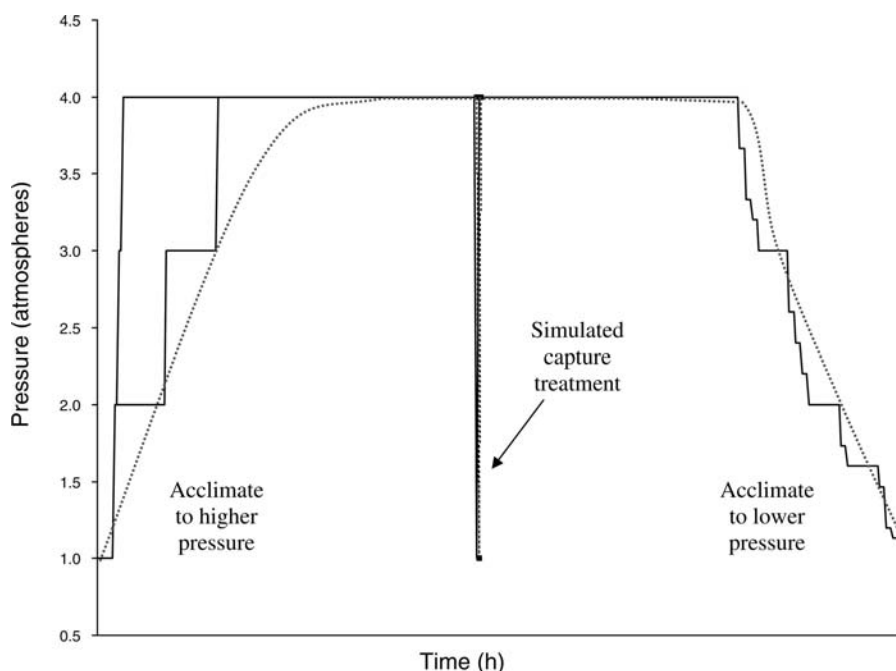


FIGURE 2.—Schematic time course of hyperbaric experiments with black and China rockfishes, showing water pressure (solid lines) and associated swim bladder pressures (dashed line) that simulate descent and ascent in the water column. Acclimation profiles were slightly different between individual and group hyperbaric chambers (solid lines). Group hyperbaric chambers were stepped up to the test pressure by 1 atmosphere absolute/d. The sharp pressure decline after acclimation indicates the time course for mortality experiments in which a simulated-capture event (forced ascent) was followed by recompression to the test pressure.

pressure drop was determined from Boyle's Law for a known expansion of 10, 20, or 30%. Each test fish provided the opportunity for multiple acclimation rate tests with incremental reductions in pressure. Once fish had come to equilibrium at 1 ATA, they were removed from the hyperbaric chamber, euthanized with tricaine methanesulfonate (MS-222), and dissected to determine physical condition of the swim bladder.

Group hyperbaric chambers.—Black rockfish (300–480 mm total length [TL]) were obtained by hook and line in coastal waters (<40 m) off the coast of Oregon, were tagged with passive integrated transponder tags, and were held for at least 3 weeks in a large (106,000-L) flow-through tank (Parker and Rankin 2003). Some black rockfish were vented (removal of excess swim bladder gas with a needle or cannula) at capture and were held for more than 2 years before experiments. We attempted to collect individuals at depths that were as shallow as possible by fishing near the surface, and we provided deep holding tanks (3 m) to minimize any barotrauma. However, because black rockfish are only available from wild collections, we could not assume that barotrauma did not occur in any individuals collected. We held all individuals for a period of at least 19 d to (1) allow fish to acclimate to and begin

feeding in captivity and (2) allow any injuries to heal. Dissection of six individuals indicated that any injured swim bladders had not ruptured or were completely healed after the holding period. Both males and females were used regardless of reproductive state. No gravid females were observed. All fish were within the size range targeted by recreational fisheries (>29 cm TL). Experiments were conducted throughout a 2-year period.

We built a large flow-through hyperbaric aquarium system consisting of an 8,700-L head tank, pumps, and the bodies of three fiberglass sand filters, which served as aquaria (1,302 L; Figure 1). The plumbing configuration and regulation of pressure for these tanks were similar to those of the small acrylic aquaria described above but were larger in scale and included a third separately regulated tank. Clear acrylic lids were fitted to the hatches so that fish behavior could be observed. Seawater (sand filtered; 9.4–16.5°C; 27–34‰) was provided from the head tank by two 3-hp pumps (1 hp = 746 W) that could generate 4.25 ATA in each tank. This design allowed a control group that did not experience the pressure changes administered to the treatment groups. Pressure in the tanks was regulated by controlling the inflow and outflow to simultaneous-

ly maintain the desired pressure and optimal flow rate (~15 L/min). It was not possible to feed the fish while they were in the sealed tanks.

For acclimation rate experiments, five fish that were acclimated to surface pressures while in the main holding tank were placed in each chamber. Pressure increases of 1 ATA/step were made before fish became neutrally buoyant at a step to maintain a strong pressure differential between the environment and the swim bladder, thereby maximizing the rate of acclimation. The time required for fish to become neutrally buoyant at 4 ATA was determined as described above.

Once the fish were acclimated to 4 ATA, decompression tests were conducted to estimate the rate of gas removal from the swim bladder. When pressure was gradually reduced, fish would begin to become positively buoyant and agitated. Pressure was then increased slightly so that fish were still positively buoyant but not agitated, usually corresponding to a predicted 10–20% increase in buoyancy according to Boyle's Law. This procedure was repeated every 4–8 h until pressures were at 1 ATA (Figure 2). Stepwise decreases in pressure were large initially but were serially reduced as larger changes in gas volume were required as pressure approached 1 ATA. At the completion of each experiment, fish were euthanized with MS-222 and dissected for evidence of physical injury. Results from these experiments defined the "control decompression regime" used in simulated-capture experiments to transition fish from 4 ATA to the surface with no visible signs of barotrauma.

Simulated capture.—To learn how pressure changes during capture affect black rockfish, we allowed five individually tagged fish to acclimate to 4 ATA in each tank as described above. The fish in the control tank remained at this pressure until the control decompression regime was implemented. Fish in the other two tanks were then exposed to pressure changes to simulate a hook-and-line capture; pressure was reduced smoothly from 4 to 1 ATA in 90 s, was held at 1 ATA for 2 min, and then was increased quickly (30 s) to 4 ATA. This simulated the pressure change and timing of a capture event that involves releasing the fish back at the depth of capture using some recompression device or allowing the fish to quickly swim back to depth. Macroscopic signs of barotrauma were recorded at each step if visible in the tank and were also observed by dissection after the experiment.

After forced decompression and subsequent recompression, all fish were held at 4 ATA for 4 d to monitor direct mortality, as suggested by Wassenberg and Hill (1993). All fish were then decompressed to surface pressures by means of the control decompression regime. Once at 1 ATA, fish were transferred to

holding tanks (4,978 L; 8.3–14.6°C; 25 L/min; flow-through seawater sterilized with ultraviolet light) and monitored for delayed mortality for at least an additional 21 d. After the monitoring period, the fish were euthanatized with MS-222 and were dissected for macroscopic evidence of pressure-related injuries and to determine the status of healing from any injuries.

Results

Comparative Experiments

The rete mirabile of black rockfish and China rockfish consists of as many as 10 individual retia, and the number may vary with the size of the fish (Figure 3). Smaller (younger) black rockfish have 6–8 separate and distinct retia that enlarge and merge as they grow. In adult black rockfish, the retia enlarge and are typically apparent as a single, dense, horseshoe-shaped unit. In contrast, China rockfish adults retain small, visually distinct retia (Figure 4). In black rockfish, rete mirabile area increases in relation to body weight (slope = 0.260; $r^2 = 0.67$; $n = 47$); the rete mirabile area in black rockfish becomes almost twice that of similar-weight China rockfish (Figure 3), whose secretory area increases more modestly with fish weight (slope = 0.096; $r^2 = 0.40$; $n = 43$).

Overall, the body density of black rockfish (1.087 g/cm³) was not significantly different from that of China rockfish (1.088 g/cm³; $t = 2.75$; $P > 0.05$; $n = 110$). The density of these two species was 5.5% greater than the density of seawater, indicating that neutrally buoyant rockfish would require a quantity of gas in the swim bladder equivalent to about 5.5% of the body volume.

The proportion of red blood cells in the blood of black rockfish averaged 32.7%, almost 50% greater than the 21.8% observed in China rockfish ($t = 8.789$; $P < 0.0001$; $n = 122$).

Acclimation Rates

Individual hyperbaric chambers.—Both rockfish species responded to increased pressure by secreting swim bladder gas to maintain a constant swim bladder volume. The rate of gas secretion was variable within and between species; all test fish showed an initial linear rate of increase, and the rate declined as the fish approached equilibrium (Figure 5). Gas secretion rates were similar among individual black rockfish during adaptation to pressure changes. Black rockfish required, on average, about 22, 80, and 87 h to become neutrally buoyant after pressure increases of 1, 2, and 3 ATA, respectively. Based on the time that each fish required to become neutrally buoyant at 50% of the test pressure, black rockfish ($n = 22$) required about 24 h to acclimate to a 1-ATA pressure increase (0.042 ATA/h;

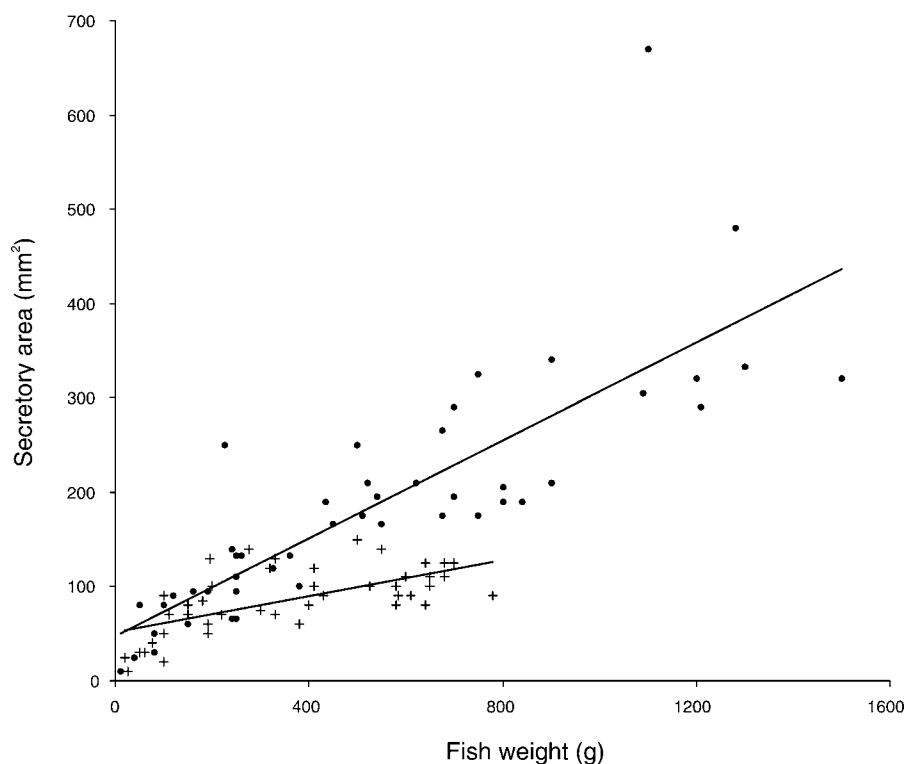


FIGURE 3.—Relations between secretory area of the rete mirabile and body weight in black rockfish (circles) and China rockfish (plus signs).

range = 10–36 h). In contrast, China rockfish ($n = 8$) were five times slower at responding to increased pressure, requiring nearly 118 h to attain neutral buoyancy after a pressure increase of 1 ATA (0.008 ATA/h; range = 65–178 h; $t = -12.18$; $df = 28$; $P < 0.001$). We did not collect data to measure the influence of fish size on acclimation rate.

In both species, the rate of gas resorption from the swim bladder was much faster than the corresponding rate of gas secretion. On average, black rockfish removed gas at a rate of 0.200 ATA/h and China rockfish removed gas much more slowly, at a rate of 0.005 ATA/h (Figure 6). The resorption rate for a pressure step was faster when starting from a higher pressure than at lower initial pressures. China rockfish resorbed gas more slowly than black rockfish and showed more variability among individuals in resorption rate with acclimation pressure (Figure 6b).

Group hyperbaric chambers with black rockfish.—Black rockfish in large hyperbaric chambers required up to 168 h for all fish to inflate their swim bladders to a volume corresponding to neutral buoyancy after a 3-ATA increase from surface pressure. Although longer than the 87-h average observed in individual hyper-

baric chambers, these experiments measured the time needed for all fish in a group of five to become neutrally buoyant and therefore represent the upper range of the time needed. We observed no difference in initial inflation rate resulting from changing the magnitude of the initial pressure increase (Figure 2). Acclimation to decreasing pressure occurred much faster; fish reached neutral buoyancy at 1 ATA after approximately 45 h of decreasing pressure steps (rate profile indicated in Figure 2). Using dissection, we found no visible physical injuries, no barotrauma, and no mortalities resulting from this 3-ATA control decompression regime.

Simulated capture.—Fish undergoing simulated-capture experiments showed barotrauma similar to that observed during recreational fishing at corresponding depths, such as bloating and exophthalmia. After recompression to 4 ATA, 2 of 90 treatment fish died in the chambers within the first 24 h. One additional fish died after 9 d (after controlled decompression and transfer to the holding tanks), yielding a $3.3 \pm 1.7\%$ total mortality rate (mean \pm SE; $n = 9$ replicates). No mortalities were observed in the control group undergoing the control decompression regime ($n = 45$).

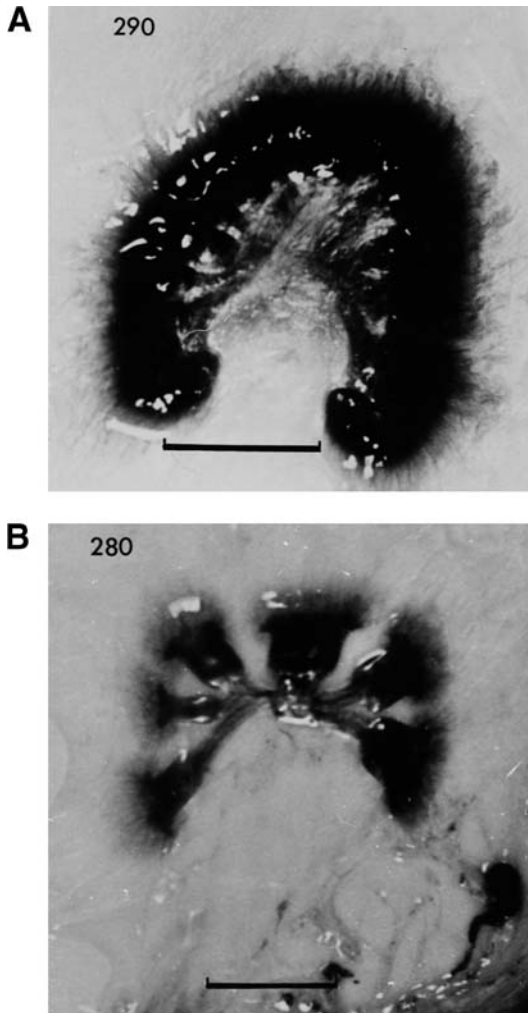


FIGURE 4.—Photographs of the rete mirabile from the swim bladders of a typical 290-mm (SL) black rockfish (top panel) and a typical 280-mm China rockfish (bottom panel). Scale bar is equal to 1 cm.

Dissection showed that short-term mortalities were probably caused by intraperitoneal vascular damage and internal bleeding. Dissections showed that 100% of fish undergoing simulated capture had ruptured swim bladders; however, by 21 d posttreatment, 77% of the swim bladders were at least partially healed and were holding gas upon dissection. There was no difference in mean size between fish with swim bladders that had healed to the point of holding gas and those whose swim bladders did not hold gas. In addition to ruptured swim bladders, organ displacement was observed in some fish exposed to simulated capture. This sometimes resulted in a segment of the intestine occupying the former swim bladder space or in fusion of the swim

bladder with the liver or intestine at injured locations. Although most swim bladders were holding gas after 3 weeks of recovery, the ventral tunica externus was often still torn and gas was retained over the injured area by the more fragile tunica internus.

Discussion

Although black rockfish and China rockfish are sympatric in distribution, the black rockfish is a semipelagic, schooling species, whereas the China rockfish is a solitary, crevice-dwelling fish (Love et al. 2002). Black rockfish make greater vertical movements (spanning a 1–2-ATA pressure gradient) and regularly move between the kelp understory, midwater, and surface (McElderry 1979). Black rockfish were faster at both gas secretion and gas resorption than were China rockfish, but both species exhibited slower rates than nonrockfish species (Harden Jones 1952; Tytler and Blaxter 1973; Harden Jones and Scholes 1985). Density of overall fish tissue was the same between the two species; therefore, differences in acclimation rates did not result from differences in gas volumes needed for individuals of similar size. The larger, more developed rete mirabile and higher red blood cell content in black rockfish enable higher swim bladder gas transfer rates and are consistent with the needs of a species that changes depth frequently (Harden Jones and Scholes 1985). These results indicate that (1) swim bladder physiology could be very different among rockfish species, depending on ecology and depth inhabited, and (2) focused experiments and a broader understanding of the physiological basis for barotrauma will be needed to determine acclimation abilities in other species.

These patterns of swim bladder physiology present some interesting constraints for semipelagic, shallow-water species, such as black rockfish, blue rockfish *S. mystinus*, and canary rockfish *S. pinniger*. Fish with physoclistic swim bladders have not evolved to reach the surface quickly or (for those species that live in shallow water) to maintain neutral buoyancy while making vertical movements (Harden Jones 1952). There is little evidence that swim bladder volume is maintained volitionally, especially over biologically meaningful pressure ranges (Harden Jones 1951; Fänge 1966). It is more likely a slow, continuous, homeostatic process of gas secretion and resorption that lags behind actual external pressure changes. The nearly 10-fold difference in the rate of gas removal than deposition means that vertically mobile species such as black rockfish, physiologically always seeking density equilibrium, would be neutrally buoyant at a depth much shallower than their mean depth. The upper extent of the vertical range would be a function of the neutral

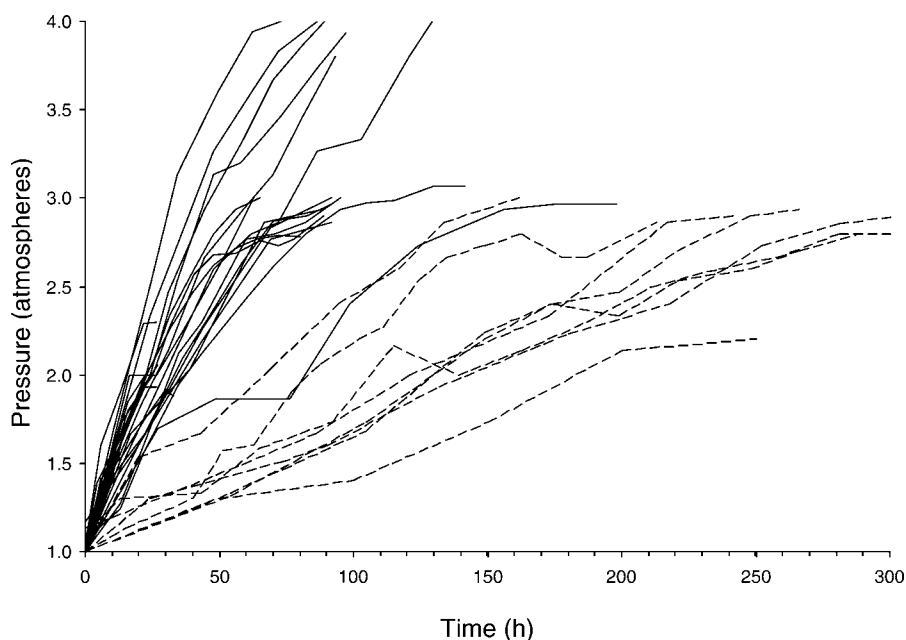


FIGURE 5.—Gas secretion rate profiles for 24 individual black rockfish (solid lines) and 8 China rockfish (dashed lines) acclimating to 2- or 3-atmosphere absolute increases in ambient pressure within a hyperbaric chamber.

buoyancy depth and the physical limits of positive buoyancy. Because capture depth will probably be closer to neutral buoyancy depth for demersal species than for semipelagic species, semipelagic individuals captured at similar depths should show less barotrauma.

Effects of Fishing

The mortality rate from decompression alone (i.e., excluding confounding factors such as handling, hook injuries, or time in air) in black rockfish was low when fish were quickly recompressed. Mortality apparently resulted from damage to the vasculature, which caused severe internal hemorrhaging in a few individuals. Rapid recompression reversed all externally visible barotrauma signs; however, the effects of handling during capture and potential predation risk upon release remain unknown, as well as any impacts on subsequent behavior or fitness. Although swim bladder rupture in itself is not lethal, associated trauma may be avoided if the gas expansion is not excessive or long lasting. Increases in volume of 30–50% may be tolerated by some rockfishes (McElderry 1979).

All of the external signs of barotrauma observed under normal fishing conditions were duplicated in the tanks at similar pressure changes. In addition to simple pressure change, there is evidence that stress induced during capture increases the severity of barotrauma, especially in the eyes (Stephens et al. 2001). Ability to resorb gas

(especially nitrogen) is limited by characteristics of plasma, as modulated by pH and pressure (Wittenburg et al. 1964; Bridges et al. 1998). When fish struggle during capture, lactate and carbon dioxide buildup in tissues and the resulting decrease in pH lead to lower solubility of blood gases and can contribute to embolism (McDonough and Hemmingsen 1985; McDonald and Milligan 1997). This physiological constraint suggests that more barotrauma may develop in fish that are forced to ascend than in fish that ascend volitionally. Such an effect may explain why some black rockfish are observed feeding at the surface, while conspecifics that are caught concurrently show barotrauma (S.J.P., personal observation). This physiological effect also means that barotrauma may continue to worsen while fish are handled in air, as blood pH will remain depressed or continue to decrease during this time (Ferguson and Tufts 1992; Cech et al. 1996). This is especially true for the eyes, given the higher oxygen pressures generated in the pseudobranch and choroid rete and the effect of pH on oxygen binding (Bridges et al. 1998; Pelster and Randall 1998). In addition, formation of gas bubbles in vasculature slows or blocks blood flow, further reducing the ability to remove carbon dioxide and nitrogen at the gills. Overall, these constraints on the physiological ability to adapt to pressure changes suggest that if physoclistic fish are to be released, they should be brought to the surface relatively quickly and then quickly sent back to depth to minimize the period of stress and time spent at low pressure.

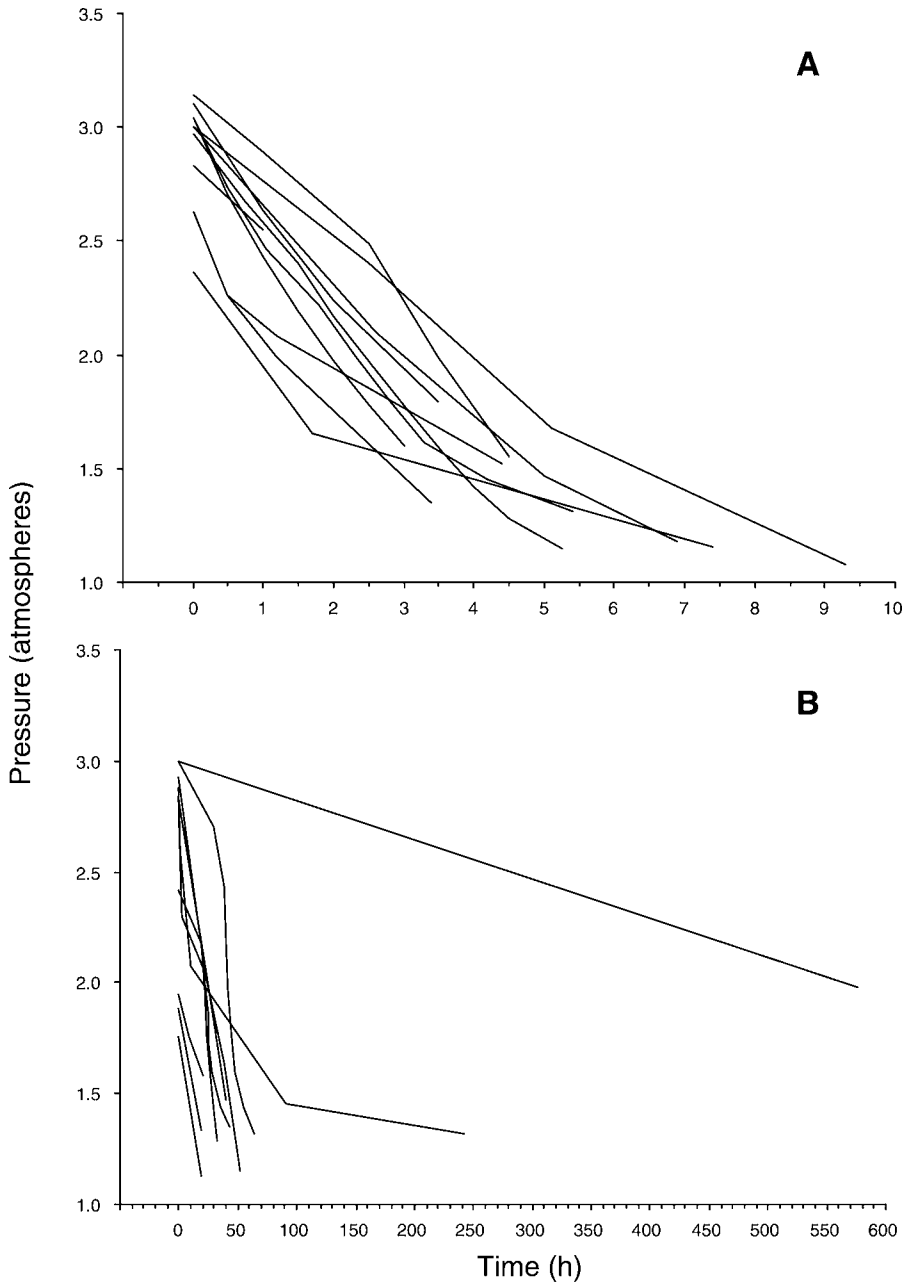


FIGURE 6.—Profiles of gas resorption rates for (A) 11 black rockfish and (B) 10 China rockfish during equilibration to sequential pressure reductions from approximately 4 atmospheres absolute (ATA) to 1 ATA in 8–36% steps within a hyperbaric chamber.

After 21 d of recovery, most black rockfish swim bladders were again holding gas and fish were neutrally buoyant in the recovery tank. Recovery of swim bladder function appeared complete and did not lead to impairment of function, as also shown in quillback rockfish *S. maliger* (Berry 2001). However, we do not

yet know whether recovery is complete for other organ systems. For example, long-term vision impairment due to embolism may affect the ability to feed or may influence long-term fitness. Damage to the tunica externus may interfere with sound production ability and may therefore have long-term impacts on behav-

ioral ecology. Behavioral impairment related to barotrauma effects could also be critically important in mark-recapture studies, where equal probability of recapture is assumed.

Because rockfish are often caught in mixed-species fisheries, species-specific harvest constraints have caused fishery closures based on the assumed low survival of discarded fish (PFMC 2004). Our data suggest that for black rockfish, survival can be much higher if techniques are used to return the fish to depth quickly. Most studies of release techniques for fish suffering from barotrauma involve venting (puncturing the swim bladder with a needle or cannula to relieve excess pressure; Keniry et al. 1996; Collins et al. 1999; Burns and Restrepo 2002). Surprisingly, studies using simple recompression via release at depth are rare and not designed to evaluate recompression as a tool (Gitshlag and Renaud 1994). Venting studies usually do not control for time at low pressure and usually compare survival rates of vented fish with those of fish released at the surface rather than those of fish that are recompressed before release (Collins et al. 1999). Moreover, some benefits of venting appear to be species specific (Burns and Restrepo 2002), indicating that physiological and ecological differences among species may influence choice of release method. Our data show that black rockfish and China rockfish cannot compensate for pressure change in any realistic time frame during forced ascent and that quick recompression may allow catch and release of black rockfish with high survival rates.

Acknowledgments

We thank the Oregon Coast Aquarium, Oregon State University facilities management for assistance with seawater supply, and Robert Anderson, Troy Buell, Eric Cassiano, Scott Malvitch, and Keith Matteson for fish culture. We also thank the Bamfield Marine Station, in particular John McNerney and Val Fletcher, for their assistance during the study. This project was made possible by funds from the National Research Council of Canada; the Western Canadian Universities Marine Biological Society; the Restoration and Enhancement Program, Oregon Department of Fish and Wildlife (Grant 01-044); and appropriations from the Oregon legislature.

References

- Alexander, R. M. 1966. Physical aspects of swimbladder function. *Biological Reviews* 41:141–176.
- Berry, M. D. 2001. Area 12 (inside) rockfish selective fishery study. Science Council of British Columbia, Report FS00-05, Vancouver. Available: <http://www.icnrc.org>.
- Bridges, C. R., M. Berenbrink, R. Müller, and W. Waser. 1998. Physiology and biochemistry of the pseudobranch: an unanswered question? *Comparative Biochemistry and Physiology A* 119:67–77.
- Brodeur, R., and W. Pearcy. 1984. Food habits and dietary overlap of some shelf rockfishes (Genus *Sebastes*) from the northeastern Pacific Ocean. *Fishery Bulletin* 82(2):269–293.
- Burns, K. M., and V. Restrepo. 2002. Survival of reef fish after rapid depressurization: field and laboratory studies. Pages 148–151 in J. A. Lucy and A. L. Studholme, editors. *Catch and release in marine recreational fisheries*. American Fisheries Society, Symposium 30, Bethesda, Maryland.
- Cech, J. J., Jr., S. D. Bartholomew, P. A. Young, and T. E. Hopkins. 1996. Striped bass exercise and handling stress in freshwater: physiological responses to recovery environment. *Transactions of the American Fisheries Society* 125:308–320.
- Collins, M. R., J. C. McGovern, G. R. Sedberry, H. S. Meister, and R. Pardiek. 1999. Swim bladder deflation in black sea bass and vermillion snapper: potential for increasing postrelease survival. *North American Journal of Fisheries Management* 19:828–832.
- Fänge, R. 1966. Physiology of the swimbladder. *Physiological Reviews* 46:299–322.
- Ferguson, R. A., and B. L. Tufts. 1992. Physiological effects of brief air exposure in exhaustively exercised rainbow trout (*Oncorhynchus mykiss*): implications for “catch and release” fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1157–1162.
- Gitshlag, G. R., and M. L. Renaud. 1994. Field experiments on survival rates of caged and released red snapper. *North American Journal of Fisheries Management* 14:131–136.
- Hallacher, L. E. 1974. The comparative morphology of extrinsic gasbladder musculature in the scorpionfish genus, *Sebastes* (Pisces: Scorpaenidae). *Proceedings of the California Academy of Sciences* 40(3):59–86.
- Harden Jones, F. R. 1951. The swimbladder and the vertical movements of teleostean fishes, I. Physical factors. *Journal of Experimental Biology* 28:553–566.
- Harden Jones, F. R. 1952. The swimbladder and the vertical movements of teleostean fishes, II. The restriction to rapid and slow movements. *Journal of Experimental Biology* 29:94–109.
- Harden Jones, F. R., and P. Scholes. 1985. Gas secretion and resorption in the swimbladder of the cod *Gadus morhua*. *Journal of Comparative Physiology B* 155:319–331.
- Keniry, M. J., W. A. Brofka, W. H. Horns, and J. E. Marsden. 1996. Effects of decompression and puncturing the gas bladder on survival of tagged yellow perch. *North American Journal of Fisheries Management* 16:201–206.
- Longbottom, S. 2000. The effect of capture depth on potential broodstock snapper (*Pagrus auratus*). Master's thesis. Curtin University of Technology, Muresk Institute of Agriculture, Perth, Western Australia, Australia.
- Love, M. S., M. M. Yoklavich, and L. Thorsteinson. 2002. *Rockfishes of the northeast Pacific*. University of California Press, Berkeley.
- McDonald, G., and L. Milligan. 1997. Ionic, osmotic, and acid–base regulation in stress. Pages 119–145 in G. K. Iwama, A. D. Pickering, J. P. Sumpter, and C. B.

- Schreck, editors. Fish stress and health in aquaculture. Cambridge University Press, UK.
- McDonough, P. M., and E. A. Hemmingsen. 1985. Swimming movements initiate bubble formation in fish decompressed from elevated gas pressures. *Comparative Biochemistry and Physiology A* 81:209–212.
- McElderry, H. I. 1979. A comparative study of the movement habits and their relationship to buoyancy compensation in two species of shallow reef rockfish (Pisces, Scorpaenidae). Master's thesis. University of Victoria, Victoria, British Columbia.
- Parker, S. J., S. A. Berkeley, J. T. Golden, D. R. Gunderson, J. Heifetz, M. A. Hixon, R. Larson, B. M. Leaman, M. S. Love, J. A. Musick, V. M. O'Connell, S. Ralston, H. J. Weeks, and M. M. Yoklavich. 2000. Management of Pacific rockfish. *Fisheries* 25(3):22–30.
- Parker, S. J., and P. S. Rankin. 2003. Tag location and retention in black rockfish (*Sebastes melanops*): feasibility of using PIT tags in a wild marine species. *North American Journal of Fisheries Management* 23:993–996.
- Pelster, B., and D. J. Randall. 1998. The physiology of the Root effect. Pages 113–139 in S. F. Perry and B. L. Tufts, editors. *Fish respiration*. Academic Press, San Diego.
- PFMC (Pacific Fishery Management Council). 2004. Status of the Pacific Coast groundfish fishery through 1999 and recommended biological catches for 2000: stock assessment and fishery evaluation. PFMC, Portland, Oregon.
- Ross, L. G. 1979. The haemodynamics of gas resorption from the physoclist swimbladder: the structure and morphometrics of the oval in *Pollachius virens* (L.). *Journal of Fish Biology* 14:261–266.
- Stephens, F. J., J. J. Cleary, G. Jenkins, B. Bones, S. R. Raidal, and J. B. Thomas. 2001. Pathogenesis and epidemiology of spontaneous exophthalmos in the West Australian dhufish, *Glaucosoma hebraicum* Richardson. *Journal of Fish Diseases* 24:515–522.
- Tytler, P., and J. H. S. Blaxter. 1973. Adaptation by cod and saithe to pressure changes. *Netherlands Journal of Sea Research* 7:31–45.
- Wassenberg, T. J., and B. J. Hill. 1993. Selection of the appropriate duration of experiments to measure survival of animals discarded from trawls. *Fisheries Research* 17:343–352.
- Wittenburg, J. B., M. J. Schwend, and B. A. Wittenburg. 1964. The secretion of oxygen into the swimbladder of fish, III. The role of carbon dioxide. *Journal of General Physiology* 48:337–355.