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The Susceptibility of Juvenile American Shad to Rapid Decompression and Fluid Shear Exposure Associated with Simulated Hydroturbine Passage

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Abstract: Throughout many areas of their native range, American shad (*Alosa sapidissima*) and other Alosine populations are in decline. Though several conditions have influenced these declines, hydropower facilities have had significant negative effects on American shad populations. Hydropower facilities expose ocean-migrating American shad to physical stressors during passage through hydropower facilities, including strike, rapid decompression, and fluid shear. In this laboratory-based study, juvenile American shad were exposed separately to rapid decompression and fluid shear to determine their susceptibility to these stressors and develop dose–response models. These dose–response relationships can help guide the development and/or operation of hydropower turbines and facilities to reduce the negative effects to American shad. Relative to other species, juvenile American shad have a high susceptibility to both rapid decompression and fluid shear. Reducing or preventing exposure to these stressors at hydropower facilities may be a potential method to assist in the effort to restore American shad populations.

Keywords: American shad; hydropower; turbine; rapid decompression; fluid shear; downstream fish passage

1. Introduction

American shad *(Alosa sapidissima)* are an anadromous, highly migratory species native to the Atlantic coast of the United States and Canada, which historically had shad runs consisting of millions of individuals, supporting valuable commercial and recreational fisheries [1–5]. The American shad is a moderately compressed fish with large green to greenish blue scales on the back, to silvery on the sides, and white on the belly. Shad have supported important fisheries in every costal state along the Atlantic coast of the United States, with the Potomac and Delaware rivers accounting for some of the largest catches [5]. They were introduced to Pacific coast rivers, including the Sacramento, Columbia, Snake, and Willamette, as early as the 1870s [6,7]. Within the native range, American shad spend most of their lives (3–6 years) in the ocean, with adults migrating upstream into coastal rivers and tributaries to spawn during the spring and early summer months. Returning adults generally reach a length of 55 cm, with females usually larger than males. In late summer and fall, the recently hatched juveniles migrate downstream to the ocean, at which point they typically range in size from 7 to 15 cm [6]. Most of these fish are iteroparous, so healthy population dynamics rely heavily on the successful downstream migration of both juveniles and adults [6,8].

Today, Pacific coast populations of American shad are very abundant, such as in the Columbia River where the average run in the last decade exceeded 3 million individuals and was the highest on record in 2019, with nearly 7.5 million returning adults [9]. However, most Atlantic coast populations are declining [10–12]. As a result, many states on the Atlantic coast have restrictions or moratoriums on American shad fishing, which prompted the development of an interstate fisheries management plan [13–15]. Factors contributing to the decline of east coast American shad populations include overfishing, habitat loss from hydropower facilities, and pollution [1,6,11,16–18]. Low passage efficiency, impassable barriers, and delays experienced at hydropower facilities during migration may add additional energetic costs, increase avian and aquatic predation, and have significant negative effects on survival and fitness [19–22].

In addition to habitat loss, fragmentation of populations, and impeded migration, hydropower facilities can lead to injury and mortality of fish during dam passage [23,24]. Migrating American shad may become disorientated, and incur significant injuries, or even mortality, from passing through turbines at hydropower facilities as they travel between freshwater and marine environments [1,4,19,25]. Migratory fish species that navigate these facilities during migrations, such as American shad, are of particular concern, since they frequently encounter hydropower facilities as they travel between freshwater and marine environments [26]. During downstream migrations, fish that become entrained in hydropower turbines may be exposed to several physical stressors including strike, rapid decompression, and shear forces [26].

Fluid shear occurs when fish pass the interface of two masses of water moving in different directions or at different velocities. Naturally occurring shear forces pose little threat of injury to fish; however, shear forces resulting from operations of hydropower facilities, in which water velocities can change significantly over short distances, may lead to injuries including descaling, tearing or bruising of tissues, and decapitation [27]. Locations within a hydropower facility where shear forces can exceed those naturally occurring within the river are spillways and turbines [28], two of the more common downstream fish passage routes available for out-migrating fish. When passing through a turbine, exposure to fluid shear can vary greatly, ranging from no exposure to strain rates or acceleration events exceeding 600 s^{-1} or 600 m s^{-2}, respectively [29,30]. Rapid decompression occurs when fish are exposed to a rapid decrease in pressure as fish pass the turbine runner or exit from underneath a sluice gate. The pressure through the turbine typically increases until the backside of the turbine blade is reached, at which point the pressure rapidly (<0.5 s) decreases before gradually increasing to surface pressure as fish enter the downstream channel [31]. Pressures can range considerably between different turbine designs and even within a single turbine, depending on where the fish passes through the turbine. These pressures have been observed to range considerably, from <10 kPa absolute to well above atmospheric pressure [29,32]. The sudden decrease in pressure may lead to a variety of barotraumas to the fish, including swim bladder rupture, exophthalmia, and emboli or emphysema throughout the organs and tissues of the fish [31,33,34]. Barotrauma injuries can result from gasses expanding within the body (explained by Boyle's Law) or bubble formation in the blood and tissues when gas comes out of solution (explained by Henry's Law) and can vary depending on the operating conditions of the hydropower facility and the species of fish [31,33,35]. Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) have been observed to sufer mortality at pressure reductions as low as 50% [31], where American eel suffered very few injuries at much greater decompression (≈90% pressure reduction) [36] and lamprey (western brook lamprey, *Lampetra planeri* and Pacific lamprey, *Entosphenus tridentatus*) exhibited no physiological or behavioral response to extreme rapid decompression (>90% pressure reduction) [24].

The objective of this study was to model the dose–response relationships for American Shad exposed to fluid shear and rapid decompression associated with downstream passage through hydropower turbines. These models make it possible to (1) estimate injury and mortality rates at hydropower facilities where the magnitude and frequency of these stressors are known, (2) provide guidelines or threshold values for turbine development and modification, and (3) guide turbine operations to reduce the likelihood that American shad are exposed to fluid shear or rapid decompression at levels likely to cause injuries or mortality. Specialized laboratory apparatuses were used to simulate exposure to fluid shear and rapid decompression on live fish. To ensure application to a wide range of known turbine designs, the apparatuses were set to expose fish to a wide range of magnitudes of each stressor. Results from exposure to fluid shear and rapid decompression were modeled to develop dose–response relationships for each stressor.

2. Methods

2.1. Fish Acquisition

Out-migrating juvenile American shad were collected by the U.S. Army Corps of Engineers using the juvenile fish collection/bypass system at McNary Dam on the Columbia River (Umatilla, OR, United States) in September of 2016 (for shear studies) and 2018 (for rapid decompression studies). Fish were transported to the Pacific Northwest National Laboratory Aquatics Research Laboratory (ARL) and held in 2000 L tanks at a stocking density of 3.5 g L^{-1} with circulating aerated water from the Columbia River at ambient temperatures (range 15.9–18.5 °C). Water quality, including total dissolved gas (mean = 101.4%), dissolved oxygen (mean = 108.7%), and temperature (mean = 17.2 °C), was maintained at consistent levels throughout the duration of the study periods. Shad were fed daily, initially with brine shrimp (*Artemia* sp.) and gradually converted to a fish feed crumb (BioVita, Bio-Oregon, Longview, WA, United States). Food was restricted 24 h prior to exposure to shear and rapid decompression. Testing was initiated 24 h after fish were collected and transported to the ARL and was conducted within one week for fluid shear testing, and four weeks for rapid decompression testing.

2.2. Fluid Shear

2.2.1. Exposure to Fluid Shear

American shad (*N* = 420), ranging in size from 53 to 85 mm (median = 62 mm) and 0.3 to 5.9 g (median = 1.4 g), were exposed to various water jet velocities (0–18 m s^{-1}) created by a submerged water jet in a rectangular flume (Table 1), hereafter referred to as the shear flume [30]. The shear flume measured 9 m long, 1.2 m wide, and was filled with water to a depth of 1.2 m. The jet was comprised of a 55.3 cm long conical stainless-steel nozzle (25.4 cm constricted to 6.35 cm diameter) bolted to a flange on one end of the shear flume [37]. The last 4.5 cm of the nozzle was a 6.35 cm diameter tube. A flow conditioner was mounted just upstream of the nozzle, and the jet was fed by a recirculating loop powered by a variable speed centrifugal pump with a programmable electronic speed controller capable of pumping up to 158 L s^{-1} [30].

Table 1. Summary of sample size and fork length for American shad exposed to a range of jet velocities and resulting strain rates or acceleration. Strain rate was calculated using Δy = 18 mm [30] and acceleration was calculated based on data acquired from Sensor Fish [38] exposed to the same jet velocities and deployment method.

Jet Velocity (m s^{-1})	Strain Rate (s^{-1})	Acceleration (m s^{-2})	*n*	Length (mm)	
				Median	Range
0	0	0	60	63	53–79
3	167	153.1	60	63	54–81
6	333	306.2	60	62	55–77
9	500	459.4	60	60	55–81
12	677	612.5	60	60	53–85
15	833	765.6	60	61	55–80
18	1000	918.7	60	64	55–76

Fish were individually exposed to fluid shear by slowly introducing them into the elevated water velocities through an induction tube (Figure 1). The induction tube was mounted at an angle of 30 degrees from the direction of flow. Experiments were initiated by capturing a fish and placing it inside of a water-filled 15 cm long, 3.8 cm diameter acrylic tube sealed with a rubber stopper on one end and a flexible polyurethane foam plug on the other end, hereafter referred to as the cartridge. The pump was turned on at the desired Hz, which had been calibrated to specific water velocities. Once the pump was up to speed, fish were released from the cartridge into the induction tube. After fish were exposed to fluid shear, the pump was turned off to ensure no additional exposure and for observation and recapture.

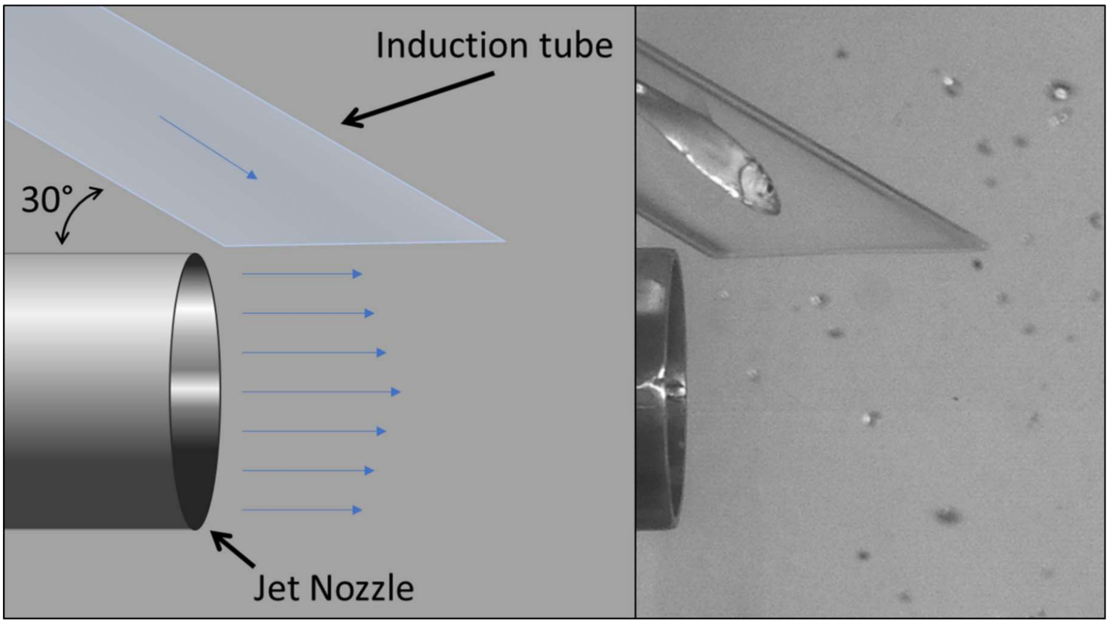

Figure 1. Diagram (**left**) and image captured from high speed video (**right**) display how fish were exposed to fluid shear by passing down the induction tube and into the water jet.

2.2.2. Fluid Shear Assessment

After exposure to fluid shear, fish were immediately observed for swimming behavior, then netted. Swimming behavior was categorized as normal, loss of equilibrium (inability to remain upright position), or erratic (exhibiting burst swimming and abnormal orientation). Once the fish were netted, they were carefully placed back into the cartridge and visually examined for injuries including percent descaling, bruising, hemorrhaging, and damage to the operculum, eyes, and gills. Fish were then transferred to holding tanks, where fish were separated based on treatment (jet velocity) and monitored for 48 h post exposure. Any fish that died or exhibited moribund behavior (prolonged swimming impairment or unrecoverable injuries) after exposure or during the post-exposure holding period were immediately euthanized, further examined for injuries, and measured.

2.3. Rapid Decompression

American shad, ranging in size from 35 to 86 mm (median = 56 mm) and 0.3 to 5.9 g (median = 1.4 g), were exposed to rapid decompression simulating passage through a hydropower turbine using four computer controlled hyper/hypobaric hydro-chambers [39]. A total of 790 American shad were examined between 20 September 2018 and 11 October 2018.

2.3.1. Exposure to Rapid Decompression

American shad can be sensitive to handling so, to prevent net damage and avoid injury or mortality prior to exposure, fish were bucketed from the general population and placed into the chambers at a concentration of 20 fish per chamber. The chambers were then pressurized to acclimate fish overnight (16 to 24 h) to a pressure of 170 or 120 kPa (all pressures reported in absolute pressure with an assumed surface pressure of 101.3 kPa), simulating a water depth of 6.8 and 1.9 m, respectively.

It is important to allow fish sufficient time to acclimate to pressure; this allows the fish to fill their swim bladder and for any gasses dissolved in the blood or tissues to stabilize. Fish that do not fill their swim bladder to a state of neutral buoyancy are less susceptible to barotrauma (or more susceptible if they overinflate the swim bladder) [39]. It is assumed that pelagic fish in a natural setting would maintain a state of neutral buoyancy and, therefore, any fish not attaining neutral buoyancy during laboratory testing are less likely to represent the natural population [31,39]. Therefore, prior to exposure to rapid decompression, fish were examined for a state of buoyancy. To avoid disturbing the fish, video cameras (HERO6 Black, GoPro, San Mateo, CA, United States) were connected to a monitor so that fish could be viewed remotely. Fish exhibiting elevated swimming effort were considered negatively buoyant if their heads were oriented up, and positively buoyant if their heads were oriented down [40]. Fish that remained horizontal with minimal swimming effort were considered neutrally buoyant. Because individual fish could not be differentiated for analysis, any trial containing fish that did not achieve neutrally buoyancy was removed from further analysis.

Once the state of buoyancy was determined, fish were exposed to pressures that mimicked downstream passage through a turbine. In general, exposure included pressure increases to about 400 kPa over a period of about 20 s to simulate travel through the turbine intake before a rapid decrease (<0.5 s) to simulate the fish passing the turbine runner. Pressure was then quickly (≈2–5 s) returned to near surface pressure (101.3 kPa) to simulate the fish exiting the facility and entering the downstream channel [34,39]. The chambers were programed so that fish were exposed to a range of rapid decompression, with a targeted nadir pressure (lowest pressure) range of 10—140 kPa. This was accomplished by changing the nadir pressure (lowest pressure) that occurs during the decompression for each trial. However, the actual nadir pressure that is achieved often differs slightly from the programed value due to the mechanical performance of the chambers.

Following exposure and return to surface pressure, the chamber lids were removed. Fish were left in the chamber for 30 min and continually assessed as alive or moribund. Fish considered moribund were immediately removed from the chamber and euthanized by submersion in a solution of MS-222 (240 mg L^{-1}) until 10 min after opercular movements had ceased. Fish that were alive after the 30 min waiting period were given a euthanizing dose of MS-222.

2.3.2. Rapid Decompression Assessment

Fish determined to be dead or moribund 30 min after exposure were measured and necropsied immediately after being euthanized. Necropsies included external and internal observations of the fish, specifically looking for barotraumas such as swim bladder rupture, exophthalmia, and emboli and hemorrhaging throughout various organs and tissues. Fish that were alive 30 min after exposure were measured and necropsied immediately after being euthanized following the same methodology.

2.4. Analysis

American shad exposed to fluid shear were evaluated using three previously designated endpoints: minor injury, major injury, and immediate mortality [30]. Fish were considered to have a minor injury if they possessed a non-life-threatening injury such as minor descaling (<20% on one side) or small bruises (<0.5 cm in diameter). Fish were considered to have a major injury if they possessed a potentially life-threating injury such as excessive scale loss (>20% on one side), large bruises (>0.5 cm in diameter), spinal fractures, lacerations with visible bleeding, injured eyes (e.g., bulged, hemorrhaged, or missing), or gill and operculum damage (e.g., inverted gill arches, torn isthmus or operculum). Immediate mortality included any fish that died or exhibited moribund behavior immediately after exposure. Because of the precautions taken to avoid a handling effect, length (fork) could not be linked to the injuries observed immediately after exposure for an individual fish. Therefore, fish length was only included in the analysis to compare the mean fork lengths of the treatment groups (ANOVA, $\alpha = 0.05$).

American shad exposed to rapid decompression were evaluated similarly to fish exposed to fluid shear and were categorized as injured, mortally injured, and immediate mortality. Fish were considered injured if they were injured in any way or died due to exposure to rapid decompression. A statistical analysis was conducted to classify specific injuries as mortal injuries [31,34,41]. Mortal injuries included injuries that were highly associated with mortality (Odds ratio >1 and Fisher's exact test $p < 0.05$; SigmaPlot v13.0) and, if highly associated, were a significant predictor of mortality (stepwise regression model $p < 0.05$; SigmaPlot v13.0).

The three different endpoints for each stressor were modeled separately using a logistic regression (SigmaPlot v13.0), where each fish was assigned a value of 1 or 0; 1 if the fish met, at a minimum, the criteria for the specified endpoint (i.e., a fish that suffered immediate mortality meets all three endpoint), 0 if the fish did not meet the criteria for the specified endpoint. The probability (p) of desired endpoint for American shad, given exposure to fluid shear or rapid decompression, can be represented as

$$P(X) = \frac{e^{\beta_0+\beta_1 S}}{1+e^{\beta_0+\beta_1 S}} \tag{1}$$

where X signifies the selected endpoint (e.g., various categorizations of injury or mortality), β_0 and β_1 are stressor-specific coefficients determined by the logistic regression analysis, and S is the magnitude of the designated stressor (i.e., fluid shear or rapid decompression). Exposure to fluid shear was expressed as both strain rate (cm s^{-1} cm^{-1} abbreviated as s^{-1}; [30]) or acceleration (m s^{-2}; [37]) and was based on the conversions listed in Table 1. Rapid decompression was expressed as the natural log of the ratio of pressure change (LRP)

$$LRP = \ln\left(\frac{p_a}{p_n}\right) \tag{2}$$

where p_a is the acclimation pressure and p_n is the nadir pressure [31]. The acclimation pressure was the pressure to which the fish became acclimated prior to exposure to rapid decompression (170 or 120 kPa for this study) and the nadir was the lowest pressure to which the fish was exposed during rapid decompression. Therefore, LRP has a direct relationship with acclimation pressure and an inverse relationship with nadir pressure; i.e., as the acclimation depth increases and/or as the nadir pressure decreases, LRP increases.

3. Results

3.1. Fluid Shear

As fluid shear exposure increased, so did the occurrences of altered behavior, injuries, and mortality (Tables 2 and 3). No fish were injured when exposed to the jet velocities of 0 (control) and 3 m s^{-1} (Table 3). All but two fish were injured when exposed to jet velocities of $\geq$ 9 m s^{-1} and all fish sustained major injuries once jet velocities reached 15 m s^{-1}. When exposed to the greatest jet velocity of 18 m s^{-1}, mortality was observed in every fish. Descaling was found to be the most prevalent injury. Mean length did not differ between treatment (jet velocity) groups (ANOVA $p = 0.335$, F ratio = 0.540; SigmaPlot v13.0).

Table 2. Summary of American shad behavior after exposure to fluid shear.

Jet Velocity (m s^{-1})	Normal	Loss of Equilibrium	Erratic
0	60 (100%)	0 (0%)	0 (0%)
3	60 (100%)	0 (0%)	0 (0%)
6	58 (97%)	1 (2%)	1 (2%)
9	56 (93%)	3 (5%)	1 (2%)
12	47 (78%)	5 (8%)	8 (13 %)
15	22 (37%)	15 (25%)	23 (38%)
18	4 (7%)	47 (78%)	9 (15%)

Table 3. Summary of observed injuries to American shad at each jet velocity tested. A total of 60 fish were tested at each jet velocity.

Jet Velocity (m s^{-1})	*n* Descaled	Mean Descaling (%)	Injuries at Various Locations				Bruises/ Cuts	Minor Injury	Major Injury	Mortality
			Eyes	Operculum	Gills	Isthmus				
0	0 (0%)	0.0	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (2%)
3	0 (0%)	0.0	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (2%)
6	15 (25%)	0.7	0 (0%)	2 (3%)	0 (0%)	0 (0%)	0 (0%)	16 (27%)	2 (3%)	2 (3%)
9	60 (100%)	8.8	2 (3%)	6 (10%)	0 (0%)	0 (0%)	2 (3%)	60 (100%)	23 (38%)	5 (8%)
12	58 (97%)	17.1	14 (23%)	19 (32%)	0 (0%)	2 (3%)	0 (0%)	58 (97%)	48 (80%)	21 (35%)
15	60 (100%)	38.2	29 (48%)	26 (43%)	0 (0%)	8 (13 %)	4 (7%)	60 (100%)	60 (100%)	42 (70%)
18	60 (100%)	54.4	51 (85%)	41 (68%)	0 (0%)	15 (25%)	8 (13 %)	60 (100%)	60 (100%)	60 (100%)

The logistic regression analysis resulted in coefficients for predicting the probability of minor injury, major injury, or mortality as a function of exposure to fluid shear, represented as strain rate (s^{-1}) or acceleration (m s^{-2}; Table 4). The models indicate that injuries began to occur when American shad were exposed a strain rate of approximately 200 s^{-1} (acceleration of approximately 180 m s^{-2}) or greater and reach an occurrence of 90% at a strain rate of approximately 465 s^{-1} (acceleration ≈ 425 m s^{-2}; Figure 2). Major injuries and mortality began to occur at strain rates of approximately 350 s^{-1} (acceleration ≈ 320 m s^{-2}) and 400 s^{-1} (acceleration ≈ 365 m s^{-2}), respectively. Major injuries and mortality reached a 90% occurrence rate at approximately 715 and 955 s^{-1} (acceleration ≈ 655 and 875 m s^{-2}), respectively (Figure 2).

Table 4. Coefficients, for the probability of minor injury, major injury, and mortality, as a function of strain rate (s^{-1}) or acceleration (m s^{-2}) for American shad exposed to fluid shear, to be used with Equation (1).

Endpoint	Strain Rate (s^{-1})		Acceleration (m s^{-2})	
	β_0	β_1	β_0	β_1
Minor Injury	−8.418	0.023	−8.520	0.025
Major Injury	−8.515	0.015	−8.773	0.017
Mortality	−6.877	0.010	−6.817	0.010

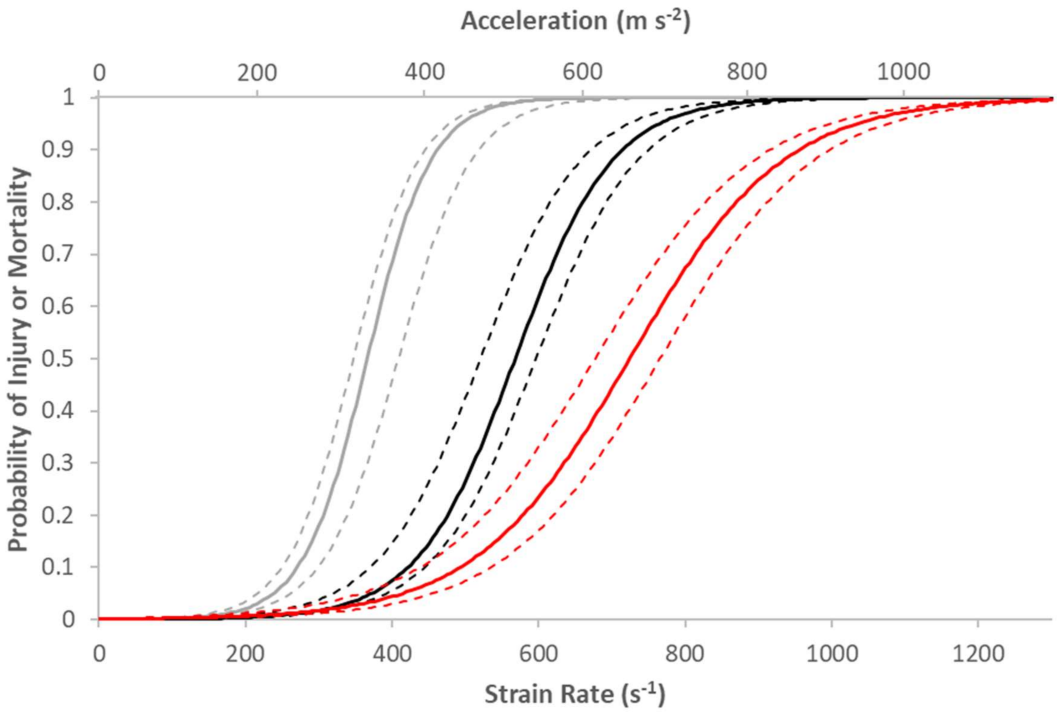

Figure 2. The probability of minor injury (grey), major injury (black), and mortality (red), as a function of strain rate (s^{-1}) or acceleration (m s^{-2}) for American shad exposed to fluid shear. Curves are a graphical representation of Equation (1) using the coefficients from Table 4 and dotted lines of the corresponding color represent the upper and lower 95% confidence intervals.

3.2. Rapid Decompression

After removing all rapid decompression trials that had negatively buoyant fish, 460 American shad remained, 138 of which were controls. Of the fish that were exposed to rapid decompression, 212 were acclimated to 170 kPa and exposed to nadir values that ranged from 11.7 to 136.5 kPa. The other 110 American shad included in the rapid decompression trials were acclimated to 120 kPa and exposed to nadir values that ranged from 17.9 to 102.0 kPa. Therefore, LRP values for all exposed fish ranged from 0.2 to 2.7. Of the 322 fish that were exposed to rapid decompression, 197 (61%) were injured, 194 (60%) of which were classified as mortally injured, and immediate mortality was observed for 140 (43%) fish.

3.2.1. Mortal Injury

Six injuries were classified as mortal injuries from the mortal injury analysis (Table 5). Seventeen other injuries were found to be highly associated with mortality (odds ratio > 1 and Fisher's exact $p < 0.05$) but were not found to be significant ($p < 0.05$) predictors of mortality when analyzed using stepwise regression (Table 5).

Table 5. For American shad, 23 injuries resulting from rapid decompression were found to be highly associated with immediate mortality. Of these injuries, six were found to be significant predictors of mortality and were considered mortal injuries for further analysis (bold, highlighted in grey).

Injury	Odds Ratio	Fisher's Exact *p*-Value	Regression *p*-Value
Swim bladder rupture	**65.2**	**1.80E-59**	**<0.001**
Renal hemorrhaging	**24.3**	**3.00E-17**	**<0.001**
Right eye emphysema *	24.1	2.00E-21	
Exopthalmia †	**22.6**	**4.00E-16**	**0.001**
Eye emphysema *	21.3	5.40E-24	
Posterior renal embolism ‡	19.3	0.0004	
Left eye emphysema *	18.6	5.40E-20	
Pectoral fin emphysema *	17.6	1.20E-08	
Mild gill embolism ‡	14.9	2.20E-05	
Anal fin emphysema *	13.2	5.40E-08	
Renal embolism ‡	**12.2**	**4.10E-11**	**0.044**
Fin emphysema *	12	5.90E-14	
Dorsal fin emphysema *	**11.7**	**9.90E-06**	**0.033**
Anterior renal embolism ‡	11.7	9.90E-06	
Mid renal embolism ‡	9.9	5.80E-07	
Pelvic fin emphysema *	9.4	0.0317	
Left eye hemorrhaging	8.8	4.80E-10	
Right eye hemorrhaging	**8.6**	**5.50E-11**	**0.003**
Gill embolism ‡	8.1	9.00E-05	
Eye hemorrhaging	7.9	4.40E-13	
Intestinal hemorrhaging	5.0	0.0003	
Hepatic hemorrhaging	4.8	0.0096	
External signs of internal hemorrhaging	3.1	0.0082	

* Emphysema is the abnormal presence of gas bubbles present within body tissues. † Exopthalmia is the abnormal bulging of the eye from the socket. ‡ Embolism is the obstruction of blood vessels by gas bubbles.

3.2.2. Susceptibility to Rapid Decompression

The logistic regression analysis resulted in coefficients for predicting the probability of injury, mortal injury, or mortality as a function of rapid decompression, represented as LRP (Table 6). The models indicate that injury and mortal injury were nearly the same and share the same intercept coefficient (Figure 3). This occurred because the majority of fish that were injured ($n = 197$) had a swim bladder rupture ($n = 173$), which was classified as a mortal injury.

Table 6. List of coefficients for Equation (1), predicting the probability of injury, mortal injury, and immediate mortality for American shad exposed to rapid decompression expressed as natural log of the ratio of pressure change (LRP).

Endpoint	β_0	β_1
Injury	−5.301	4.921
Mortal Injury	−5.301	4.825
Immediate Mortality	−3.851	2.349

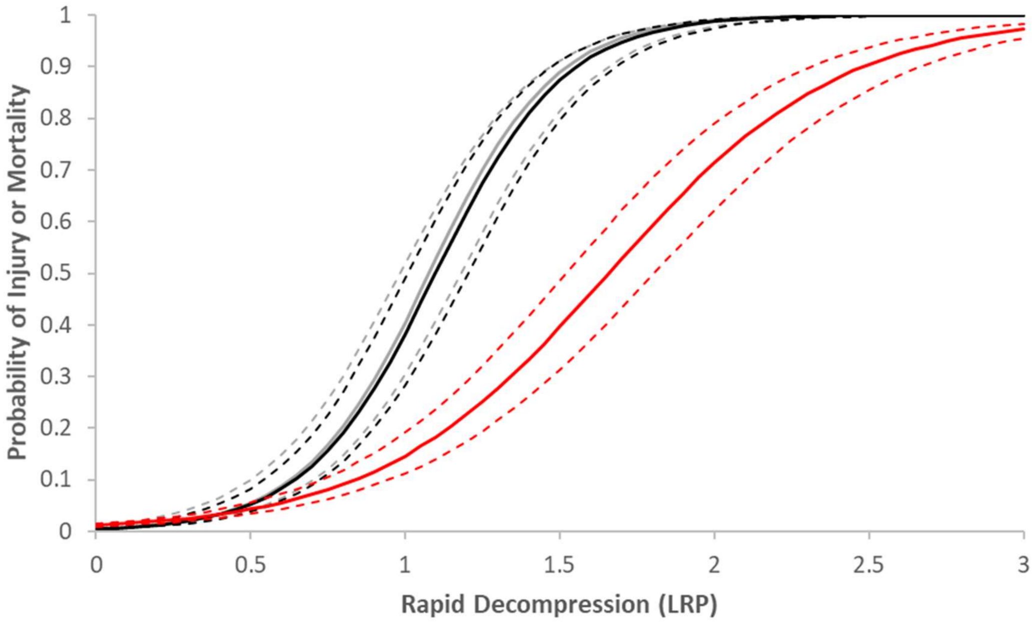

Figure 3. A graphical representation of Equation (1) using the coefficients from Table 6 to estimate the probability of American shad injury (grey), mortal injury (black), and immediate mortality (red), as a function of rapid decompression expressed as LRP. Dotted lines of the corresponding color represent the upper and lower 95% confidence intervals.

4. Discussion

Juvenile American shad were found to be susceptible to both fluid shear and rapid decompression associated with passage through hydropower turbines. Chinook salmon also migrate to the ocean as juveniles and are the only species to have been examined extensively and similarly for susceptibility to both fluid shear [30,37] and rapid decompression [31]. When compared to juvenile Chinook salmon, juvenile American shad, such as those used in this study, are more susceptible (Figure 4). Juvenile American shad tested in this study are also more susceptible to effects of shear and rapid decompression than other fish species, such as silver and yellow phase American eel (*Anguilla rostrata*), juvenile lamprey (*Lampetra* spp.), juvenile rainbow trout (*Oncorhynchus mykiss*), and a few Australian species, which have been examined similarly [24,30,34,36]. This suggests that measures (i.e., turbine designs or operational modifications) taken to protect juvenile salmonids, or other fish species at hydropower facilities may not be sufficient to protect juvenile American shad.

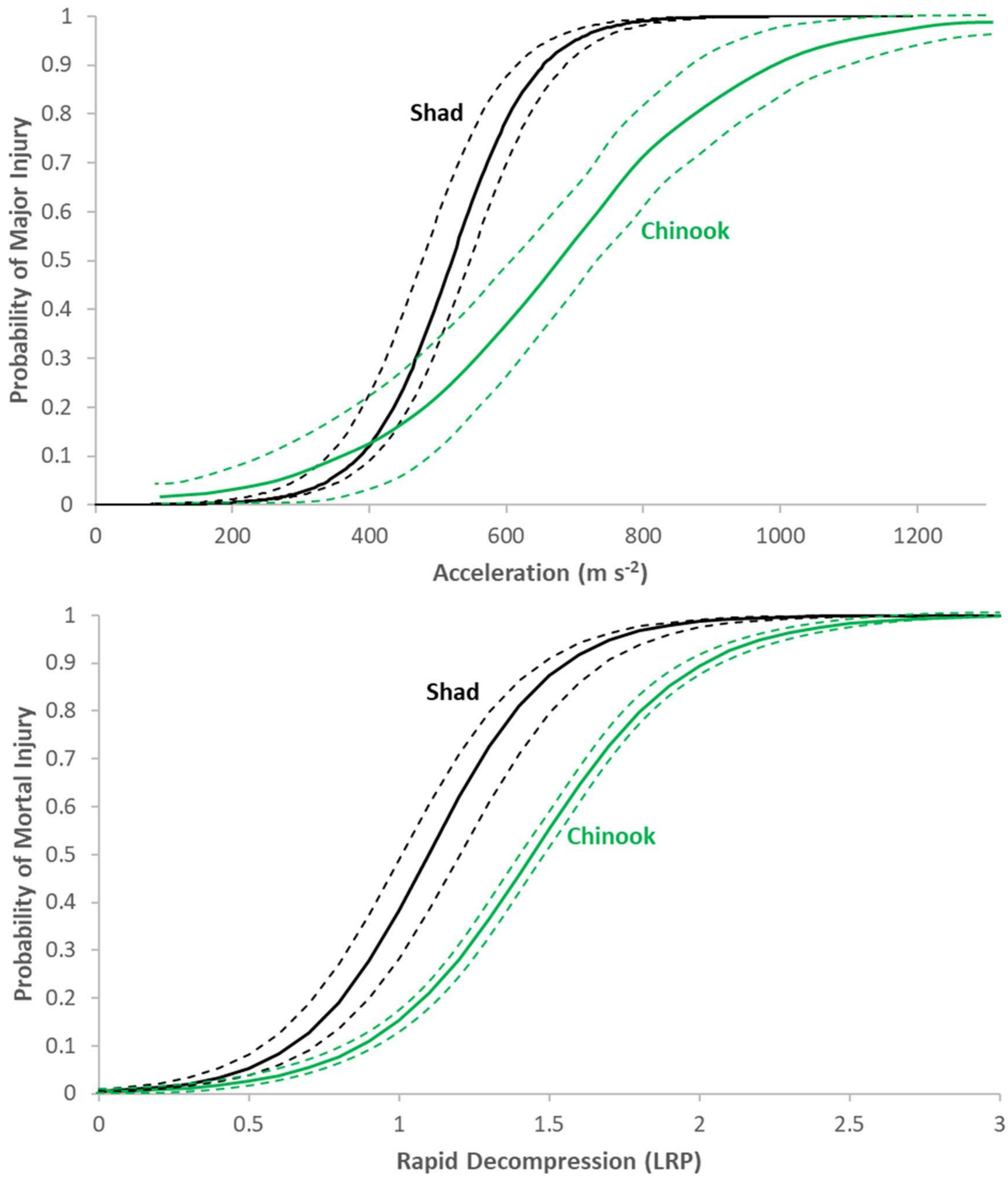

Figure 4. Comparison between the susceptibility of juvenile American shad (black) and juvenile Chinook salmon (green) to fluid shear (top) and rapid decompression (bottom). Curves for juvenile Chinook salmon exposed to fluid shear and rapid decompression were extracted from Deng et al. [37] and Brown et al. [31], respectively. Dotted lines of the corresponding color represent the upper and lower 95% confidence intervals.

Considerable progress has been made in the design of fish-friendly hydropower turbines [26,42]. Dose–response relationships to turbine stressors, such as those developed as part of this study, have been used to guide the development of new turbines [43,44]. Additionally, by providing managers and operators with these dose–response relationships, operating conditions for currently installed turbines may be set within certain parameters in hopes of reducing injury or mortality for passing fish.

Along the Atlantic Coast of the United States, within the native range of American shad, there are 343 hydropower projects located in areas in which American shad are present [45]. The Northeast region of the United States alone has 275 of these hydropower projects, many of which are nearing the end of a Federal Energy Regulatory Commission (FERC) License [45]. The 343 hydropower plants account for 945 turbines with an installed capacity of 11,058 MW [45]. Though currently not federally listed, in many areas along the East Coast, American shad numbers are well below historical numbers and some runs are considered to be at an all-time low [10–12]. If populations continue to decline, there is potential that American shad could be added to the federal list of endangered and threatened wildlife, at which point they would fall under the protection of the Endangered Species Act. If American shad become listed, the FERC licensing process for any of the hydropower projects within the East Coast would be greatly affected as FERC could potentially become liable in the result of the injury or death of any listed species as the result of a license [46].

4.1. Fluid Shear

Scale loss and damage to the eyes and operculum are three of the most common injuries inflicted on fish exposed to fluid shear [30] and juvenile American shad are particularly susceptible to these injuries. It is no surprise that juvenile American shad were susceptible to scale loss, as the proportionally large deciduous scales are easily shed with minimal handling. Juvenile American shad also have a relatively large operculum, which spans vertically across approximately 80% the fishes' head. The physical shape of shad, laterally compressed with the maximum body depth occurring just posterior to the operculum, makes the operculum easily affected by fluid shear, particularly when flow velocities relative to the fish increase in a tail-to-head direction. Additionally, juvenile American shad have relatively large eyes, which protrude slightly from the head, making them easily affected by fluid shear.

4.2. Rapid Decompression

The susceptibility of a fish species to rapid decompression is greatly dependent on the type of swim bladder they possess [31,40]. American shad and other clupeoids are physostomous, meaning that they have a pneumatic duct that connects the swim bladder with the esophagus, which allows for the rapid expulsion of excess gas from the swim bladder. However, even physostomous fish may not be capable of venting excess gas in response to the rapid pressure reductions that occur during turbine passage [47] When excess gas is not expelled, fish can incur mortal injuries such as swim bladder rupture, exophthalmia, and emboli and hemorrhaging in tissues [31]. Swim bladder rupture was also classified as a mortal injury for Chinook salmon, another physostome, and the difference in susceptibility between the two species is likely a result of different swim bladder morphology, particularly a unique feature of the shad swim bladder.

The swim bladder often improves hearing capabilities in most teleost fish [48]. This is particularly the case for American shad and other clupeids, which have an offshoot of the swim bladder that connects with the utricles of the inner ear [49]. This morphological trait may be the reason that juvenile American shad are more likely to rupture their swim bladder as compared to juvenile Chinook salmon, and why swim bladder rupture is likely to cause mortality of American shad. If an American shad survives a swim bladder rupture, or if damage to the swim bladder occurs without rupturing, the fish may be severely impaired. The unique swim bladder appears to be specifically tuned to detect ultrasound in the range emitted by dolphins, which are a major predator of shad [49–53]. Therefore, any damage to the swim bladder from rapid decompression may result in an increased susceptibility to predation.

5. Conclusions

When compared to other fish species, American shad are highly susceptible to fluid shear and rapid decompression. As the demand for lower-impact hydropower increases, it is critical that dose–response relationships, such as the ones developed in this study for American shad, are considered in the hydropower turbine and facility design process. As additional measures are considered for reducing the impacts of hydropower on fish populations, testing the susceptibility of additional species to rapid decompression and fluid shear should be considered to better understand how different morphological features may affect a fish's susceptibility. Applying these dose–response relationships to turbine operation as a method to reduce exposure to stressors may also provide fish passage benefits. This could be particularly beneficial for migratory species like American shad, which may only be present at a facility during specific times of the year, when operations could be altered to be safer for passing fish.

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