Quantifying mortality and injury susceptibility for two morphologically disparate fishes exposed to simulated turbine blade strike

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Abstract:

Passage of fishes through hydropower turbines and water pumping stations may cause mortal injury as the result of exposure to blade strike impact. Laboratory trials of simulated blade strike on two morphologically distinct fishes, American eel (*Anguilla rostrata*) and bluegill sunfish (*Lepomis macrochirus*) were undertaken to assess injury and mortality rates. We hypothesized that bluegill would have comparable rates of injury and mortality to other laterally compressed fishes while anguilliform American eel would be more resistant to injury. American eel had low observed mortality rates at the highest velocity tested (13.6 m/s), but many fish were observed with vertebral fractures which we categorized as functionally dead individuals. Bluegill were more susceptible to blade strike with high rates of mortality regardless of blade thickness, velocity, or impact conditions (location, angle, or fish orientation). These data have broadened our understanding of the range of responses among entrained fishes exposed to blade strike and represent species with low (American eel) and high (bluegill) susceptibility to injury and mortality. Our blade strike data can help inform safer turbine designs or prioritization of pumps that minimize traumatic injury and mortality of fishes during non-volitional passage through hydropower turbines or water pumping stations.

Keywords: hydropower, entrainment, water pumping stations, American eel, bluegill sunfish, passage trauma

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Introduction

Controlled movement of water to generate electricity, manage flooding, or provide irrigation are all important components of water management worldwide. These activities have also impacted riverine connectivity, altered stream hydrology, and sometimes have lethal consequences to fish passing through hydropower (Pracheil et al., 2016a) or water pumping stations (van Esch et al., 2014). Field studies have confirmed that turbine passage is frequent at many dams (Hostetter et al., 2011; Pracheil et al., 2015; Mueller et al., 2017) and at water pumping stations (McNabb et al., 2003; Baumgartner et al., 2009; van Esch, 2012), so industry developers have been tasked with redesigning hydropower turbines to reduce the risk of major injury or death (Čada, 2001) or prioritizing use of safer pumps (van Esch, 2012). Fishes at the highest risk of passage are those that undergo migrations to (adults) or from (juveniles) spawning habitat including anadromous salmonids or clupeids, catadromous anguillids, and potamodromous fishes (Grubbs & Kraus, 2010; Binder et al., 2011; McIntyre et al., 2016) although resident fish are also often entrained. The remarkable diversity of form (shapes, size, and other morphometrics) among migratory fishes, and disparate geological and hydrological features at each dam or pumping station, make it impossible to design a one-size-fits-all strategy to reduce passage at all sites.

To reduce or eliminate passage, some facilities have installed fishway passage structures, exclusion devices, or actively collect and transport certain species (e.g., salmonids smolts) safely around the dam or pumping station (Čada, 2001; van Esch, 2012). Some fishways and operations may help fish avoid passage, but none of the current solutions are 100% effective making passage unavoidable at many sites. When fish do pass through turbines, they are faced with a suite of stressors that may cause traumatic injury or death including, barotrauma from rapid decompression, hydraulic shear, cavitation, turbulence, blade strike, or collisions with structures (Colotelo et al., 2017). Similarly, traumatic injury caused by passage through water pumping stations has also been linked with mechanical damage, shear, and pressure fluctuations.(van Esch et al., 2014). Linking traumatic injury and death to a specific stressor following turbine passage during field trials is problematic because the exact exposure conditions of each fish are unknown. To that end, laboratory experimentation that investigates each stressor separately is the best alternative to better inform safer turbine designs that minimize injury and mortality during turbine passage.

Physical impact of blades striking fish represents one of the most likely avenues of injury or mortality when fish pass through hydropower turbines or water pumping stations. The risk and severity of injury from blade strike has been associated with turbine type, with Francis and Kaplan-types being the most common turbines found in hydropower dams globally (Uria-Martinez et al., 2018). Francis turbines are often associated with higher rates of mortality because they have more turbine blades and operate at higher RPMs than Kaplan turbines (Fu et al., 2016; Martinez et al., 2019). Mortality of fish passing through pumping stations is linked with pump type and operation conditions, with axial pumps have the highest mortality when flow rates exceed 200 m^3/min (van Esch, 2012). In contrast, Hidrostal pumps often have low mortality which is likely a result of using lower flow rates and having fewer, thicker blades (McNabb et al., 2003; Helfrich et al., 2004). In addition, velocity and leading-edge thickness of the blades also factors into probability of mortality from strike impact. The movement, orientation, and size of passing fish in combination with location and angle of blade strike must also be accounted for when predicting rates of injury and mortality. Ideally, one could account for all blade strike variables at once and provide a multiplicative probability estimate of injury or mortality for each species. However, probability of injury or mortality from blade strike is only one of multiple stressors, each with its own suite of exposure conditions, that would factor into estimates of total turbine passage mortality. Logistic constraints prohibit estimating injury and mortality rates for every exposure condition and stressor because both are also dependent on fish species (Colotelo et al., 2017).

Among species, marked variation in body shape, skeletal composition or architecture, muscle thickness, and integument quality (e.g., skin thickness or scale-type) are important factors influencing susceptibility to injury or mortality (Pracheil et al., 2016b). Laboratory data have shown that susceptibility to mortality in gizzard shad *Dorosoma cepedianum* (Lesuer, 1818) and rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) is markedly higher compared to hybrid striped bass (striped bass *Morone saxatilus* [Walbaum, 1792] × white bass *Morone chrysops* [Rafinesque, 1820]) or white sturgeon *Acipenser transmontanus* (Richardson, 1836), especially at higher blade strike velocities and thinner blade widths (Turnpenny, 1998; EPRI, 2008, 2011; Bevelhimer et al., 2019). Injuries linked with blade strike trauma may include scale loss, trauma to internal organs and musculature (hemorrhage, lacerations, contusions, or rupture), and skeletal fractures including the vertebrae (Turnpenny, 1998; Bevelhimer et al., 2019). Within a species, injury susceptibility and mortality is also affected by size of entrained fish (Coutant & Whitney, 2000) making size an important covariate in blade strike studies. Previous work in EPRI (2008, 2011) showed that survival of fish was related to the L/t ratio (fish total length divided by the blade thickness) and blade strike velocity. For example, fish that were struck by blades as thick or thicker than their total length ($L/t \leq 1.0$) tended to have higher survival than fish struck by thinner blades ($L/t > 2.0$) moving at similar velocities (EPRI, 2008, 2011). The diversity of form among fishes likely impacts their susceptibility to injury or death from turbine blade strike and suggests each species (or guild representative) must be investigated to best inform turbine design.

American eel *Anguilla rostrata* (Lesueur, 1817) is an elongate, migratory species that may be susceptible to turbine passage in the USA. Anguillid eels are well known catadromous species that migrate down freshwater rivers to reach spawning grounds in the Sargasso Sea (Grubbs & Kraus, 2010; Binder et al., 2011; Haro, 2014). This species has a wide geographic range throughout Eastern North America where it is found as far north as coastal Canada, down into the Gulf coast states in the southeastern USA, and up the Mississippi River drainage (Haro, 2014; Froese

& Pauly, 2019). Its distribution and migratory behavior increase the likelihood that eel will become entrained which has been observed in some rivers (Carr & Whoriskey, 2008; Eyler et al., 2016), especially coastal rivers of the eastern USA where many hydroelectric facilities are found (Jager et al., 2013; USACE, 2018). American eel is an IUCN listed endangered species with documented declines in historical abundance as result of overfishing and habitat loss, but population decline is likely confounded by dams disrupting riverine connectivity (Haro, 2014). Field studies have confirmed that anguillid eels (American and European eels) pass through turbines, and observations of eels that have been completely severed in half are not uncommon (B. Pracheil, *personal observation*). European eels *Anguilla anguilla* [Linnaeus, 1758], a closely related species, is also known to pass through pumping stations and passage trials showed that this species did not experience mortality until velocity was >8.0 m/s (van Esch et al., 2014). Laboratory data suggest American eel are markedly resistant to blade strike impact up to 12.2 m/s, though no internal injury assessments were performed that might link specific injuries to death (EPRI, 2008). More information is needed for eels exposed to more strike conditions and detailed injury assessments would also be beneficial so trauma could be linked with blade strike characteristics to better elucidate the susceptibility of eels to blade strike.

Bluegill sunfish *Lepomis macrochirus* (Rafinesque, 1819) is often found in the same freshwater habitat as eel, where its pelagic nature could increase its risk of turbine passage. Bluegill have a markedly wider distribution than American eel with a native range in Eastern and Central USA where it is an abundant representative of the ichthyofauna (Cooke & Philipp, 2009; Froese & Pauly, 2019). Unlike eel, sunfish do not make characteristic mass migrations of any notable distance or destination, but they are common in reservoirs (Froese & Pauly, 2019) including dams with hydropower facilities (Pracheil et al., 2016b). Bluegill represent a typical centrarchid species: laterally compressed, with a deep body, relatively short total length, and pronounced spines on the dorsal, pelvic, and anal fins (Cooke & Philipp, 2009). This species has a unique shape for which little information is available related to susceptibility to turbine passage including blade strike. The limited data from field trials showed that bluegill mortality may approach 57%, but entrainment appeared to be more haphazard and not because of volitional turbine passage (Keefer et al., 2013). To our knowledge, there is no other field or laboratory data available on bluegill or any centrarchid that relates turbine blade strike conditions to probability of injury or mortality.

This study aims to increase our knowledge about the effects of blade strike on susceptibility to injury and mortality through investigation of two fishes with high risk of turbine entrainment. Responses of American eel and bluegill to blade strike will vary as a result of their morphologically distinct nature; however, injury and mortality rates of both species will likely be higher when struck perpendicular to the blade on the mid-body, lateral surface, i.e., the worst-case-scenario relative to other strike locations (Bevelhimer et al., 2019). To that end, the objectives of this study are: 1) assess short-term mortality of bluegill and American eel after exposure to multiple treatment combinations of blade width, velocity, strike location, orientation, and impact angle, 2) document external and internal injuries of all fish, and 3) analyze these data using univariate statistics and logistic regression to better model injury and mortality rates related to simulated blade strike.

Materials and Methods

Simulated Blade Strike

The blade strike apparatus and protocol used to generate simulated blade strike followed methods reported in Bevelhimer et al., 2019, though modifications were made to accommodate our study species. Briefly, we used a spring-powered blade arm that accommodated blades of different thicknesses and generated velocities up to 13.6 m/s. Major strike variables used for both species included strike location (head or mid-body), fish orientation (lateral, dorsal, or ventral), and impact angle (45, 90, or 135°; Figure 1). Tail strikes were not included in this study because previous work found low mortality across multiple species suggesting tail strikes would have negligible impacts on fish survival (EPRI, 2008; Bevelhimer et al., 2019). Blade widths of 19, 26, or 52 mm in this study and strike velocities used for both species represented conditions typical of velocities between the hub and blade tip, i.e., average turbine passage conditions (Bevelhimer et al., 2019). A high-speed camera system (Model IL4, Fastec Imaging, San Diego, California) filmed every impact at 1000 frames per second to confirm blade strike velocity, location, and impact angle as well fish orientation. Average blade strike velocity (± 0.10 m/s) was estimated from two velocity check videos (one before and one after each experimental group) and from three fish treatment videos in each group using Kinovea software (v0.8.15, www.kinovea.org). Treatment groups varied by blade width, velocity, location, orientation, and impact angle to cover as many exposure scenarios as possible because exact conditions of turbine passed fish are unknown. Upon arrival to laboratory, fish were evenly distributed into separate 680-liter, circular fiberglass tanks which received constant water supply, aeration, and were fed daily. Fish were not fed 24 hours prior to experimentation to avoid tank fouling. Our design used 20 fish per group though some groups contained <15 fish so that more scenarios could be included to provide additional inferences about injury and mortality rates of each species. In addition, each treatment group contained 2-3 fish used as experimental controls and were pooled together by species.

Study Species

Wild-caught American eel with an average mass of 266.7 g (141.0 – 422.3 g) and total length of 53.9 cm (45.7 – 67.5 cm) were purchased from a commercial supplier in Pennsylvania (Delaware Valley Fish Company, Norristown, Pennsylvania, USA). Preliminary trials suggested blade strike was not injurious until velocities reached 12.0 m/s which became the lowest blade strike velocity, so eel were exposed to 12.0 and 13.6 m/s using the 19- and 26-mm blades. Blade strike location for American eel was restricted to the anterior portion of the body (up to 22% of TL) using the pectoral fin to demarcate a head strike (4 – 11% TL) and mid-body strike (13 – 22% TL). A mid-body strike on an eel was closely associated with location of most internal organs including the heart, liver, gall bladder, stomach, swim bladder, and kidney. Due to the lower number of available fish, we did not include 45 or 135° strikes and prioritized impacts at 90°. A total of 156 treatment fish in 11 exposure groups and 20 control fish were used for eel analyses (N = 176; Table 1).

Bluegill sunfish were received from a commercial supplier in Alabama (Southeastern Pond Management, Saginaw, Alabama, USA) and sorted into three size groups: "small" (n = 73; average TL = 11.8 ± 1.49 cm; average mass = 30.4 ± 12.48 g), "medium" (n = 377; average TL = 16.0 ± 1.02 cm; average mass = 80.7 ± 10.28 g), and "large" (n = 19; average TL = 17.5 ± 1.18 cm; average mass = 113.6 ± 33.32 g). Preliminary trials on bluegill suggested use of

26- and 52-mm wide blades with blade strike velocities of 4.7 – 9.1 m/s. An impact to the head was considered at any point between the snout and trailing edge of the operculum (i.e., head length). A mid-body strike occurred between the operculum and leading edge of the anal fin which is also associated with most of the visceral mass. A total of 422 treatment fish in 26 exposure groups and 48 control fish were used for bluegill analyses (N = 470; Table 1).

Blade Strike Protocol

Pairs of fish were anesthetized in a 14-L water bath containing a solution of pure clove oil extract dissolved in 95% ethanol (1:10) and diluted with dechlorinated tap water. Concentrations of clove oil for anesthesia were 60 ppm for bluegill and 120 ppm for American eel (Javahery et al., 2012) to ensure fish reached deep anesthesia (i.e., Stage III, Plane 3) denoted by loss of equilibrium, lack of movement, and rare gill ventilations (Sneddon, 2012). Anesthetized fish were removed from the bath and visually inspected for external injuries or deformities. Following visual inspection, fish were randomly assigned treatment condition and placed on the strike platform at the intended treatment position. Neutrally buoyant fish were placed onto the strike platform and loosely held in place with flexible tubing designed to allow fish to move freely after blade impact. A final check of correct treatment conditions was proceeded by initiation of high-speed videography and the triggered release of the blade. Control fish were exposed to the exact same conditions as treatment fish but did not receive a blade strike. Following blade impact and removal from tank, the fish was tagged in the lower jaw with a numbered, T-bar anchor tag (Floy Tag & Mfg. Inc., Seattle, Washington), photographed, placed into a 450-liter fiberglass recovery tank containing freshwater with aeration, and observed for up to 1-hour. Individual observations of gill ventilation, maintenance of upright position, discoloration, swimming ability, and hemorrhaging were noted every 15-minutes. Fish were categorized based on their condition including 1) individuals that appeared normal with no obvious signs of distress which were considered survivors, 2) early removal of any fish that appeared to be severely injured or moribund fish with irregular or labored gill ventilation, loss of equilibrium, or labored swimming, 3) fish that were removed right at the one-hour mark with signs of severe injury or appeared to be moribund, and 4) fish that were considered dead within hour observation (i.e., direct mortality). *Observed mortality* for each treatment group included direct mortalities (category 4) plus moribund individuals removed early (categories 2 and 3). All fish including those considered dead, were then placed in the euthanasia bath. Euthanasia was accomplished with a 250-ppm clove oil solution for bluegill and a 420-ppm solution for American eel. After gill ventilations were no longer observed (i.e., usually after 10 minutes) all fish were placed on ice prior to necropsy.

Detailed injury assessments were performed via external and internal necropsy on all fish following euthanasia. Mass (± 0.1 g) and total length (± 0.1 cm) of each fish was recorded. The external examination included identifying potential hemorrhaging, lacerations, contusions, or discoloration associated with the fins, snout, eyes, operculum, and integument. Degree of descaling was also noted when applicable. The internal examination began with a traverse cut using the cloaca (vent) and continued anteriorly until reaching the isthmus of the operculum. Next, another incision continued dorsally along the trailing edge of the operculum until reaching the vertebral column. The final incision cut along the spine posteriorly until reaching the area above the vent, followed by an incision in the ventral direction until the entire flank was removed. Sex was noted when it could be easily determined from existing gonad condition. Soft tissues assessed included the heart, liver, gall bladder, stomach, intestines, gonads, swim bladder, and kidney. Specific injuries were categorized as hemorrhage, laceration, contusion, clotting, edema, rupture, or avulsion. Partial or complete fracture of skeletal elements including the vertebral column, ribs (bluegill only), or haemal spines (eel only) were also noted. Spinal fractures, regardless of location, was considered a major injury for both species and was used as an indicator of functional death. Functional mortality (i.e., ecological death) was considered for fish with spinal fractures as they would most likely be unable to escape conditions that would lead to their death or impair their ability to capture food. *Combined mortality* for each treatment group included functional and observed mortalities. The assessor performed necropsies without knowledge of which treatment individual fish had received.

Data Analyses

Mortality rates (observed and combined) were calculated for both species across all treatments groups and pair-wise comparisons were made using Chi-square test with Yates correction according to the following equation:

$$\chi^2_{Yates} = \frac{(|ad - bc| - 0.5N)^2 N}{mnrs} \tag{1}$$

where *a* and *b* are the number of mortalities for treatments 1 and 2, respectively, *c* and *d* are the number of survivors for treatment 1 and 2, respectively, *m* is the total number of mortalities and *n* is the total number of survivors for both treatments, *r* and *s* are the total number of fish for each treatment, and *N* is the total number of fish in the comparison (Campbell, 2007). The Yates corrections to Chi-square tests was used because it accounts for treatment groups with <5 expected mortalities or survivors (Campbell, 2007). Chi-square tests were used to compare groups that were similar in all but one category to assess effects of blade width, blade strike velocity, strike location, orientation, and impact angle on mortality. One-tailed p-values were used to test significance comparing treatment groups to controls, and two-tailed p-values for tests between treatment groups. We assumed $\alpha = 0.05$.

A second analysis was performed to determine the effect that velocity had on observed and combined mortality rates between groups of bluegill that only varied by average total length. We used a four-parameter log-logistic function to model the dose-response of velocity and mortality according to the following equation (Ritz et al., 2015):

$$f(x; b, c, d, e) = c + \frac{d - c}{1 + \left(\frac{x}{e}\right)^b} \tag{4}$$

where *f(x; b, c, d, e)* is predicted proportion of fish that would not survive, *b* is the slope or inclination point, *c* is the lower bound which was fixed at 0.0, *d* is the higher bound which was fixed at 1.0, and *e* is the effective dose for 50% mortality of the population (E_{50}) or the blade strike velocity at which 50% of the population would not be expected to survive. The log-logistic dose response curve was used to analyze two subsets of bluegill that received mid-body, lateral strikes at 90° with at least four blade strike velocities. The subsets differed in average length – i.e., small (11.7 cm; n = 57) and medium-sized fish (16.1 cm; n = 70). Dose-response regression analysis and goodness of fit tests were performed using the "*drc*" package (Ritz et al., 2015) in *R v3.5.1* (R Core Team, 2018).

Finally, a logistic regression analysis was performed using generalized linear model (*glm*) with a logit link function available in *R v3.5.1* (R Core Team, 2018). The analyses were performed using observed or combined mortality as the binary predictor variable for both eel and bluegill. Logistic regression is well suited for data that contain a combination of continuous, discrete, categorical, or binary variables with a binary response bounded between 0 and 1 (Hilbe, 2016). Continuous variables included, blade velocity (m/s), mass (g), and total length (cm). Categorical variables included blade width (19, 26, and 52), location (M; mid-body or H; head) of blade strike, fish orientation (L; lateral, D; dorsal, or V; ventral), and impact angle (45, 90, 135°). The last group of variables with binary outcomes were linked with injuries pooled together by anatomical structure. For example, if an individual was observed with hemorrhaging and contusions on the liver it was considered a "1" for the liver category otherwise it was assigned "0" if no injuries were present. Injury categories found in both species included integument, head, fins (all paired and medial fins), gills, viscera (visceral mass as a whole), heart, liver, spleen, swim bladder, kidney, muscle, internal decapitation, and vertebral column. Mouth cavity (including the mouth, buccal surfaces, and palate), gall bladder, stomach, and haemal spines were included in the American eel analysis, whereas eye, opercula, intestines, gonads, and ribs were only included in the bluegill analysis. Only one size-based variable (mass or total length) was included in the analysis because of collinearity among these data. Outliers were detected by centering and scaling size data (mass or length) and removing values with z-scores less than -3.29 or greater than 3.29. Two statistical analyses were performed: 1) blade strike conditions regressed against combined mortality in treatment fish only (n = 151 eels and 400 bluegill) and 2) injury categories regressed against observed mortality including controls (n = 175 eels and 465 bluegill). Akaike model selection criteria (AIC) and stepwise variable selection was used to select the best fitting model. We used a train to test data ratio of 80:20 for both species. Receiver operating (ROC) plots and area under the curve (AUC) estimates were used to test the ability of our models to predict injury or mortality.

Results

Confirmation of Blade Strike Velocity and Impact

High speed videography confirmed that blade velocity and strike impact conditions (location, orientation, and impact angle) were consistently replicated. Estimates of blade velocity indicated our system had a precision of ± 0.1 m/s within treatment groups. During video confirmation of strike impacts, we found that some fish were not struck as intended, either due to initial misplacement or drifting out of alignment as the blade approached the fish. As a result, about 5% (n = 9) of American eel were analyzed in a different than intended treatment group. Similarly, ~5% of bluegill (n = 25 fish) were not struck as intended. Twenty bluegill that moved could not be placed into one of the 26 original treatment groups, so they were excluded from Chi-square analyses; however, these individuals were included in the logistic regression relating injury to mortality because this model accommodated all variations of treatment conditions. The remaining five bluegill were excluded from all analyses because interaction with holding brackets may have caused injury unrelated to treatment conditions. Nearly all bluegill ($n = 465$) and every American eel ($n = 176$) were used in our statistical analyses.

Mortality

A total of 626 fish across both species were successfully exposed to one of 39 treatment conditions including controls (Table 1). No control fish of either species (20 American eel and 48 bluegill) died at any point in our experiment including brief handling, anesthesia, or tagging procedures (i.e., mortality rates = 0.0). Most observed mortalities were the result of removing moribund fish during the 1-hr post-strike observation and not direct death. Some moribund fish exhibited marked hyperpigmentation on the skin that usually affected only one part of the body and was clearly demarcated from normal skin near the impact site. Hyperpigmentation was not a good predictor of survivorship for either species because abnormal pigmentation disappeared immediately during euthanasia and it was not observed in all fish. Moribund fish were often observed resting on the tank bottom and made few efforts to swim unless stimulated by the assessor. We also observed labored swimming with an inability to maintain upright position in the water column (for bluegill only) which prompted early removal.

American eel had low overall mortality across all treatment groups for fish exposed to velocities up to 13.6 m/s. The highest observed mortality rate was 45.5% when struck on the dorsal surface of the head with the 19-mm blade moving at 13.6 m/s and was the only group (trial #7; Table 1) with significantly ($p \ll 0.001$) higher mortality compared to control fish. One group (trial #4; Table 1) of eels had no observed instances of mortality, but this trial had a significantly higher combined mortality rate of 100% ($p \ll 0.001$). Mortality (observed and combined) for fish exposed to 19- and 26-mm blades (Trial #1 & #9; 12.0 m/s, mid-body, lateral strike) were statistically indistinguishable from one another (Table 2). Velocity groups (12.0 versus 13.6 m/s) tested had low observed mortality but high rates of combined mortality, though none of the comparisons differed significantly. Location had a modest effect when fish struck on the head experienced significantly higher observed mortality compared to mid-body strikes (Trial #4 & #7; 19 mm blade, 13.6 m/s; $p = 0.021$), though this was not true for combined mortality or any other comparisons (Table 2). All eel struck on the dorsal surface had significantly higher combined mortality rates compared to controls ($\geq 73\%$; $p \ll 0.001$) and to fish struck on the lateral ($p \leq 0.014$) or ventral surfaces ($p \ll 0.001$). No other comparisons yielded significant results (Table 2).

Overall rates of mortality (observed and combined) among bluegill was notably higher than American eel, and mortality was >90% on multiple occasions at moderately low velocities. Most observed and combined mortality rates among treatment groups were significantly higher than control fish (Table 1). Combined mortality rates of 100% were detected in at least five treatment groups at low velocities (i.e., 6.1 m/s). No significant affect was detected between the 26- and 52-mm blades because mortality (observed and combined) was high in both groups. Significantly higher observed and combined mortality was not detected until velocity exposure groups differed by ≥ 1.0 m/s, though this was not true for all velocity treatment groups (Table 2). Mid-body strikes had significantly higher mortality (observed and combined) than head strikes at 7.1 and 8.0 m/s, but not at 9.0 m/s because mortality was high at both strike locations at this velocity (Table 2). Observed and combined mortality rates were significantly higher when fish were struck on the lateral compared to the ventral surfaces at velocities near 7.5 m/s, but rates were high at all orientations above 8.7 m/s. Mortality was high regardless of impact angle, though only combined mortality was significantly higher for lateral strikes to the head at 90° compared to 45° ($p << 0.001$). Large bluegill (trial #22; Table 1) had observed and combined mortality rates of 100% when exposed to a mid-body, lateral strike at 90° with the 52-mm blade moving at 6.4 m/s. In a comparable trial for medium-sized fish (trial #19; Table 1), observed mortality rate of 50.0% was significantly lower ($p = 0.002$) than large fish. The small size group (trial #19; Table 1) had a slightly higher observed mortality rate (71.4%) and was not significantly different from medium or large fish. Combined mortality rates increased to 83.3% in medium fish and was 100% for both small and large bluegill and did not vary significantly among groups.

Injury Assessment

Dissections of both species revealed that many individuals survived with major internal injuries which were not observed externally. Some moribund fish exhibited marked hyperpigmentation on the skin that usually affected only one part of the body and was clearly demarcated from normal skin near the impact site. In addition to hyperpigmentation, the most common external injury was hemorrhaging from the mouth or the opercular cavity of eel, while minor abrasions and descaling were common among bluegill. We observed fractures of the vertebral column in both species, which was considered a major injury and was used to indicate functional mortality. Nearly 15% of bluegill and 20% of American eel were observed with vertebral fractures but did not exhibit any signs of stress to indicate it was moribund and should be removed early. The most severe vertebral fracture in both species was observed when the 1st pre-caudal vertebrae was forcefully separated from the posterior edge of the cranium, i.e., internal decapitation. In both species, internal decapitation was often associated with external and internal signs of hemorrhaging near the fracture site. Hemorrhaging or clotting within the visceral mass (i.e., internal organs excluding the heart and kidney) was used as an indication of internal bleeding and was detected in both species. No other general trends across both species were observed.

Though only 16 American eel died during this study, > 25% of all eel dissected showed some signs of severe trauma to the vertebral column. Only the internal decapitation injury group had significantly higher observed mortality (33.3%; $p = 0.002$) than the overall eel mortality rate of 9% (Table 3). Localized hemorrhaging in the buccal cavity and pooling of blood against the palate was also observed as result of internal decapitation when fish were struck on dorsal surface of the head. Gill hemorrhaging was observed from strikes to lateral or ventral surface of the head but had low observed mortality. The most common internal injury among eel was hemorrhaging, lacerations, or contusions to the liver for fish exposed to mid-body lateral and ventral strikes. Some livers were so severely damaged that the hepatic tissue became friable and fell apart during dissection. Fractures to the caudal vertebrae and haemal spines were also common for fish receiving mid-body lateral and dorsal strikes, but only one of these fish was confirmed dead. Five fish with vertebral fractures also had hemorrhaging from damaged kidney tissue which caused blood to pool inside the swim bladder. Muscle injuries (mainly contusions and clotting) where only found in fish that also had concurrent bone fractures in the mid-body region. Organ avulsion ($n = 1$) was only observed in the spleen, while rupture ($n = 5$) was observed in both the spleen and gall bladder, though only one fish was confirmed dead. Internal hemorrhaging and clotting of the viscera was likely from damage to the liver or spleen. One eel that died had no obvious external or internal injuries and was excluded from logistic regression.

Three-quarters of all bluegill tested were observed with one or more injuries. Damage to the eye, operculum, fins, and muscle had mortality rates statistically indistinguishable from the overall rate 50.2% (Table 3). Mortality rates among fish observed with internal decapitation was also similar to the overall rate (58.3%) and nearly half of these survived the assessment period. Vertebral fracture was the most common injury observed in bluegill including the small fish exposed to the lowest velocity (i.e, 4.7 m/s). Nearly ¼ of all bluegill with vertebral fractures had two or three separate fractures along the entire vertebral column. While no external signs of fractures were evident, moderate to severe hemorrhaging and clotting along the vertebral column against the swim bladder was observed internally. Source of hemorrhaging was difficult to pinpoint, but may have originated from vessels along the spine, trauma to the kidney, or combination of both. Swim bladder damage had a significantly higher rate of mortality (82.1%; $p << 0.001$) and was the second most common injury observed. Rupture of gonadal tissue had significantly higher rates of mortality (71.7%; $p = 0.002$) and was observed in both sexes. Damage to the viscera did not have significantly higher levels of mortality and was only detected in 12% of bluegill. All fish observed with broken ribs ($n = 30$) also had at least one complete fracture of the vertebral column. Fish with gill damage had significantly higher mortality ($p = 0.011$) but this injury was only detected in nine fish. Damage to integument (e.g., minor descaling) was associated with significantly higher rates of mortality (72.3%; $p << 0.001$) but was most likely not the direct cause of mortality. All injuries with significantly higher rates of mortality were also observed with high incidence of vertebral fractures (≥ 75%) which was likely the cause of death for these fish. Injuries to the head and intestine were rare ($n = 2$ fish) and were excluded from logistic regression.

Dose-Response

The dose response analyses of mortality rate against blade strike velocity produced two significant models with good fit for both small ($p << 0.001$) and medium ($p = 0.004$) sized bluegill. The log-logistic models predicted 0 – 100% mortality over a 3 – 4 m/s range in velocity (Figure 2a). Both curves had approximately the same shape and slope (b), but smaller fish were expected to reach 50% mortality at a velocity 0.7 m/s lower than the medium-sized group. Predicted models fit our dose-response data better than the fully parameterized model and one-way analysis of variance (ANOVA) of average mortality across velocity exposure groups ($p >> 0.05$).

The log-logistic models of combined mortality against blade strike velocity was also significant for both small and medium sized fish ($p << 0.001$). Both models predicted 0 – 100 percent mortality over a 3 – 4 m/s velocity range, but small and medium E50 values decreased (Figure 2b). Functional death was predicted to occur at lower velocities overall compared to observed mortality, and small fish experienced major injuries at velocities ~1.0 m/s lower than medium bluegill. The shape of the small and medium curves was also similar but the separation between curves was greater than observed mortality data. Both predictive models fit combined mortality rate data better than the fully parameterized model and one-way ANOVA across velocity exposure groups ($p >> 0.05$).

Logistic Regression

Logistic regression of blade strike conditions against combined mortality found a significant effect among American eel and bluegill data. Stepwise variable selection chose the model containing only blade width and orientation for American eel (AIC = 85.81) while velocity, location, and orientation were the best predictors of combined mortality in bluegill (AIC = 270.62; Table 4). Eel struck on the lateral or ventral surface had higher odds of survival compared to individuals struck on the dorsal surface. Similarly, strikes with the 26 mm blade at fixed orientation would have 85% higher odds of survival compared to strikes with the 19 mm blade. At average velocity and fixed orientation, bluegill would be ~80X more likely to die when struck in the mid-body compared to the head. Similarly, fish struck on the lateral surface were ~45X more likely to die (at average velocity and fixed location), whereas individuals struck on the ventral surface were 77% more likely to survive. For every 1.0 m/s increase in blade strike velocity (at fixed location and orientation) fish would be ~3X more likely to perish. Fish size (e.g., total length, mass, or L/t ratio) did not have a significant impact on mortality for American eel or bluegill across the entire range tested; therefore, it was dropped from the most parsimonious model during stepwise regression. The ROC curves suggested our logistic models had high specificity (high probability of correctly predicting combined mortality), and AUC values ≥ 0.882 indicated both eel and bluegill models properly classified combined mortality as a result of blade strike conditions (Figure 3a, b).

We only found a significant effect of injury category on observed mortality among bluegill data. Stepwise variable selection produced a model containing integument, operculum, viscera, liver, swim bladder, internal decapitation and vertebral fracture as the best predictors of observed mortality among bluegill (AIC = 275.92; Table 4). Fish with vertebral fractures or internal decapitations with fixed rates of integument, operculum, viscera, and liver injuries were >18X more likely to die. Fish with damage to the integument and fixed rates of operculum, viscera, liver, swim bladder, internal decapitation and vertebral fracture injuries were nearly 2X more likely to die as a result. Damage to the operculum and swim bladder were both important to our parsimonious model but neither were a significant predictor of mortality by itself (Table 4). The ROC curve suggested our logistic model had high specificity and an AUC score of 0.847 suggested the injury model properly classified observed mortality related to injury category.

Discussion

Pairwise comparisons were unable to clearly separate overall trends in our data which highlights the limitations of univariate statistics and not a lack of an actual relationship between blade strike conditions and mortality. For example, logistic regression indicated that thicker blades had higher odds of survival in eel but not in bluegill (Table 4), while results of chi-square tests were less conclusive for both species (Table 2). Lack of significance in bluegill was likely the result of high rates of mortality overall though only two widths were used in this study. Blade strike velocity is likely to have effect on eel mortality, but it was not detected in our study which included only a limited range of blade strike velocities (e.g., 12.0 and 13.6 m/s). In contrast, chi-square and logistic regression analyses indicated that mortality was significantly higher in bluegill when blade strike increased by ≥ 1.0 m/s. Orientation had a clear effect on American eel mortality while location did not – dorsal strikes had higher odds of mortality than lateral or ventral strikes regardless of location. Mid-body lateral strikes were associated with higher odds of mortality in bluegill which was also shown in rainbow trout, gizzard shad, and hybrid striped bass (Bevelhimer et al., 2019). Bluegill had high mortality (≥ 80.0%) at all impact angles with no obvious trend, and no other angles were tested or analyzed for American eel. In general, our data indicates that eel may resist blade strike at velocities near 12.0 m/s, though dorsal strikes at or below this velocity would still be severely injurious. Bluegill mortality data fit expected trends of higher mortality with mid-body lateral strikes, but the effects of blade width and impact angle were not obvious. Furthermore, while bluegill data covered more exposure scenarios, the effect of blade width should not be completely dismissed because only two widths were tested in our experiment. Furthermore, lack of significance among bluegill does not indicate lower susceptibility, rather mortality rates were high overall suggesting this species is more intolerant of blade strike conditions compared to eel.

American eel and bluegill data presented here fall within the lower and upper range of survival data published for other species. Bluegill exposed to 6.4 m/s and struck on the mid-body, lateral side at 90° experienced significantly higher mortality than hybrid striped bass which did not die from these conditions (Bevelhimer et al., 2019). Mortality rates of bluegill and gizzard shad were both equivalently high (>60%) when exposed to a 52-mm blade moving at ~7.4 m/s, and impacting the mid-body, lateral surface at 90° (Bevelhimer et al., 2019). Bluegill exposed to comparable strike conditions (~4.7 m/s, mid-body, lateral strikes at 90°) as rainbow trout had similarly low observed mortality rates (Turnpenny, 1998; EPRI, 2008). Low rates of observed mortality was also found in American eel at velocities up to 12.2 m/s; however, overall mortality after a 96-hr observation period increased to 70% for mid-body strikes specifically (EPRI, 2008). White sturgeon had significantly higher mortality (~50%) from similar turbine blade strike conditions (12.0 m/s velocity, 26-mm blade, mid-body, lateral strike at 90°) suggesting sturgeon may be more susceptible to turbine passage than American eel (EPRI, 2011). Across all studies discussed so far, it appears bluegill and gizzard shad are the most susceptible, followed by rainbow trout and hybrid striped bass, while white sturgeon and American eel are the most resistant species tested to date.

The marked range in response to blade strike is mirrored by the anatomically and morphologically distinct body types of American eel and bluegill. American eel are elongate with total length far exceeding body depth and have incredibly flexible bodies that facilitate its anguilliform mode of swimming (Helfman et al., 2009; Haro, 2014). In contrast, bluegill is short with a laterally compressed body and high surface area to maximize acceleration, turning behavior, and maneuverability (Collar & Wainwright, 2009). Review of highspeed video revealed that both species wrapped around the blade to some degree after contact, but eel wrapped more completely with seemingly minimal negative effect. The only instance this was not true for eel was during all dorsal strikes which often had low observed mortality but ≥73% were considered functionally dead due to spinal fractures, indicating dorso-ventral flexibility is limited. Bending in bluegill was exceedingly traumatic and many fish had more than one vertebral fracture at low velocities (~ 5.0 m/s). The exact degree to which each species can bend with minimal vertebral damage was not measured; however, vertebral morphology has been linked with C-start curvature and swimming performance (Swain, 1992; Brainerd & Patek, 1998). More specifically, the number of, and angle between, each vertebrae influences maximum curvature and is one measure of stiffness among fishes (Brainerd & Patek, 1998). The second component includes the role of interconnected skin, tendons, and muscles around the skeletal elements and their affect on overall stiffness (Long & Nipper, 1996). While whole body stiffness was also not measured, we know American eel has 103 – 111 vertebrae compared to only 28 – 33 found in bluegill (Nelson et al., 2016; Froese & Pauly, 2019) which likely contributes to the enhanced flexibility of American eel under most strike scenarios. Injury severity and mortality may also be related to proximity of blade strike to a species center of gravity. Blade strike impacts near the center of gravity may be especially traumatic because there would be less deflection and more force transmitted to the fish (Turnpenny et al., 1992; Bevelhimer et al., 2019). This relationship may not apply to American eel because the center of gravity is not located near the visceral mass, but mid-body strikes in this study did target the area with concentrated soft tissues. The center of gravity for bluegill is located roughly 40% of its total length (Tytell & Lauder, 2008) which also coincides with the location of most internal organs of the visceral mass. We observed more severe organ damage in American eel which could related to its lack of skeletal protection (i.e., ribs or intramuscular bones), whereas bluegill has an extensive protective network that provides enhanced protection to soft tissues. Investigations into anatomical and biomechanical properties (e.g., flexibility or center of gravity) related to strike location are needed to better elucidate how fish may resist injury caused by blade strike.

Fish size was also compared between different size groups and across the entire range of fish tested suggesting size may affect mortality, but not necessarily in the same way described previously or under all conditions. EPRI (2008) was the first to demonstrate that fish survival was linked to the total length to blade width ratio (i.e., L/t ratio). Average American eel L/t ratio in our study (28.8) had no observed mortality and matched comparable trials (L/t = 31.8; velocity = 12.2 m/s) with no instantaneous mortality described in EPRI (2008). The average L/t ratios for small (2.25), medium (3.10), and large (3.36) bluegill all had observed mortality >50%, though large fish had significantly higher observed mortality compared to medium fish. Combined mortality rates were higher for all bluegill L/t ratios (≥ 83%) and no obvious trend was detected. Our dose-response curves suggest that observed and functional mortality for 50% of small bluegill would occur at notably lower velocities than medium bluegill (Figure 2). Dose response analyses indicated that small fish are more susceptible to blade strike than larger individuals, which contrasts with lower mortality observed in small compared to larger rainbow trout (EPRI, 2008). No further comparisons can be made because of our limited number of L/t ratio groups and lack of direct comparison with our study species. Interestingly, logistic regression models suggested that size did not significantly impact mortality, which was influenced more by location, orientation, and velocity of blade strike impact. For eel, lack of significant effect on size may be related to the narrow range of sizes used (45 – 65 cm), whereas size is less important to bluegill provided that all sizes of fish tested experienced notably high mortality rates. Regardless, fish size is likely an important predictor of mortality, but other factors (e.g., species morphology or proximity of strike to center of gravity) should also be factored into estimates of mortality when accounting for size effects within or among species.

Many individuals of both species (39 American eel and 63 bluegill) survived at least one hour with one or more vertebral fractures which necessitated redefining mortality based on functional (ecological) death. While these animals were technically considered survivors in our study, they would be less likely to escape predation and capturing food would also be challenging. More importantly, there were no obvious external signs of this severe injury that could be observed consistently. The logistic regression of injuries suggested many other internal injuries were significant predictors of mortality, but these injuries were always associated with high prevalence of fractured vertebrae in bluegill (Table 4). This is especially important to consider during turbine passage studies in the field because the assessor would be unable to detect functionally dead individuals without performing internal necropsies. To our knowledge, field studies do not perform internal necropsies suggesting that some apparent survivors may be functionally dead after the observation period ends. For example, American eel mortality increased to nearly 70% during a 96-hr observation period which was attributed to an unspecified internal injury (EPRI, 2008). Combined mortality rates >70% were detected in American eel when mortality estimates included functionally dead fish which suggests this endpoint is more indicative of long-term eel survival. To that end, we suggest internal exams should be a component of field and laboratory studies because it provides a more accurate estimate of injury and mortality rates. Inclusion of functionally dead fish should increase accuracy of mortality estimates, but we are uncertain that all vertebral fractures are lethal and unrecoverable provided some fish were observed with partial vertebral fractures. Additional trials that observe fishes for longer periods of time (i.e., ≥ 96 hours) would also help elucidate how functional death relates to changes in fish health, growth, or behavioral impairment following exposure to blade strike impact.

Conclusions

The data presented in this study will provide additional insights into how susceptible riverine fishes are to blade strike impact that may be experienced during passage through hydropower turbines or water pumping facilities. Our system is not meant to mimic complete turbine passage conditions like studies involving scale models and live fish. Instead, the blade strike apparatus used in this study was designed to expose fish to a blade with a similar shape, leading edge thickness, and strike velocity of a hydropower turbine blade during average turbine passage conditions (Bevelhimer et al., 2019). Leading edge width and velocity of our blade is also within the specifications of radial, mixed flow, and Hidrostal pumps used at water pumping stations worldwide (McNabb et al., 2003; Helfrich et al., 2004; van Esch, 2012). The operation of both hydropower turbines and water pumping stations would also affect estimates of mortality as operators adjust flow rate or runner speed to maximize generation ability or water movement. Our methodology was also developed to cover as many exposure scenarios as possible with the given number of fish because strike conditions that occur to each fish passing through turbines or pumps is unknown. In addition, we designed our system to allow for precise, repeatable exposure of fishes to blade strike conditions to better account for variation and decrease uncertainty in our estimates of mortality. Fish struck by our stimulated turbine blade were not constricted in any way and were allowed to move freely after initial contact was made with the turbine blade. Prior studies used monofilament tethers to hold fish in place to better control where the blade impacted fish; as a result, this method also lead to estimates of mortality that were confounded by a tether that restricted fish movement (EPRI, 2008, 2011). The apparatus and methodologies used here may be less realistic than in-situ passage studies, but our design maximizes the ability to control dose (e.g., blade width and strike velocity) to provide more accurate estimates of mortality.

Our system was well suited to quantify blade strike dose-responses that will parameterize the Biological Performance Assessment (BioPA) model and Hydropower Biological Evaluation Toolset (HBET) – both are being developed to inform safer turbine designs (Richmond et al., 2014; Hou et al., 2018). Development of safer turbine designs using biologically relevant data is not a new concept and has already led to design and implementation of more fish friendly systems (Čada, 2001). Our data are of growing importance as dam operators are faced with the rigors of relicensing through the Federal Energy Regulatory Committee (FERC) which stipulates renewal of licenses every 30 – 50 years. Part of this renewal process includes detailed and costly environmental impact assessments which always includes a component of turbine passage and survival of fishes most likely to become entrained. The native ranges of American eel and bluegill put them in direct contact with nearly 50% of all hydropower projects in the USA, suggesting the risk of entrainment and turbine passage is high for both species (ORNL, 2019). While more detailed and holistic estimates of mortality and dose-response models will be released in the future, we suggest the following to maximize utility of our data presented as is. To date, no exposure conditions tested with our system or others has been able to replicate the severe trauma (e.g., eels severed in half) observed at some dams. To that end, we suspect that grinding and tearing of eels via pinch points is the more likely cause of these kinds of injuries compared to the internal injuries we observed which were more likely to be caused by direct blade strike. Mortality of eels is more likely if passage through turbines or pumping stations includes blade characteristics that are moderately thin (< 26 mm) and moving at velocities ≥ 12.0 m/s. Bluegill, which is much less resistant to blade strike, will likely experience high mortality under most scenarios because strike velocities as low as 5.0 m/s were lethal. Furthermore, our data indicate that fish species is an important consideration in mortality estimates and suggests that size effects may be confounded by species anatomical and morphology disparities. Future research should include more blade widths for both species a wider range of strike velocities in eel specifically to better elucidate how blade strike effects mortality. We also recommend continued investigations into more morphologically distinct species and account for fish biomechanics to better understand how blade strike impact affects mortality or riverine fishes.

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Figure captions

Fig. 1 Diagram depicting major blade strike conditions related to the fish body and impact of the blade. Major variables included location (head or mid-body), orientation of fish (lateral, ventral, or dorsal), and impact angle (45, 90, or 135°). See Table 1 for more detailed information on exposure conditions of each treatment group

Fig. 2 Dose-response relationships between blade strike velocity (m/s) and observed (a) and combined (b) mortality in small (dashed line) or medium sized (solid line) bluegill. Lines represent a four-parameter log-logistic regression (*c* and *d* fixed at 0.0 and 1.0, respectively) while points are group mortality rates according to blade strike velocity

Fig. 3 Receiver operating plots (ROC) of logistic regression models fitted to combined mortality and blade strike conditions for (**a**) bluegill and (**b**) American eel or (**c**) observed mortality and injury category among bluegill. Presented with area under the curve (AUC) values. Values of AUC closer to 1.0 are considered to have good predictive ability compared to values closer to 0.5

Figure

Click here to access/download;Figure;Fig.1 - Blade strike conditions.docx

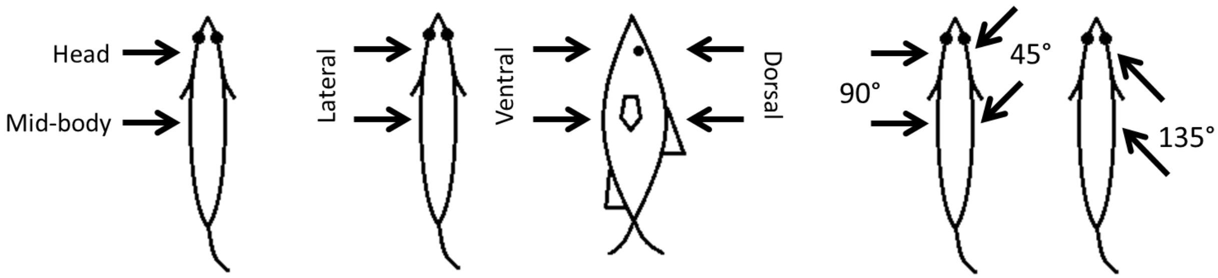

Fig. 1

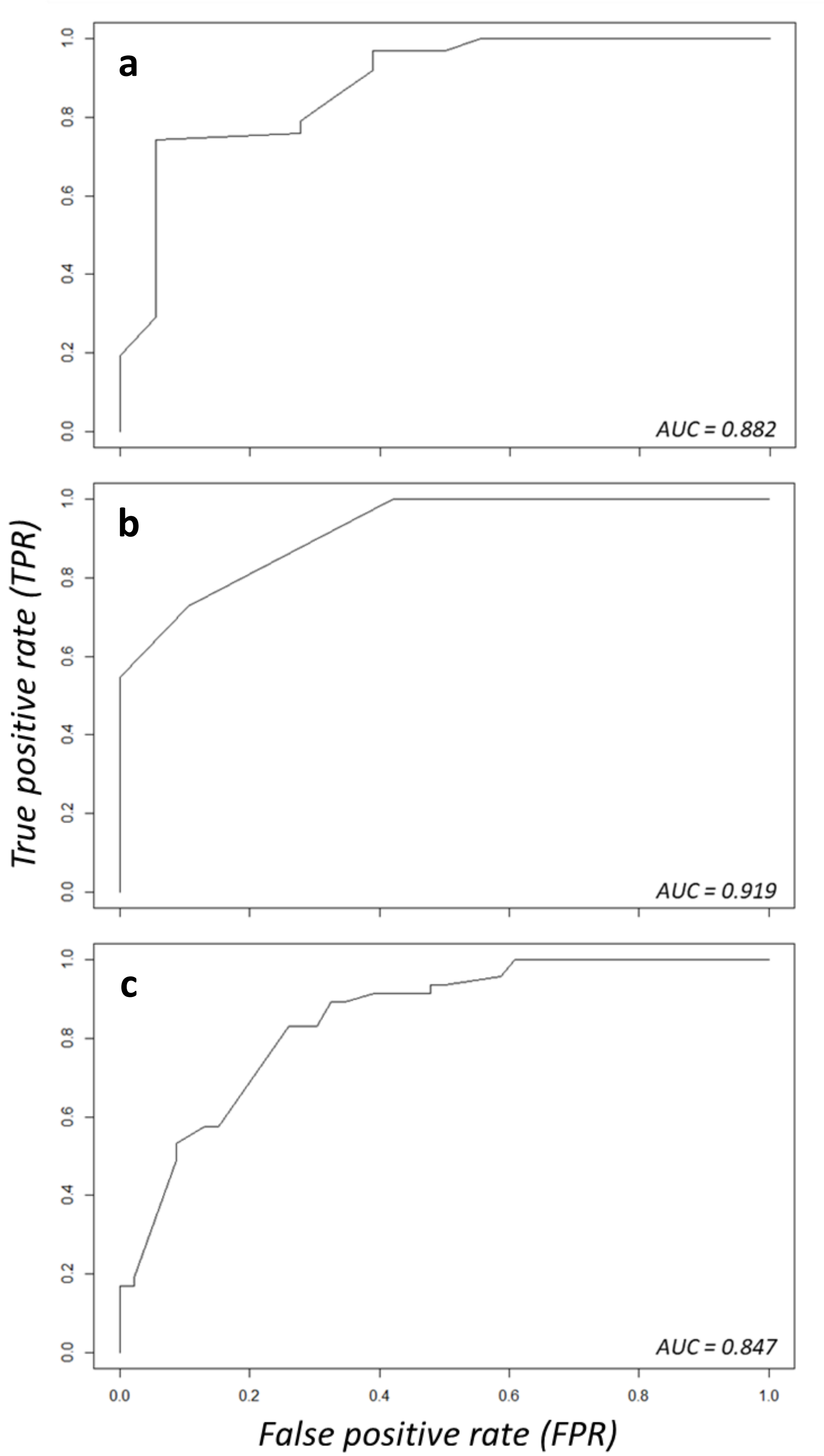
a
b
c
AUC = 0.882
AUC = 0.919
AUC = 0.847
True positive rate (TPR)
False positive rate (FPR)
0.0
0.2
0.4
0.6
0.8
1.0

Fig. 3

Table 1. Experimental overview of the study including all 37 treatment groups and two control (C) groups for American eel and bluegill. Size classes are reported for bluegill only (Sma; small, Med; medium, and Lar; large). Blade strike characteristics including blade width (Wid; mm), velocity (Vel; m/s), impact angle (Ang), location (Loc, with M; mid-body or H; head), orientation (Ort, with L; lateral, D; dorsal, and V; ventral). The total number in each group (N) is reported along with counts of observed (OMort), functional (FMort), and combined mortalities (CMort). Rates were calculated for observed and combined mortalities only. Results of one-tailed Chi-square test with Yates correction are presented as p-values for observed and combined mortality of each treatment group tested against the species' control group. We assumed α = 0.05; significant comparisons are in bold.

#	Species	Size	Wid	Vel	Ang	Loc	Ort	N	Number of Deaths			Rates			
									OMort	**FMort**	**CMort**	**OMort**	**p-value**	**CMort**	**p-value**
C	American eel	--	--	--	--	--	--	20	0	0	0	0.0	--	0.0	--
1	American eel	--	19	12.0	90	M	L	11	0	3	3	0.0	1.000	27.3	**0.034**
2	American eel	--	19	12.0	90	M	D	10	0	9	9	0.0	1.000	90.0	**<0.001**
3	American eel	--	19	13.6	90	M	L	20	3	3	5	15.0	0.115	25.0	**0.028**
4	American eel	--	19	13.6	90	M	D	11	0	11	11	0.0	1.000	100.0	**<0.001**
5	American eel	--	19	13.6	90	M	V	13	1	0	1	7.7	0.413	7.7	0.413
6	American eel	--	19	13.6	90	H	L	19	3	1	4	15.8	0.106	21.1	0.051
7	American eel	--	19	13.6	90	H	D	11	5	9	10	45.5	**0.003**	90.9	**<0.001**
8	American eel	--	19	13.6	90	H	V	16	0	0	0	0.0	1.000	0.0	1.000
9	American eel	--	26	12.0	90	M	L	15	1	0	1	6.7	0.442	6.7	0.442
10	American eel	--	26	12.0	90	H	L	15	0	0	0	0.0	1.000	0.0	1.000
11	American eel	--	26	12.0	90	H	D	15	3	11	11	20.0	0.138	73.3	**<0.001**
C	Bluegill	--	--	--	--	--	--	48	0	0	0	0.0	--	0.0	--
12	Bluegill	Med	26	7.7	90	M	L	18	16	17	18	88.9	**<0.001**	100.0	**<0.001**
13	Bluegill	Med	26	8.6	90	M	L	36	35	35	35	97.2	**<0.001**	97.2	**<0.001**
14	Bluegill	Sma	52	4.7	90	M	L	14	1	8	8	7.1	0.254	57.1	**<0.001**
15	Bluegill	Sma	52	5.3	90	M	L	15	5	13	13	33.3	**<0.001**	86.7	**<0.001**
16	Bluegill	Sma	52	6.1	90	M	L	14	10	13	14	71.4	**<0.001**	100.0	**<0.001**

17	Bluegill	Sma	52	7.3	90	M	L	14	12	14	14	85.7	**<0.001**	100.0	**<0.001**
18	Bluegill	Med	52	5.5	90	M	L	18	2	3	4	11.1	0.062	22.2	**0.003**
19	Bluegill	Med	52	6.4	90	M	L	18	9	15	15	50.0	**<0.001**	83.3	**<0.001**
20	Bluegill	Med	52	7.3	90	M	L	17	15	14	16	88.2	**<0.001**	94.1	**<0.001**
21	Bluegill	Med	52	9.1	90	M	L	17	16	14	16	94.1	**<0.001**	94.1	**<0.001**
22	Bluegill	Lar	52	6.4	90	M	L	18	18	18	18	100.0	**<0.001**	100.0	**<0.001**
23	Bluegill	Med	52	7.3	45	M	L	15	14	10	14	93.3	**<0.001**	93.3	**<0.001**
24	Bluegill	Med	52	8.0	45	M	L	15	13	14	14	86.7	**<0.001**	93.3	**<0.001**
25	Bluegill	Med	52	7.3	135	M	L	15	11	12	14	73.3	**<0.001**	93.3	**<0.001**
26	Bluegill	Med	52	8.0	135	M	L	15	12	9	13	80.0	**<0.001**	86.7	**<0.001**
27	Bluegill	Med	52	7.5	90	M	D	9	0	0	0	0.0	1.000	0.0	1.000
28	Bluegill	Med	52	8.7	90	M	D	17	10	11	13	58.8	**<0.001**	76.5	**<0.001**
29	Bluegill	Med	52	9.4	90	M	D	9	5	8	9	55.6	**<0.001**	100.0	**<0.001**
30	Bluegill	Med	52	7.5	90	M	V	9	0	0	0	0.0	1.000	0.0	1.000
31	Bluegill	Med	52	8.7	90	M	V	17	3	3	5	17.6	**0.011**	29.4	**<0.001**
32	Bluegill	Med	52	9.4	90	M	V	9	5	3	5	55.6	**<0.001**	55.6	**<0.001**
33	Bluegill	Med	52	7.1	90	H	L	14	0	0	0	0.0	1.000	0.0	1.000
34	Bluegill	Med	52	8.8	90	H	L	17	2	8	9	11.8	0.055	52.9	**<0.001**
35	Bluegill	Med	52	9.0	90	H	L	14	11	10	13	78.6	**<0.001**	92.9	**<0.001**
36	Bluegill	Med	52	8.0	45	H	L	15	1	8	9	6.7	0.268	60.0	**<0.001**
37	Bluegill	Med	52	8.3	45	H	L	13	0	0	0	0.0	1.000	0.0	1.000

Table 2. Results of two-tailed, pairwise comparisons using Chi-square test with Yates correction for observed and combined mortality rates of American eel and bluegill. Trials (treatment groups separated by a comma) being compared are referenced from data in Table 1. The main variable to be tested (Var) is listed with blade strike characteristics including blade width (Wid; mm), velocity (Vel; m/s), impact angle (Ang), location (Loc, with M; mid-body or H; head), orientation (Ort, with L; lateral, D; dorsal, and V; ventral). Rates of observed (OMort) and combined mortalities (CMort) are provided with p-values (p) for each comparison. We assumed α = 0.05; significant comparisons are in bold.

Species	**Var**	**Trials**	**Wid**	**Vel**	**Ang**	**Loc**	**Ort**	**OMort**		***p***	**CMort**		***p***
American eel	Wid	1, 9	19, 26	12.0	90	M	L	0 (0.0)	1 (6.7)	*0.873*	3 (27.3)	1 (6.7)	*0.374*
	Vel	1, 3	19	12.0, 13.6	90	M	L	0 (0.0)	3 (15.0)	*0.474*	3 (27.3)	5 (25.0)	*0.771*
		2, 4	19	12.0, 13.6	90	M	D	0 (0.0)	0 (0.0)	*1.000*	9 (90.0)	11 (100.0)	*0.961*
	Loc	3, 6	19	13.6	90	M, H	L	3 (15.8)	3 (15.8)	*0.707*	5 (21.1)	4 (21.1)	*0.930*
		4, 7	19	13.6	90	M, H	D	0 (0.0)	5 (45.4)	***0.021***	11 (100.0)	10 (90.9)	*0.500*
		5, 8	19	13.6	90	M, H	V	1 (7.1)	0 (0.0)	*0.473*	1 (7.1)	0 (0.0)	*0.203*
	Ort	1, 2	19	12.0	90	M	L, D	0 (0.0)	0 (0.0)	*1.000*	3 (27.3)	9 (90.0)	***0.014***
		3, 4	19	13.6	90	M	L, D	3 (15.0)	0 (0.0)	*0.474*	5 (25.0)	11 (100.0)	***<0.001***
		3, 5	19	13.6	90	M	L, V	3 (15.0)	1 (7.1)	*0.751*	5 (25.0)	1 (7.1)	*0.598*
		4, 5	19	13.6	90	M	D, V	0 (0.0)	1 (7.1)	*0.932*	11 (100.0)	1 (7.1)	***<0.001***
		10, 11	26	12.0	90	H	L, D	0 (0.0)	3 (20.0)	*0.224*	0 (0.0)	11 (73.3)	***<0.001***
Bluegill	BW	12, 20	26, 52	~7.5	90	M	L	16 (89.9)	15 (88.2)	*0.638*	18 (100.0)	16 (94.1)	*0.978*
		13, 21	26, 52	~8.8	90	M	L	35 (97.1)	16 (94.1)	*0.827*	35 (97.2)	16 (94.1)	*0.827*
	Vel	12, 13	26	7.7, 8.6	90	M	L	16 (89.9)	35 (97.1)	*0.529*	18 (100.0)	35 (97.2)	*0.721*
		18, 19	52	5.5, 6.4	90	M	L	2 (11.1)	9 (50.0)	***0.030***	4 (22.2)	15 (83.3)	***<0.001***
		18, 20	52	5.5, 7.3	90	M	L	2 (11.1)	15 (88.2)	***<0.001***	4 (22.2)	16 (94.1)	***<0.001***
		18, 21	52	5.5, 9.1	90	M	L	2 (11.1)	16 (94.1)	***<0.001***	4 (22.2)	16 (94.1)	***<0.001***
		19, 20	52	6.4, 7.3	90	M	L	9 (50.0)	15 (88.2)	***0.038***	15 (83.3)	16 (94.1)	*0.638*
		19, 21	52	6.4, 9.1	90	M	L	9 (50.0)	16 (94.1)	***0.012***	15 (83.3)	16 (94.1)	*0.638*
		20, 21	52	7.3, 9.1	90	M	L	15 (88.2)	16 (94.1)	*1.000*	16 (94.1)	16 (94.1)	*0.466*

	27, 28	52	7.5, 8.7	90	M	D	0 (0.0)	10 (58.8)	***0.012***	0 (0.0)	13 (76.5)	***<0.001***
	28, 29	52	8.7, 9.4	90	M	D	10 (58.8)	5 (55.6)	*0.797*	13 (76.5)	9 (100.0)	*0.312*
	27, 29	52	7.5, 9.4	90	M	D	0 (0.0)	5 (55.6)	***0.035***	0 (0.0)	9 (100.0)	***<0.001***
	30, 31	52	7.5, 8.7	90	M	V	0 (0.0)	3 (17.6)	*0.487*	0 (0.0)	5 (29.4)	*0.198*
	31, 32	52	8.7, 9.4	90	M	V	3 (17.6)	5 (55.6)	*0.122*	5 (29.4)	5 (55.6)	*0.379*
	30, 32	52	7.5, 9.4	90	M	V	0 (0.0)	5 (55.6)	***0.035***	0 (0.0)	5 (55.6)	***0.035***
	23, 24	52	7.3, 8.0	45	M	L	14 (93.3)	13 (86.7)	*1.000*	14 (93.3)	14 (93.3)	*0.464*
	25, 26	52	7.3, 8.0	135	M	L	11 (73.3)	12 (80.0)	*1.000*	14 (93.3)	13 (86.7)	*1.000*
	33, 34	52	7.1, 8.8	90	H	L	0 (0.0)	2 (11.8)	*0.553*	0 (0.0)	9 (52.9)	***0.005***
	34, 35	52	8.8, 9.0	90	H	L	2 (11.8)	11 (78.6)	***<0.001***	9 (52.9)	13 (92.9)	***0.041***
	33, 35	52	7.1, 9.0	90	H	L	0 (0.0)	11 (78.6)	***<0.001***	0 (0.0)	13 (92.9)	***<0.001***
Ang	20, 23	52	7.3	90, 45	M	L	15 (88.2)	14 (93.3)	*0.909*	16 (94.1)	14 (93.3)	*0.522*
	20, 25	52	7.3	90, 135	M	L	15 (88.2)	11 (73.3)	*0.909*	16 (94.1)	14 (93.3)	*0.522*
	23, 25	52	7.3	45, 135	M	L	14 (93.3)	11 (73.3)	*0.464*	14 (93.3)	14 (93.3)	*0.464*
	24, 26	52	8.0	45, 135	M	L	13 (86.7)	12 (80.0)	*1.000*	14 (93.3)	13 (86.7)	*0.464*
	34, 37	52	~8.6	90, 45	H	L	2 (11.8)	0 (0.0)	*0.588*	9 (52.9)	0 (0.0)	***0.006***
Loc	20, 33	52	~7.2	90	M, H	L	15 (88.2)	0 (0.0)	***<0.001***	16 (94.1)	0 (0.0)	***<0.001***
	21, 35	52	~9.1	90	M, H	L	16 (94.1)	11 (78.6)	*0.455*	16 (94.1)	13 (92.9)	*0.554*
	24, 36	52	8.0	45	M, H	L	13 (86.7)	1 (6.7)	***<0.001***	14 (93.3)	9 (60.0)	*0.084*
Ort	20, 27	52	~7.4	90	M	L, D	15 (88.2)	0 (0.0)	***<0.001***	16 (94.1)	0 (0.0)	***<0.001***
	20, 30	52	~7.4	90	M	L, V	15 (88.2)	0 (0.0)	***<0.001***	16 (94.1)	0 (0.0)	***<0.001***
	21, 29	52	~9.3	90	M	L, D	16 (94.1)	5 (55.6)	*0.064*	16 (94.1)	9 (100.0)	*0.742*
	21, 32	52	~9.3	90	M	L, V	16 (94.1)	5 (55.6)	*0.064*	16 (94.1)	5 (55.6)	*0.064*
	27, 30	52	7.5	90	M	D, V	0 (0.0)	0 (0.0)	*1.000*	0 (0.0)	0 (0.0)	*1.000*
	28, 31	52	8.7	90	M	D, V	10 (58.8)	3 (17.6)	***0.034***	13 (76.5)	5 (29.4)	***0.016***
	29, 32	52	9.4	90	M	D, V	5 (55.6)	5 (55.6)	*0.635*	9 (100.0)	5 (55.6)	*0.089*

Table 3. Observed mortality (OMort) among American eel and bluegill related to major injury categories for each species. One-tailed p-values were calculated from Chi-square test with Yates correction between the observed mortality rates of each injury category against mortality rate of total injured & uninjured fish of both species. We assumed α = 0.05. Significant comparisons are in bold. Notes provide additional injury or analysis details for observed mortalities.

Species	Category	Total	OMort	Rate	p-value	Notes
American eel	Injured & uninjured	176	16	0.091	--	--
	Integument	39	2	0.051	*0.312*	--
	Head	24	5	0.208	*0.080*	--
	Mouth cavity	40	8	0.200	***0.044***	7 of 8 had internal decapitation
	Pectoral fin	69	9	0.130	*0.247*	--
	Gill	4	0	0.000	--	Sample size too small to test
	Viscera	9	1	0.111	*0.349*	--
	Heart	4	0	0.000	--	Sample size too small to test
	Liver	51	3	0.059	*0.329*	--
	Gall bladder	2	0	0.000	--	Sample size too small to test
	Spleen	11	1	0.091	*0.294*	--
	Swim bladder	3	0	0.000	--	Sample size too small to test
	Stomach	1	0	0.000	--	Sample size too small to test
	Kidney	5	0	0.000	*0.463*	--
	Muscle	29	1	0.034	*0.255*	--
	Haemal spines	18	0	0.000	*0.188*	--
	Internal decapitation	21	7	0.333	***0.002***	--
	Caudal vertebrae	26	1	0.038	*0.301*	--
Bluegill	Injured & uninjured	450	226	0.502	--	--
	Integument	143	102	0.713	***<0.001***	94 of 102 had vertebral damage
	Head	1	0	0.000	--	Sample size too small to test
	Eye	34	17	0.500	*0.439*	--
	Operculum	11	7	0.636	*0.283*	--
	Fins (all)	13	6	0.462	*0.497*	--
	Gill	9	8	0.889	***0.025***	8 of 8 had vertebral damage
	Viscera	67	41	0.612	*0.061*	35 of 41 had vertebral damage
	Heart	18	8	0.444	*0.405*	--
	Liver	20	11	0.550	*0.425*	--
	Spleen	12	5	0.417	*0.385*	--

Intestine	1	1	1.000	--	Sample size too small to test
Swim bladder	224	184	0.821	***<0.001***	182 of 184 had vertebral damage
Gonads	53	38	0.717	***0.002***	36 of 38 had vertebral damage
Kidney	62	42	0.677	***0.007***	36 of 42 had vertebral damage
Muscle	74	41	0.554	*0.242*	--
Ribs	30	28	0.933	***<0.001***	28 of 28 had vertebral damage
Internal decapitation	36	15	0.583	*0.223*	--
Vertebrae	276	213	0.772	***<0.001***	--

Table 4. Results of a logistic regression of combined mortality and strike impact conditions and observed mortality and injury categories for bluegill and American eel. Coefficient estimates (Coeff; log odds), standard error (SE), odds ratio (OR) with 95% confidence interval (CI), p-value (p) assuming α = 0.05, and Akaike Information Selection Criteria (AIC) are provided using stepwise model selection. Significant variables are in bold.

Model	Variable	Coeff	SE	OR	OR (95% CI) Lower	OR (95% CI) Upper	p	AIC
Strike impact								
American eel	(Intercept)	3.01	0.775	--	--	--	**<0.001**	85.81
	Orientation [L]	-4.35	0.806	0.013	0.002	0.051	**<0.001**	
	Orientation [V]	-6.09	1.281	0.002	0.000	0.019	**<0.001**	
	Blade [26 mm]	-1.91	0.840	0.15	0.021	0.64	**0.023**	
Bluegill	(Intercept)	-13.89	2.114	--	--	--	**<0.001**	270.62
	Location [M]	4.37	0.578	79.3	27.3	266.7	**<0.001**	
	Orientation [L]	3.84	0.645	46.7	13.9	177.7	**<0.001**	
	Orientation [V]	-1.46	0.575	0.23	0.07	0.70	**0.011**	
	Velocity	1.16	0.189	3.2	2.2	4.7	**<0.001**	
Injury category								
Bluegill	(Intercept)	-3.57	0.446	--	--	--	**<0.001**	275.92
	Integument	1.33	0.392	3.80	1.81	8.50	**<0.001**	
	Operculum	1.72	1.138	5.57	0.75	65.5	0.131	
	Viscera	1.13	0.542	3.10	1.11	9.44	**0.037**	
	Liver	1.54	0.751	4.66	1.10	20.8	**0.040**	
	Swim bladder	0.88	0.503	2.43	0.88	6.49	0.078	
	Int. decapitation	2.93	0.603	18.7	5.94	64.3	**<0.001**	
	Vertebral fracture	3.68	0.601	39.5	12.7	140.6	**<0.001**	

Note: The logistic regression of American eel injury category against observed mortality was not significant and was omitted (see text for detail).