Rev Fish Biol Fisheries
DOI 10.1007/s11160-015-9416-8

REVIEWS

A fish-eye view of riverine hydropower systems: the current understanding of the biological response to turbine passage

Brenda M. Pracheil · C. R. DeRolph · M. P. Schramm · M. S. Bevelhimer

Received: 2 April 2015 / Accepted: 29 December 2015
© Springer International Publishing Switzerland (outside the USA) 2016

Abstract One-way connectivity maintained by fish passing through hydropower turbines in fragmented rivers can be important to population dynamics, but can also introduce a new and significant source of mortality. Sources of mortality during turbine passage can come from several sources including blade strike, shear forces, cavitation, or pressure decreases and parsing the contributions of these individual forces is important for advancing and deploying turbines that minimize these impacts to fishes. We used a national hydropower database and conducted a systematic review of the literature to accomplish three goals: (1) report on the spatial distribution of turbine types and generation capacities in the USA, (2) determine fish mortality rates among turbine types and fish species and (3) examine relationships between physical forces similar to those encountered during fish turbine passage and fish injury and mortality. We found that while Francis turbines generate 56 % of all US hydropower and have the highest associated fish mortality of any turbine type, these turbines are proportionally understudied compared to less-common and less injury-associated Kaplan turbines, particularly in the Pacific Northwest. While juvenile salmonid species in actual or simulated Kaplan turbine conditions were the most commonly studied, the highest mortality rates were reported from percid fishes passing through Francis turbines. Future studies should focus on understanding which species are most at-risk to turbine passage injury and mortality and, subsequently, increasing the diversity of taxonomy and turbine types in evaluations of turbine injury and mortality.

Keywords Turbine mortality · Barotrauma · Hydropower · River · Fish · Fish passage

This manuscript has been authored by UT-Battelle, LLC under Contract No. DE-AC05-00OR22725 with the US Department of Energy. The United States Government retains and the publisher, by accepting the article for publication, acknowledges that the United States Government retains a non-exclusive, paid-up, irrevocable, world-wide license to publish or reproduce the published form of this manuscript, or allow others to do so, for United States Government purposes. The Department of Energy will provide public access to these results of federally sponsored research in accordance with the DOE Public Access Plan (http://energy.gov/downloads/doe-public-access-plan).

Electronic supplementary material The online version of this article (doi:10.1007/s11160-015-9416-8) contains supplementary material, which is available to authorized users.

B. M. Pracheil (✉) · C. R. DeRolph · M. P. Schramm · M. S. Bevelhimer
Oak Ridge National Laboratory, Environmental Sciences Division, Oak Ridge, TN 37831-6036, USA
e-mail: pracheilbm@ornl.gov

Introduction

Fragmentation of fish populations by dams has been linked to population declines of many fish species (Reidy Liermann et al. 2012). Although the obstructive

Published online: 13 January 2016

properties of dams are fundamental to discussions of the impacts of dams on fish populations, some biological connectivity can remain between segments of dam-fragmented populations even in the absence of mitigated fish passage. Hydropower dams, for instance, allow for one-way connectivity as upstream populations are connected to downstream populations via turbine entrainment; that is, movement of fish through hydropower turbines of dams into downstream habitats. Numbers of fish entrained can be substantial and may be important to maintaining population dynamics (Jager 2006; Pracheil et al. 2014). However, turbine entrainment injury and mortality can be substantial even at facilities with mitigated fish passage, potentially having population-level effects. For instance, turbine entrainment mortality for some fish species can exceed 25 % for some turbine types and blade velocities (GeoSense 2011). Conversely, turbine entrainment mortality can also be relatively low for other types (3–5 %; Čada 2001), suggesting that decreases in turbine injury and mortality rates are possible.

Turbine-associated injury and mortality comes from a variety of forces encountered by fish in the turbine environment, namely, shear forces, turbulence, cavitation, pressure, and blade strike or other mechanical wounding of fish (Čada 2001; Fig. 1). Primary sources of injury and mortality vary with fish age and size. For example, shear and turbulence are important sources of mortality for fish during early life history while blade strike or other mechanical wounding becomes more important as fish get older and larger (Coutant and Whitney 2000). Barotrauma caused by rapid pressure change can affect fish of all ages, although it may be more important at specific points in life history than in others (Brown et al. 2014). There is some understanding of how relationships among injury and mortality sources and fish life history might interact, but these understandings are largely qualitative and unsynthesized across studies. Focused quantitative studies or models that can extrapolate our understanding of turbine-associated injury and mortality across projects, turbine types, or turbine operating efficiencies are precluded as a result.

Quantifying injury and mortality rates and how they are partitioned among sources is critical for helping turbine manufacturers, water resource engineers, and regulators understand how to cost-effectively evaluate and reduce these risks to fishes. Modifying turbine operation schemes (e.g., flow rates, wicket gate setting, daily timing, etc.) and designing new turbines that minimize fish injury and mortality requires quantifying biological thresholds at both the individual (i.e., dose–response relationships between discrete physical forces and individual fish injuries or mortality) and population (i.e., percentage of fish injured or killed during turbine entrainment) levels that can allow parameterization of fish injury and mortality models. Unfortunately, our current understanding of the biological response to turbine designs between and among sources of entrainment injury or mortality has not been informed by a diversity of fish species, life history stages, or sizes. Moreover, relationships between and among these physical forces and variations in fish morphology, behavior or life history stage are complex and not well-quantified leaving many knowledge gaps that must be filled as we create and test new advanced turbine technologies and hydropower generation schemes.

To contribute to a better understanding of how fish are affected by turbine passage that can lead to further development of fish-friendly technologies, we present a baseline understanding of the biological response of fishes to turbine passage at both individual and population scales. Specifically, we (1) evaluated fish mortality rates among turbine types and fish species, (2) examined relationships between physical forces similar to those encountered during fish turbine passage and fish injury and mortality. We also determined geographic regions and fish taxa most at risk to turbine passage.

Ultimately, the impact of injury and mortality to turbine passed fish will need to be evaluated in a population-level context. Understanding the relationships between the magnitude of various stressors and individual fish response as presented in this paper is a critical first step in parameterizing population models that can be used to evaluate species management and conservation concerns. In addition, characterizing these relationships by taxa and turbine type will allow for a much larger inference space and development of models that can be more tailored to a specific species.

Materials and methods

Systematic review of fish species and life history stages reported as entrained by turbines

We conducted a systematic review of the literature using established criteria for inclusion or exclusion of

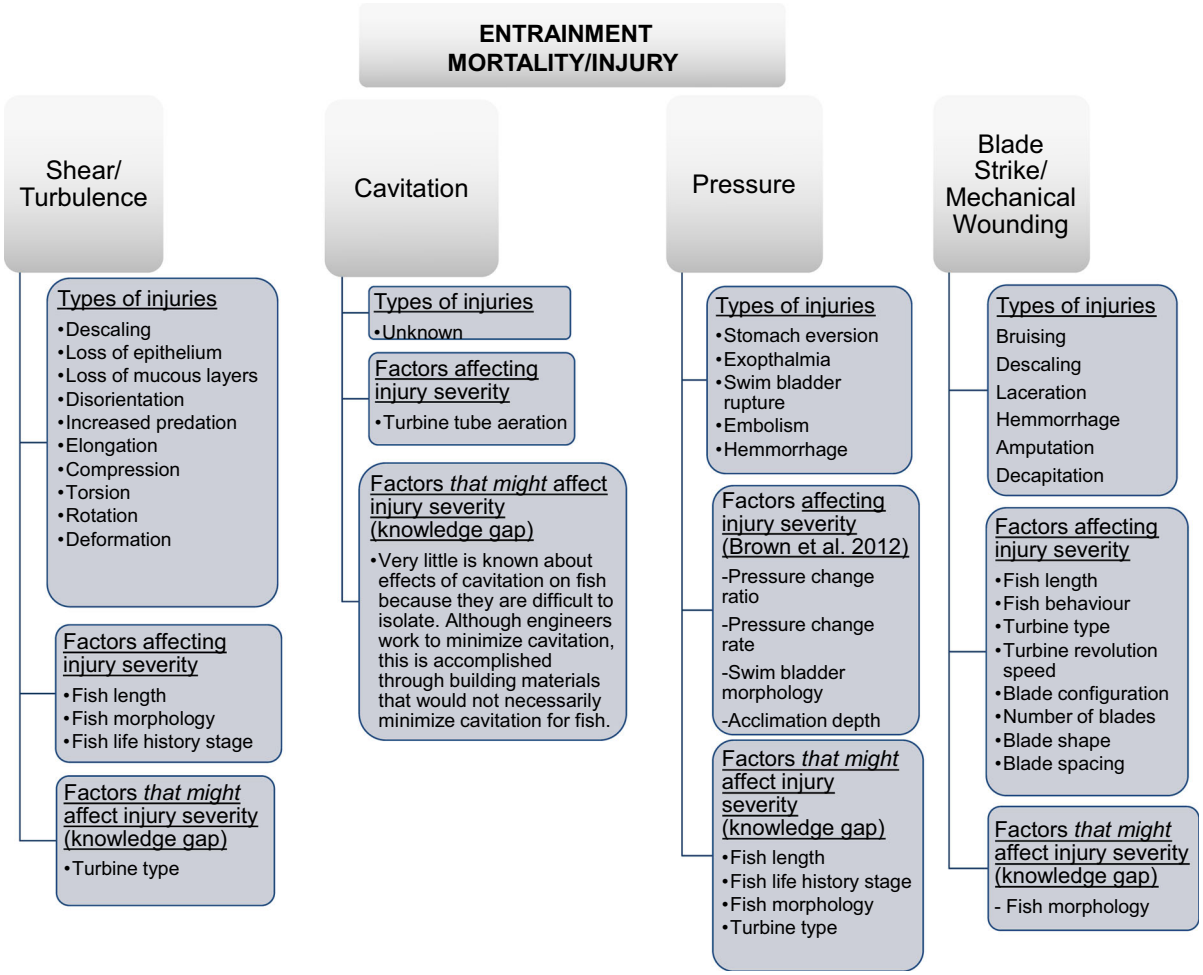

Fig. 1 Types of injuries, factors contributing to injury, and knowledge gaps among physical forces contributing to injury and mortality during downstream fish passage through turbines

studies in the database prior to beginning the study (CEE 2013). We conducted our search using Google Scholar accessed 15–16 December 2014 using the first 200 results from each of the search terms "hydropower entrainment", "hydropower fish entrainment", and "fish turbine entrainment". We additionally searched the literature cited sections of references found in the Google Scholar search. Although our Google Scholar search turned-up 600 records (3 search terms × 200 results), we identified 377 potentially related references, 23 of which contained useful data on fish turbine entrainment (e.g., fish species names and/or numbers indicating how many fish were entrained) that were entered into our database and summarized (Appendix A of supplementary material). In cases where two references used the same data, such as a report and a peer-review publication from the same study or a report that used data from multiple sources (e.g., Normandeau Associates Inc. and Gomez and Sullivan Engineers, P.C. 2012), we included data from the most inclusive source only. In Appendix A of supplementary material, each line represents findings from one life stage of one species in one study.

Systematic review of physical force and turbine-associated injury and mortality

We conducted a systematic review of the literature using established criteria for inclusion or exclusion of studies in the database prior to beginning the study (Collaboration for Environmental Evidence (CEE) 2013). We conducted our search using Google Scholar

accessed 15–30 January, 2014 using the first 200 results from each of the search terms "fish pressure", "fish pressure injury", "fish pressure mortality", "fish barotrauma", "fish barotrauma injury", "fish barotrauma mortality", "fish blade strike", "fish blade strike injury", "fish blade strike mortality", "fish shear", "fish shear injury", "fish shear mortality", "fish cavitation", "fish cavitation injury", "fish cavitation mortality", "fish turbine injury", and "fish turbine mortality". We additionally searched the literature cited sections of references found in the Google Scholar search. Although the Google Scholar search turned-up 3400 records (17 search terms × 200 results), we identified 200 potentially related references, 26 of which contained useful data on turbine-induced injury and turbine passage survival that was entered into our database (e.g., provided pressure and or force values as well as fish injury or mortality descriptions that could be used in a meta-analysis; Appendix B of supplementary material). In cases where two references used the same data, such as a report and a peer-review publication from the same study, we included data from the more extensive source only, which was typically the report. We did not restrict the spatial extent of the studies included, but nearly all studies were from North America. In Appendix B and C of supplementary material, each line of data represents treatment means or treatment percentages from one life stage of one species in one study.

From the articles identified in our systematic review, we extracted common and scientific names, life history stage, fish length (mm), number of fish included per treatment/trial/species group (each treatment group constituted a separate record in the database), mean depth of fish in experiment (m), maximum pressure (kPa), minimum pressure (kPa), pressure change (maximum pressure-minimum pressure), proportional pressure change (maximum pressure/minimum pressure), reported survival rate (%), survival rate evaluation period (h), injury rate (% of population) with particular types of injuries (stomach eversion, exophthalmia, ocular emphysema—specifically corneal emphysema, fin membrane emphysema, prolapsed cloaca, swim bladder expansion, swim bladder rupture, hemorrhage, organ torsion, arterial embolism). This database table contained 186 records from 17 studies (Appendix B of supplementary material). Our search terms also returned many studies on impacts of rapid pressure decreases associated with commercial and recreational harvest, some of which were also included in this database.

Our database also contained a table of published literature reports of physical force-associated injury and mortality. From these articles, we extracted species' common and scientific names, life history stage, fish length, number of fish included per treatment/trial/species group (each treatment group constituted a separate record in the database), turbine type, location, river, dam head height (m), turbine discharge (m^3s^{-1}), mortality rate (%), mortality rate evaluation period (h), barotrauma rate (%), blade strike rate (%), and scale loss rate (%). This database contained 502 records from 10 studies (Appendix C of supplementary material).

Spatial analysis of turbine passage

To provide spatial and taxonomic context to our understanding of the biological response to hydropower turbine passage, we merged data collected during our systematic review with hydropower project data from the National Hydropower Asset Assessment Program (NHAAP; Kao et al. 2014) database. The NHAAP database contains spatial data on hydropower plants including nameplate capacity, turbine types, and mode of operation (i.e., hydropeaking, run-of-river, reregulating, etc.). We also merged the NHAAP database with the NatureServe North American freshwater fish database—a database giving spatial range extent information for nearly all freshwater fish species in the USA—to determine which species had the greatest potential exposure to turbine passage as measured by the number of turbines in a species range. We used this information to determine (1) the spatial distribution of hydropower across the United States by turbine type and plant nameplate capacity, (2) the spatial distribution of fish genera tested in turbine mortality studies for Francis and Kaplan turbines (the two most common turbine types), and (3) the fish species with the greatest number of Francis turbines (the most abundant turbine) within their species ranges. We did not examine the spatial distribution of barotrauma studies because studies simulating instantaneous pressure drops characteristic of hydropower turbine passage must be conducted in a laboratory setting and the effects of barotrauma such as that encountered in a hydropower system have been

studied for few species. More than 80 % of the data points in the turbine mortality database focused on Francis and Kaplan turbines. All other single turbine types represented <10 % of the observations in the database, so we restricted our spatial analysis to Francis and Kaplan turbines.

Meta-analysis

We hypothesized that turbine mortality would differ among turbine types and fish species. To determine how turbine-associated fish mortality varied among turbine type, we calculated mean (±SE) survival of fish passing through all turbine types where there were >10 records. These means were calculated as the mean (±SE) percent survivals reported across studies. We also calculated the mean (±SE) survival of fish by family and genus for each turbine type.

We searched for thresholds and relationships between physical forces encountered by fish during turbine passage and injury and mortality. Specifically, we visually inspected plots for threshold relationships between physical forces and mortality rates. We used a simple linear regression analysis to describe relationships between the percent of fish in a study treatment with a particular injury type (i.e., exophthalmia, ocular emphysema, membrane emphysema, hemorrhage, stomach eversion) and percent survival. We hypothesized that increasing the ratio of maximum to minimum pressure would result in decreasing survival and conducted a simple linear regression to test this hypothesis. We also conducted a simple linear regression between percent survival reported in a study and the percent of a study population with an injury type to determine injury severity. The rationale here was that the most serious decompression injuries would be associated with high average mortality on a population-level.

Results

Fish species and life history stages involved in turbine entrainment studies

Our review of fish entrainment literature showed that entrainment of juvenile salmonid fishes is far and away the most commonly studied or reported on fish species or life stage in entrainment studies- (Fig. 2). This is likely because juveniles are the primary life stage of salmonids making downstream migrations and downstream migrations are intrinsic to completing their life cycle. In fact, juvenile fishes are the most common life stage examined or reported as entrained in entrainment studies for nearly all species of fish even though some adult fish undergoing spawning migrations may "fall back" after passing upstream past a dam and pass back through turbines. A small percentage of adult steelhead called kelts, will spawn multiple times and will perform multiple downstream migrations through turbines (Colotelo et al. 2013).

Spatial distribution of hydropower

Hydropower is not homogeneously located among US hydrologic regions; by far, the most hydropower is generated in the Pacific Northwest (Fig. 3). The second most hydropower is generated in the California hydrologic region, although the nameplate capacity in the California hydrologic region is less than half that of the Pacific Northwest.

Francis turbines are the most frequent turbine type and are also capable of generating the most power—56 % of all potential conventional hydropower generation in the USA is provided by Francis turbines (Fig. 3). Not only are Francis turbines the most common overall in the USA, but they are also the most common in every hydrologic region except the Mid-Atlantic where Deriaz turbines—a propeller turbine similar to a Kaplan turbine with inclined blades suitable for higher heads—are more common.

Turbine mortality

Francis turbines were associated with the highest mortality and Kaplan turbines the lowest (Fig. 4). Cross flow turbines had similar associated mortality rates to Francis turbines, although we found reports of mortality rates for only four taxa compared to 20 taxa for Francis turbines and 13 taxa for Kaplan turbines (Fig. 4, Table 1). Most taxa whose entrainment mortality has been reported for Francis turbines had mean mortality rates >20 % and several taxa had >30 % mean mortality including *Notropis* sp., *Sander* sp., *Perca* sp., *Salmo* sp., *Salvelinus* sp. (>50 % mean mortality, but only one study included), and unspecified salmonids (Table 1).

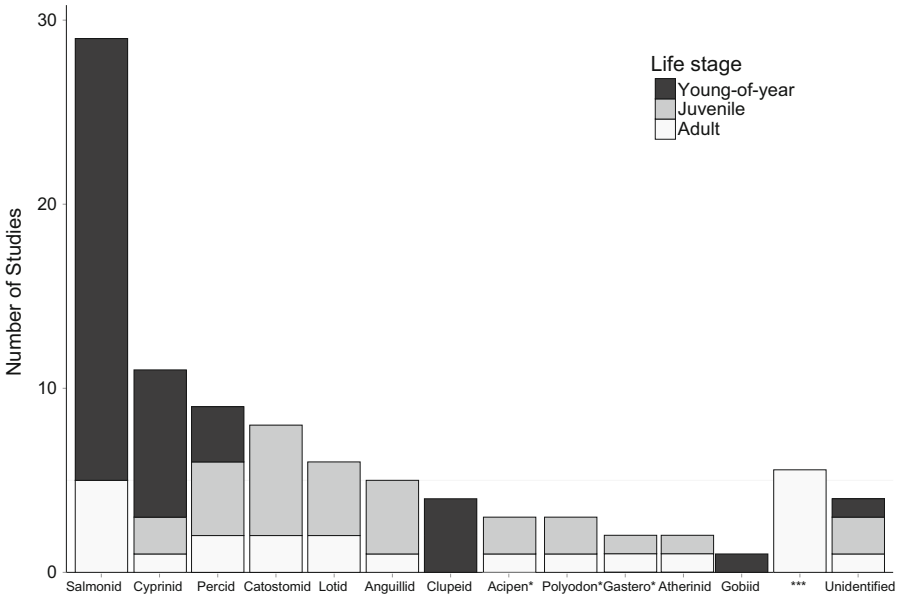

Fig. 2 Number of studies reporting turbine entrainment of listed fish families by life history stage. If a study reported entrainment of more than one life history stage, that study was counted toward totals of all life history stages included. *Abbreviated families are as follows: *Acipen* Acipenseridae, *Polyodon* Polyodontidae, *Gastero* Gasterosteidae. ***Contains information from six families: Petromyzontidae, Phycidae, Pleuronectidae, Scophthalmidae, Stromateidae, and Syngnathidae—each with one study containing only adults

We found few fish species with mortality rates reported for multiple turbine types, so we were unable to make direct comparisons of mean mortality rates among turbine types for most taxa. Turbine-associated mortality has been studied in Francis and Kaplan turbines for both *Perca* sp. and *Sander* sp. and mean mortality rates associated with Kaplan turbines are much lower (Table 1). For instance, the mean mortality of *Perca* sp. was only 5 % in Kaplan turbines compared to 31 % in Francis turbines (Table 1). Similarly, mean mortality of *Sander* sp. was 14 % in Kaplan turbines compared to 39 % in Francis turbines (Table 1). Two salmonid genera, *Onchorhynchus* and *Salmo* have mean mortality rates reported for all three turbine types discussed in this study (Table 1). Interestingly, crossflow turbines have the highest mean mortality rates in *Oncorhynchus* sp. (Francis: 26.2 %, Kaplan: 8.6 %, crossflow: 32.4 %) and Francis turbines have the highest mean mortality rate in *Salmo* sp. (Francis: 30.1 %, Kaplan: 9.2 %, crossflow: 12.1 %; Table 1). Mean mortality rates are similar in both genera for Francis and Kaplan turbines.

Studies conducted on turbine mortality of Francis and Kaplan turbines focus on different hydrologic regions and different types of species. Studies reporting turbine mortality of Francis turbines are focused in the eastern US, particularly in the Great Lakes hydrologic region where the number of studies was nearly an order of magnitude greater than in any other hydrologic region (Fig. 5). In contrast, the greatest number of studies of Kaplan turbines occurred in the Pacific Northwest hydrologic region where there were three times as many studies conducted as in the second most studied region (the Great Lakes; Fig. 5). This is especially interesting because the Pacific Northwest has the capacity to generate more hydropower than any other hydrologic region and a majority of its hydropower is generated by Francis turbines (Fig. 3). This is a common pattern, in fact, where the frequency of turbine type studied is not reflective of the relative abundance of turbines in a hydrologic region. Kaplan turbines are also proportionally oversampled in the Tennessee and New England hydrologic regions, but are proportionally under-sampled in the Ohio hydrologic region.

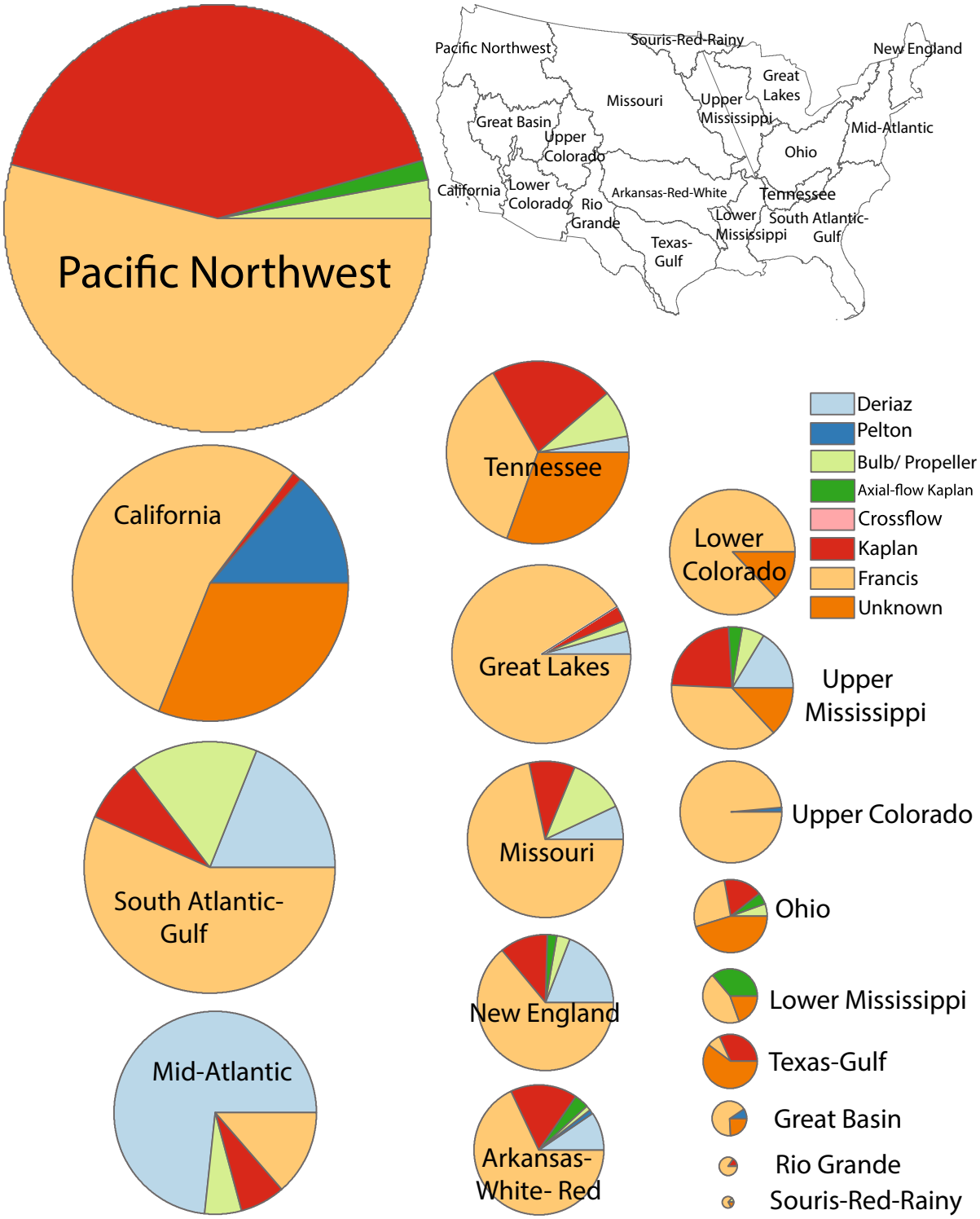

Fig. 3 Hydropower nameplate capacity by turbine type (MW of installed capacity) and USGS Hydrologic Region (HUC-2) and includes both Federal Energy Regulatory Commission (FERC) licensed hydropower projects and FERC license exempt federal hydropower projects. Totals were compiled from the National Hydropower Asset Assessment Program (NHAAP) database. Size of *pie graph* represents relative amount of hydropower produced in a HUC-2

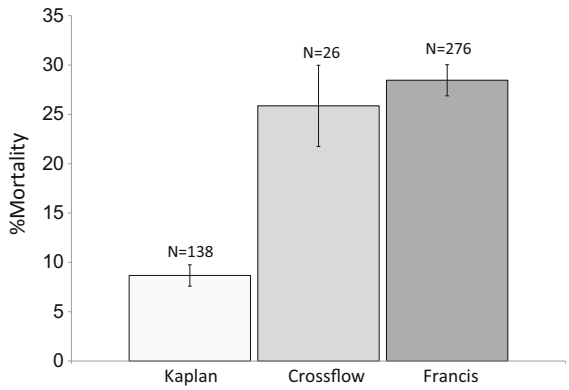

Fig. 4 Percent mortality ± standard error from literature reported values of turbine-associated mortality by turbine type. N is the number of data points. In many cases, multiple data points were obtained from a single study

Values of fish injury and mortality related to pressure changes

Although we set out to measure the biological effects of multiple physical forces encountered by fishes as they move through turbines, we uncovered very few studies on forces other than pressure. As a result, the results of our meta-analysis are restricted to the effects of pressure changes on fishes. However, because fish are exposed to multiple stressors during turbine passage and our systematic review process did not discover or include all reports and journal articles for a variety of reasons (i.e., published after Google Scholar accession date, internal reports that did not appear in our Google Scholar searches, not found via keyword searches), we added additional references to allow for discussion of additional turbine stressors on fishes.

We recorded 10 different injuries in response to rapid pressure decreases from 186 records we extracted from 17 studies (Table 1). Our efforts resulted in 56 instances of stomach eversion, 72 of exophthalmia, 58 of tight swim bladders, 52 of hemorrhage, 36 of corneal emphysema, 32 of membrane emphysema, 20 of prolapsed cloaca, 20 of arterial embolism, 14 of ruptured swim bladders, and 14 of organ torsion. Exophthalmia, ocular emphysema, and prolapsed cloaca were the most severe pressure-associated injuries each having <35 % of the population with those injuries surviving (Table 1). Swim bladder distention was the least serious injury and was associated with >70 % of the population with this injury surviving (Table 2).

Thresholds and relationships between physical forces encountered by fish during turbine passage and injury and mortality

The data we compiled from the literature was insufficient to identify thresholds between in-turbine physical forces encountered by fish and biological responses. However, we were able to identify direction of relationship between pressure and several injury types. We found that as the ratio of maximum pressure to minimum pressure encountered by a fish increased, survival decreased ($r^2 = 0.342$, $P < 0.001$, 120 *df*; Fig. 6), and certain injuries, namely, exophthalmia ($r^2 = 0.211$, $P < 0.001$, 72 *df*; Fig. 7), ocular emphysema ($r^2 = 0.223$, $P = 0.004$, 34 *df*; Fig. 7), and stomach eversion ($r^2 = 0.305$, $P < 0.001$, 56 *df*; Fig. 7) increased.

Discussion

This is the first synthesis of studies reporting turbine-associated mortality across turbine types. Large standard deviations relative to the means for mortality rates of several species, especially for Francis turbines, suggest that mortality rates can be highly variable among projects and hydropower generation regimes. More field and laboratory work that examines a wider range of species at a wider range of operating conditions and efficiencies can help to lend an understanding of operating conditions and plant and turbine specifications associated with the highest and lowest fish mortalities for creating more fish-friendly hydropower. However, turbine-associated injury and mortality rates may have high natural variability. High natural variability may be expected even among individuals of the same fish species being entrained through the same turbine because of the many possible paths fish may take during entrainment and the wide-ranging stressor values that may be encountered during entrainment (Garrison et al. 2002; Deng et al. 2005; Cada et al. 2006). Pressure, for instance, can vary several orders of magnitude across the turbine surface such that even two fish of the same species that pass through a turbine at virtually the same time can experience very different pressure-related injuries (Richmond et al. 2014).

The basic, if not, rudimentary relationships in some cases between stressors and injury or mortality rates

Table 1 Per treatment mean % ±SD of turbine-associated mortality from the literature by fish family and genus by turbine type

Family	Genus	Studies	Mean mortality ± SD (%)
Francis			
Anguillidae	***Anguilla***	**5**	**10.9 ± 13.0**
Catostomidae	*Catostomus*	20	16.3 ± 23.0
Centrarchidae	*Ambloplites*	1	96
	Lepomis	22	14.8 ± 19.8
	Micropterus	8	14.0 ± 9.6
	Pomoxis	1	100
	Unspecified	7	29.4 ± 32.5
Clupeidae	***Alosa***	**11**	**24.3 ± 2.3**
Cyprinidae	*Notemigonius*	2	13.1 ± 9.8
	Notropis	3	31.8 ± 7.2
	Unspecified	7	12.5 ± 4.5
Esocidae	*Esox*	5	22.7 ± 15.5
Ictaluridae	*Ictalurus*	1	6.0
Percidae	*Perca*	9	31.0 ± 26.6
	Sander	7	39.4 ± 28.5
	Unspecified	11	45.5 ± 24.2
Salmonidae	***Oncorhyncus***	**47**	**26.2 ± 21.0**
	Salmo	**8**	**30.1 ± 26.9**
	Salvelinus	**1**	**57**
	Unspecified	**17**	**31.3 ± 28.3**
Kaplan			
Anguillidae	***Anguilla***	**3**	**25.7 ± 10.6**
Centrarchidae	*Lepomis*	6	8.3 ± 5.9
	Micropterus	3	2.7 ± 0.6
	Unspecified	6	4.7 ± 2.1
Clupeidae	***Alosa***	**12**	**7.2 ± 6.0**
Cyprinidae	*Notemigonius*	1	8.0
Esocidae	*Esox*	2	22.5 ± 4.9
Ictaluridae	*Ictalurus*	4	10.8 ± 5.7
Percidae	*Perca*	4	5.0 ± 2.9
	Sander	4	13.8 ± 2.8
Salmonidae	***Oncorhyncus***	**68**	**8.6 ± 16.5**
	Salmo	**8**	**9.2 ± 6.9**
	Unspecified	**6**	**5.3 ± 4.6**
Crossflow			
Clupeidae	***Alosa***	**1**	**10.0**
Moronidae	***Morone***	**4**	**15.9 ± 2.4**
Salmonidae	***Oncorhyncus***	**17**	**32.4 ± 23.4**
	Salmo	**4**	**12.1 ± 7.3**

We included only the three most commonly studied turbine types: Kaplan, Francis, and crossflow. Marine, brackish and anadromous fishes are shown in bold. Each treatment in a study = one data point

within or among fish species may not have adequately high precision on which to base endangered species and other regulatory decisions or to evaluate turbine technologies, but the estimates and relationships derived in our meta-analysis are still quite valuable. Relative relationships and numbers we present can provide useful starting values in population and other models used to evaluate the impacts of hydropower on

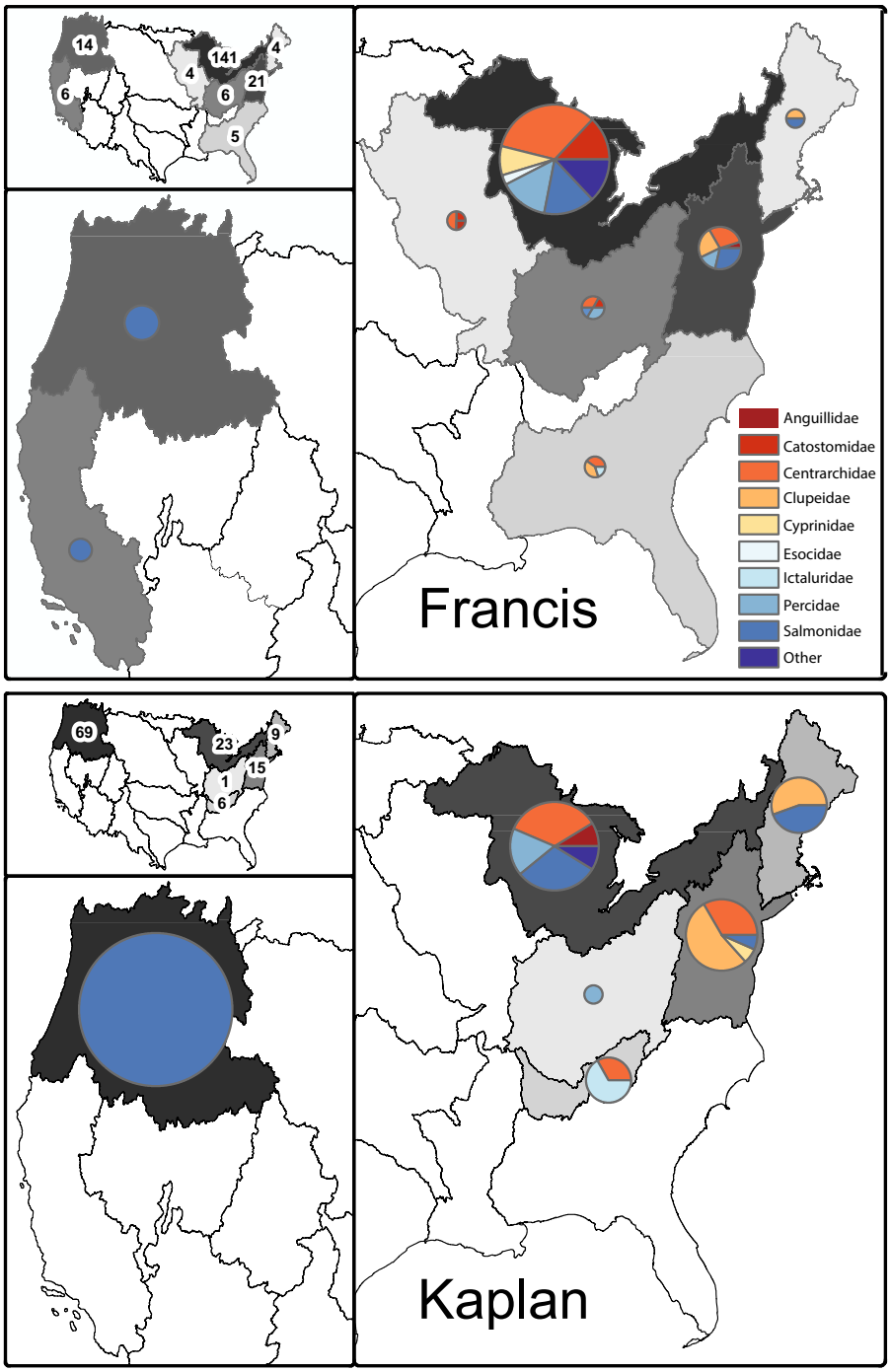

Fig. 5 Distribution of turbine mortality studies by turbine type (Francis: *top set of maps*, Kaplan: *bottom set of maps*) and fish family. Size of *pie charts* is representative of number of study treatments in a USGS hydrologic region. Numbers in *upper left panel* represent numbers of study treatments conducted in a region

fish populations. Injury and mortality rates as well as injury types and prevalence vary widely among turbine types and fish species. Scaling our understanding from the individual fish-level—where experiments are conducted—to the population-level—where regulatory actions are taken—is the ultimate

Table 2 Average per treatment percent survival ± SD of fish with an injury type after subjection to pressure decreases (mean ± SD) irrespective of fish species

Injury	Average % survival
Swim bladder distention	73.80 ± 26.44
Membrane emphysema	66.43 ± 34.28
Stomach eversion	66.34 ± 30.56
Arterial embolism	63.41 ± 35.12
Hemorrhage	47.39 ± 31.14
Organ torsion	45.79 ± 23.29
Swim bladder rupture	37.52 ± 31.39
Exophthalmia	32.12 ± 26.37
Ocular emphysema	30.02 ± 22.51
Prolapsed cloaca	26.65 ± 24.49

The ratio of mean max absolute pressure: mean min absolute pressure across these studies was 5.1 ± 3.3

step in understanding the true impacts of hydropower on fish. Currently, there are not published estimates of mortality by species and turbine type that are useful for informing models that extrapolate impacts of hydropower from the individual to the population-level. When models are constructed, estimates are often borrowed from other species or turbine types. The estimates we provide add an additional layer of reality to population models seeking to understand the effects of downstream turbine passage on fish populations such as those developed for white sturgeon and other riverine fishes in general (Jager et al. 2001; Jager 2006).

Most of our knowledge of the biological impacts of fish entrainment and in-turbine conditions on fish comes from passage of juvenile salmonid fishes through Kaplan turbines: study species and conditions that are not broadly representative of US fish species and hydropower in general. For example, Kaplan turbines have the lowest associated mortality of any turbine examined in this study, with an average of 8 % mortality across species reported in the literature. Francis turbines, on the other hand, have an average of approximately 28 % mortality across species reported in the literature. Furthermore, Francis turbines are linked to significant mortality of many taxa of concern including salmonids and percids that may have >30 % mortality. Species in these families are frequently of conservation concern and also contain highly valuable sport fishes such as all species of trout and salmon (Salmonidae) and walleye and yellow perch (Percidae) that may be the source of regulatory concern during the relicensing process. It is therefore clear that future studies should focus on gaining a more comprehensive understanding of biological responses of

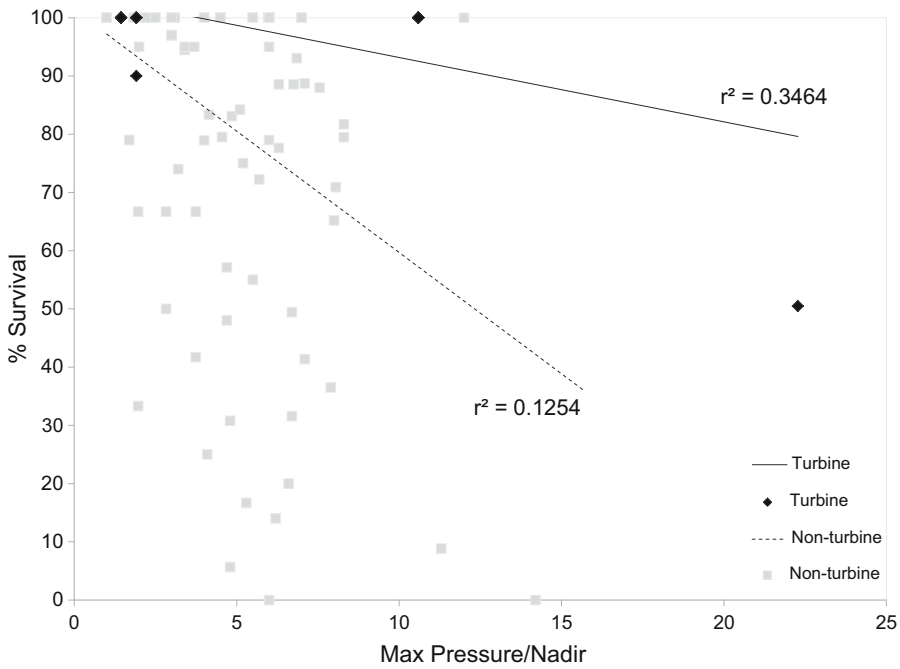

Fig. 6 Percent of study population surviving following a decrease in absolute pressure for studies simulating in-turbine conditions with instantaneous pressure drops (*black diamonds*, *solid best-fit line*) and those from studies of recreational and commercial fishing barotrauma (*gray squares, dashed best-fit line*)

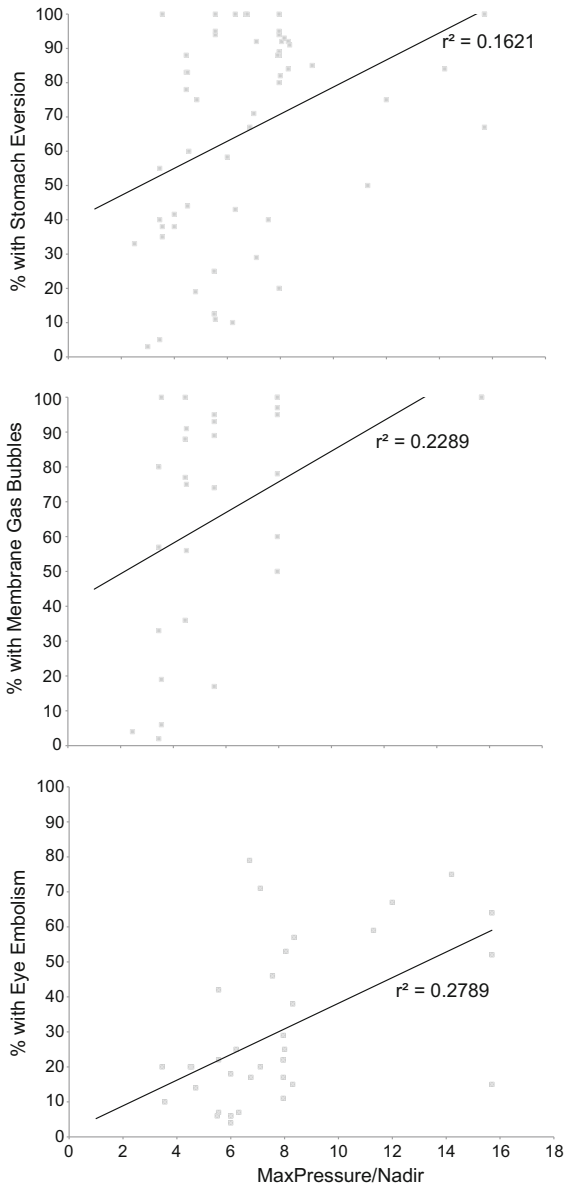

Fig. 7 Percent of study population that developed stomach eversion (*top panel*), fin membrane emphysema (*middle panel*) or ocular emphysema (*bottom panel*) as a result of rapid absolute pressure decreases. Only data from studies of recreational and commercial fishing barotrauma are shown due to lack of data in studies simulating in-turbine conditions

fishes to Francis turbines. Also interesting was the lack of studies looking at fish mortality associated with Deriaz turbines—a common turbine-type across the eastern US that is similar to Kaplan turbines, only suitable for dams with higher head pressures. Mortality estimates from Kaplan turbines may also provide fair, but likely under- estimates, of mortality caused by Deriaz turbines.

Eel, such as the American eel *Anguilla rostrata* were of particular interest in our summary of turbine passage mortality because they are currently a candidate species for federal endangerment status in the USA. If the conservation status of American eel is elevated to federally endangered, their protection has the potential to impact approximately 1/3 of US hydropower generation, particularly that on the Atlantic coast portion of their range (Jager et al. 2013). Contrary to findings for most fish taxa, our meta-analysis suggests that adult eels incur higher mortality passing through Kaplan turbines (25.7 ± 10.6 %) versus Francis turbines (10.9 ± 13.0 %). Downstream passage is of primary concern for this species because adult American eel make multiple spawning migrations throughout their lifetime potentially exposing them to turbine passage several times as adults return to the ocean. The potentially imminent federal listing of this species points to the need for a highly accurate understanding of adult eel mortality rates particularly with respect to Deriaz turbines which are common on the east coast. An enhanced understanding of this relationship potentially through expanded field and laboratory studies is especially important because published literature suggests that eel movement through Deriaz turbines may yield high mortality rates due to their similarity to Kaplan turbines.

Many forces are responsible for fish injury and mortality during turbine passage including shear, pressure, blade grinding, pinching and/or strike (Fig. 1). While it is not clear from these studies exactly what factor or factors are responsible for differences in mortality rates among turbine types, we suspect that blade strike may be the most significant factor. For example, prior studies have shown that both Kaplan (Trumbo et al. 2014) and Francis (Duncan and Carlson 2011) turbines can have an absolute nadir pressure near 0 kPa which can cause severe barotrauma. Despite similar pressure profiles between these turbine types, Francis turbines have a much higher mortality rate (Fig. 4). Moreover, the distribution of pressures across a turbine surface show that very low pressures such as those associated with barotrauma are rare across a turbine surface and are not commonly encountered by fish (Richmond et al. 2014). Similarly, cross-flow turbines have many more

blades than a Kaplan turbine but operate at much lower head pressures, and likely nadir pressures, than typical Francis or Kaplan turbines. Cross-flow turbines, nevertheless, also have substantially higher mortality than Kaplan turbines. Blade spacing and number are two of key components of models that estimate fish blade strike (along with fish length; e.g., Ferguson et al. 2008; Deng et al. 2007), and Francis and crossflow turbines contain many more blades that are closer together than Kaplan turbine blades. Future work should focus first on characterizing the range of forces exerted by stressors on fishes across many turbine types. This would allow for the design of laboratory experiments that seek to understand the biological impacts of in-turbine stressors that can be used to reduce environmental impact of new and existing turbines.

Literature describing effects of rapid pressure decreases on fish were abundant compared to that examining effects of other forces (e.g., shear force, cavitation). Even so, with the exception of one study that provides a dose–response relationship for juvenile Chinook salmon (Brown et al. 2012a), but not for adults that could be subject to "fall-back" entrainment through turbines while migrating upstream, an informative, dose–response curve could not be constructed for any species or across species from literature data alone. There have also been several studies examining the effects of shear forces on juvenile Salmonids, that found both major and minor injuries could occur within the range of shear conditions present in a turbine with injuries ranging from scale loss to torn opercles to increased predation (Neitzel et al. 2004; Deng et al. 2005; Richmond et al. 2009; Deng et al. 2010). As a result, more laboratory and field studies are needed to generate data over a wider range of physical conditions and species to create models that can inform the design of new turbines and the hydropower regulatory community.

In general, as the ratio of maximum pressure to minimum pressure to which a fish is exposed increases, the population injury and mortality rate increases (Figs. 6, 7). Brown et al. (2012a, b) also found this relationship between pressure ratios and embolism, exophthalmia, and hemorrhage. Specifically, they found that these injuries are due to rapid decompression rather than just decompression in general because slow decompression did not induce injury or mortality. Brown et al. (2012a, b) focused on physostomous Chinook salmon that can burp air from their swim bladders potentially making them less susceptible to decompression injury than physoclistous fishes that slowly dissolve swim bladder gases into the blood through concentrated areas of blood capillaries called the *rete mirabile*. However, the relationship between swim bladder gas regulation and decompression injury has not been explicitly tested. Among the barotrauma studies we summarized, all fish species from non-turbine condition studies were physostomous and also showed high mortality from the rapid decompression that results from fish harvest. While Brown et al. (2012a, b) concluded that Chinook salmon may fare reasonably well if decompression is slow, our meta-analysis suggests that physoclistous fish, such as the majority of those included in Appendix B of supplementary material, have high mortality even from relatively slower decompression that results from retrieval by angling. This suggests that physoclistous fishes may fare poorly during the near instantaneous decompression that can occur during turbine passage. Similarly, Tsvetkov et al. (1972) reported that for physoclistous fishes, the magnitude of pressure decrease is more important than the rate of pressure decrease for determining pressure-related injury. In physoclistous fishes, pressure equilibrium is achieved through diffusion of gases through a capillary network (the *rete mirabile*) rather than by burping air as occurs in physostomous fishes. Pressure equilibrium is thus, achieved much more slowly and, theoretically, any rate of pressure decrease that is greater than the rate of pressure acclimation for a fish can potentially cause damage to a fish. Although we cannot provide precise dose–response relationships for physoclistous fishes from these data, our meta-analysis featuring fish that underwent much less rapid decompression suggests that physoclistous fishes subjected to the near instantaneous decompression inside of a turbine could have substantially higher barotrauma-associated mortality than those reported for Chinook salmon. However, it could also be that slower but sustained pressure decreases like that experienced by fish when they move from the high-pressure environment near the bottom of a reservoir into a relatively low-pressure environment at or near the surface of the water in the tailwater, similar to that depicted by trawler and angling studies, may also cause substantial mortality. Future studies should focus on comparing injury and mortality rates across

a gradient of decompression rates, especially for physoclistous fishes.

Pelagic percid species, such as walleye and yellow perch (i.e., the taxa with the highest turbine mortality rates) have typically been included in entrainment studies presumably due to their relative abundance and widespread distribution compared to other taxa in that family. Many percids, such as darters and log perch, are of conservation concern but percid mortality rates reported here may not be accurate for many of the small-bodied percids because they are not pelagic and, therefore, likely not as susceptible to entrainment. Potentially walleye and yellow perch represent the percid species at greatest risk of turbine entrainment due to habitat use and their large species range. Future work evaluating pelagic life stages of other percid species may be necessary to evaluate their vulnerability to turbine entrainment, injury and mortality. This is especially important because while their small body size reduces their risk of injury from blade strike, they may still experience high mortality via barotrauma because of their physoclistous swim bladders. Turbine mortality rates from other physoclistous taxa such as Centrarchidae, suggest that rates could be quite high even for smaller-bodied fishes. Future studies should assess the risk of percids other than walleye and yellow perch to entrainment and, if necessary, evaluate the physical effects of turbine passage on these fishes.

Fish entrainment is mostly an unavoidable reality associated with riverine hydropower generation. Successful downstream passage technologies have been recently demonstrated at the Rocky Reach Hydro Project on the Columbia River, USA with installation of a juvenile fish bypass and at Swift Dam on the Lewis River, USA with installation of a floating surface collector to concentrate juvenile fish for passage, but these technologies have yet to be widely deployed or ordered as part of regulatory requirements. Population connectivity created via turbine passage can be important for population dynamics, especially for migratory fishes (Jager 2006; Pracheil et al. 2012, 2014), and while putting up fish screens and exclusion devices may be a cost-effective way of minimizing entrainment problems, they may create others in severing population connectivity. Moving toward more environmentally sustainable hydropower will require creating operating schemes, turbine designs, and downstream bypasses whose physical forces exist within the physiological limits of fishes such as advanced turbine designs that reduce injury and mortality to turbine passed fishes (Cada 2001; Hogan et al. 2014). Current costs and incentives for installing most downstream passage and advanced turbines are high enough that they have not yet been widely ordered for power producers required to mitigate entrainment losses. Future policy directives aimed at increasing fish-friendly riverine hydropower might work towards creating subsidies or other incentives for manufacturers and power producers alike that would be easier on fish while minimally impacting their bottom line.

Acknowledgments We thank Alison Colotelo and Ryan McManamay for comments on this manuscript. This study was funded by the US Department of Energy (DOE) Energy Efficiency and Renewable Energy Office, Wind and Water Power Technologies Program through Oak Ridge National Laboratory, which is managed by UT-Battelle, LLC, for the DOE under contract DE-AC05-00OR22725. Opinions expressed are those of the authors and do not reflect those of their employers.

References

Brown RS, Carlson TJ, Gingerich AJ, Stephenson JR, Pflugrath BD, Welch AE, Langeslay MJ, Ahmann ML, Johnson RL, Skalski JR, Seaburg AG, Townsend RL (2012a) Quantifying mortal injury of juvenile Chinook salmon exposed to simulated hydro-turbine passage. T Am Fish Soc 141:147–157

Brown RS, Pflugrath BD, Colotelo AH, Brauner CJ, Carlson TJ, Deng ZD, Seaburg AG (2012b) Pathways of barotrauma in juvenile salmonids exposed to simulated hydroturbine passage: Boyle's law vs Henry's law. Fish Res 121:43–50

Brown RS, Colotelo AH, Pflugrath BD, Boys CA, Baumgartner LJ, Deng ZD, Silva LGM, Brauner CJ, Mallen-Cooper M, Phonekhampeng O, Thorncraft G, Singhanouvong D (2014) Understanding barotrauma in fish passing hydro structures: a global strategy for sustainable development of water resources. Fisheries 39:108–122

Čada GF (2001) The development of advanced hydroelectric turbines to improve fish passage survival. Fisheries 26:14–23

Čada G, Loar J, Garrison L, Fisher R Jr, Neitzel D (2006) Efforts to reduce mortality to hydroelectric turbine-passed fish: locating and quantifying damaging shear stresses. Environ Manage 37:898–906

Collaboration for Environmental Evidence (CEE) (2013) Guidelines for systematic review and evidence synthesis in environmental management version 4.2. Environmental evidence: http://devtestsite.co.uk/cee/wp-content/uploads/2014/06/Review-guidelines-version-4.2-final.pdf

Colotelo AH, Jones BW, Harnish RA, McMichael GA, Ham KD, Deng ZD, Squeochs GM, Brown RS, Weiland MA, Ploskey GR, Li X, Fu T (2013) Passage distribution and federal Columbia River power system survival for steelhead kelts tagged above and at Lower Granite Dam. PNNL-22101 http://www.salmonrecovery.gov/Files/Comprehensive%20Evaluation/Colotelo-etal_2013_-%20Kelt-Passage-Distribution-Survival_PNWD-22101.Pdf. Accessed 10 Aug 2015

Coutant CC, Whitney RR (2000) Fish behavior in relation to passage through hydropower turbines: a review. Trans Am Fish Soc 129:351–380

Deng Z, Guensch GR, McKinstry CA, Mueller RP, Dauble DD, Richmond MC (2005) Evaluation of fish-injury mechanisms during exposure to turbulent shear flow. Can J Fish Aquat Sci 62:1513–1522

Deng Z, Carlson TJ, Richmond MC (2007) Six-degree-of-freedom sensor fish design and instrumentation. Sensors 7:3399–3415

Deng Z, Mueller RP, Richmond MC, Johnson GE (2010) Injury and mortality of juvenile salmon entrained in a submerged jet entering still water. N Am J Fish Manage 30:623–628

Duncan JP, Carlson TJ (2011) Characterization of fish passage conditions through a Francis turbine, spillway, and regulating outlet at detroit dam, oregon, using sensor fish, 2009. Pacific Northwest National Laboratory, Richland

Ferguson JW, Ploskey GR, Leonardsson K, Zabel RW, Lundqvist H (2008) Combining turbine blade-strike and life cycle models to assess mitigation strategies for fish passing dams. Can J Fish Aquat Sci 65:1568–1585

Garrison LA, Fisher Jr., RK, Sale MJ, Cada GF (2002) Application of biological design criteria and computational fluid dynamics to investigate fish survival in Kaplan turbines. In: Proceedings of HydroVision

GeoSense (2011) Report on fish entrainment and mortality at Mason Dam, OR. Technical Report for Mason Dam Hydroelectric Project (FERC No. 12686)

Hogan TW, Cada GF, Amaral SV (2014) The status of environmentally enhanced hydropower turbines. Fisheries 39:164–172

Jager HI (2006) Chutes and ladders and other games we play with rivers. I. Simulated effects of upstream passage on white sturgeon. Can J Aquat Sci 63:165–175

Jager HI, Chandler JA, Lepla KB, Van Winkle W (2001) A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. Environ Biol Fish 60:347–361

Jager HI, Elrod B, Samu N, McManamay RA, Smith BT (2013) ESA Protection for the American Eel: Implications for US Hydropower (No. ORNL/TM-2013/361). Oak Ridge National Laboratory (ORNL)

Kao S, McManamay RA, Stewart KM, Samu NM, Hadjerioua B, DeNeale ST, Yeasmin D, Pasha MFK, Oubeidillah AA, Smith BT (2014) New stream-reach development: a comprehensive assessment of hydropower energy potential in the United States. GPO DOE/EE-1063, Wind and Water Power Program, Department of Energy, Washington, DC

Neitzel DA, Dauble DD, Čada GF, Richmond MC, Guensch GR, Mueller RP, Abernethy CS, Amidan B (2004) Survival estimates for juvenile fish subjected to a laboratory-generated shear environment. Trans Am Fish Soc 133:447–454

Normandeau Associates, Inc. and Gomez and Sullivan Engineers, P.C. (2012) Estimation of survival of adult American shad passed through Francis and Kaplan turbines. Study for Conowingo Hydroelectric Project Federal Energy Regulatory Commission relicensing. FERC project number 405. August 2012

Pracheil BM, Pegg MA, Powell LA, Mestl GE (2012) Swimways: protecting paddlefish through movement-centered management. Fisheries 37:449–457

Pracheil BM, Mestl GE, Pegg MA (2014) Movement through dams facilitates population connectivity in a large river. Riv Res Appl. doi:10.1002/rra.2751

Reidy Liermann CA, Nilsson C, Robertson J, Ng RY (2012) Implications of dam obstruction for global freshwater fish diversity. BioSci 62:539–548

Richmond MC, Deng Z, McKinstry CA, Mueller RP, Carlson TJ, Dauble DD (2009) Response relationships between juvenile salmon and an autonomous sensor in turbulent flow. Fish Res 97:134–139

Richmond MC, Serkowski JA, Ebner LL, Sick M, Brown RS, Carlson TJ (2014) Quantifying barotrauma risk to juvenile fish during hydro-turbine passage. Fish Res 154:152–164

Trumbo BA, Ahmann ML, Renholds JF, Brown RS, Colotelo AH, Deng ZD (2014) Improving hydroturbine pressures to enhance salmon passage survival and recovery. Rev Fish Biol Fish 24:955–965

Tsvetkov VI, Pavlov DS, Nezdoliy VK (1972) Changes of hydrostatic pressure lethal to young of some freshwater fish. J Ichthyol 12:307–318