FINAL REPORT

Section A. Summary

Title of Project: Investigating fish energy use and swimming behavior in turbulent flows: Guiding restoration of Lake Michigan tributaries

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Abstract:

Freshwater ecosystems worldwide are currently at risk due to anthropogenic habitat loss and degradation. This is particularly true for areas where the landscape is dominated by agriculture, such those surrounding Lake Michigan. Because tributary habitat is important for many fish species, healthy fisheries in the Great Lakes require a watershed-scale approach to ecosystem conservation and restoration. Placement of in-stream structures is a common means of habitat restoration within tributary streams. However, the design of the habitat improvement structures is based primarily on engineering and geomorphic rather than biological criteria. Given the limited understanding of the advantages and disadvantages of various structure types and designs for fish, we sought to examine the influence of turbulent flow, generated by simulated in-stream restoration structures, on fish energetics and behavior. Our goals were to identify key turbulent flow parameters that define energetic cost and space use of fish swimming around such structures, and to develop and test a quantitative explanatory model. To this end, we carried out laboratory and field experiments across a range of spatial scales and environmental contexts, structure dimensions, orientation, and complexity: small-scale lab experiments to relate fish oxygen consumption (energy use) to acceleration; large-scale lab experiments to develop models linking characteristics of turbulent flow generated by structures to fish energy use and space use; and field experiments to test these models in a real riverine environment. The small-scale lab experiments indicated that in presence of in-stream structures of any type fish displayed more stable swimming (smaller changes in acceleration) and, as a result, experienced lower energetic cost. On the other hand, the large-scale lab experiments suggested that, when free to choose swimming position around structures, fish chose positions with reduced velocity but elevated turbulence, and experienced higher energetic cost compared with control conditions. Together, this research provides new insights into the interactions of fish with in-stream restoration structures, and contributes to a novel approach to restoration science, which uses fish energetics as a means to assess the effectiveness of structure design. Thus, our findings will serve to increase the success of restoration activities by contributing to better understanding of the characteristics of instream restoration structures that lead to flow conditions that are energetically beneficial for fish.

Key Words:

fish energetics; turbulence; accelerometry; instream structures; river restoration; habitat management

Lay Summary:

Many of the fish species important for both recreational and commercial fishing in Lake Michigan depend on the streams and rivers that feed into the lake, and need these in order to complete their life cycle. However, human activity has lead to ecological degradation of these streams and has impacted their ability to provide the habitat that fish need. Restoration is a suite of actions that are used to reverse these negative impacts, and often involves installing physical structures that are meant to provide habitat for fish. However, we know very little about how fish actually use and interact with these structures, and the designs for these projects typically focus on the intended physical changes to stream environment, assuming that they will benefit fish. This is concerning because installing restoration structures changes the environmental conditions within streams in many ways and can be costly.

To improve our understanding of links between restoration structures, the changes they make within the stream environment, and how such changes affect fish, we used a combination of experiments conducted within the laboratory and within an actual stream. We tested two popular sportfish species, smallmouth bass and rainbow trout, and created simulated restoration structures. We measured how these structures changed the average velocity of water flowing past them and how they generated turbulence (swirling eddies and fluctuating flow velocities), and then studied how these habitat characteristics changed fish swimming behavior and the energy they used to swim. We were interested in how fish spent energy because when swimming requires a greater energy investment, fish then have less left over for activities like reproduction. Ultimately, we have found that the interactions between fish and these structures vary, and whether they cause fish to spend more or less energy to swim may depend on how closely fish are interacting with structures. In some case, fish spend less energy when swimming with structures. In other cases, fish spend more energy when swimming with structures, but still choose to stay near structures, which suggested that there could be some other benefit that they may be seeking to derive, possibly unrelated to the energetic cost of swimming.

Section B. Accomplishments

1. Introduction

Tributary streams serve many critical roles that allow fish communities of the Great Lakes to complete their life histories (Goodyear, 1982). Such streams provide spawning, nursery, and rearing habitat (Biette *et al.*, 1981; Fausch and White, 1986). However, extensive damming, channelization, stream crossing construction, dredging, large wood removal, and land use-related sedimentation in these streams have resulted in alteration of their hydrological and geomorphic characteristics (Rutherford, 2008). These changes, in turn, have translated into negative impacts on the quality and connectivity of habitat for Great Lakes fishes (Rutherford, 2008). This kind of physical degradation of stream habitat has been identified as the leading cause of freshwater biodiversity loss (Collen *et al.*, 2014). According to a recent assessment, over 30% of tributaries in the Great Lakes region were classified as impaired in terms of habitat quality (Riseng *et al.*, 2010). Moreover, recent estimates indicate that there are over 7000 dams on tributaries of the Great Lakes and 38 times as many stream crossings, out of which only 36% were deemed fully passable to fish (Januchowski-Hartley *et al.*, 2013).

The physiological and behavioral aspects of swimming provides a critical link between this kind of physical habitat alterations and fish community response. Any changes in streamflow, channel shape, or roughness are reflected in the hydraulic forces fish of a given species encounter as they feed, migrate, or interact with their aquatic environment. For example, channels simplified through channelization and/or large wood removal have swift currents, due to decreased hydraulic roughness, and reduced hydraulic heterogeneity in flow (Douglas Shields and Smith, 1992; Rhoads *et al.*, 2003). As a result, fish need to expend more energy to swim or maintain their position against the flow and cannot take advantage of sharp velocity gradients generated by a complex channel boundary (Fausch, 1984; Wall *et al.*, 2016). In addition, operation of dams may alter thermal characteristics of habitat (Horne *et al.*, 2004), which further amplifies the metabolic cost of swimming (Enders and Boisclair, 2016). Finally, placement of culverts at road crossings often increases current velocity, which may impede the ability of fish to move between complementary habitats (Castro-Santos, 2004; Haro *et al.*, 2004). Different fish species can respond differently to habitat alteration, depending on their morphological, biomechanical, and behavioral traits (Bisson *et al.*, 1988; Blake, 2004).

The restoration of fish habitat in tributary streams plays a critical role in improving Great Lakes ecosystem health. The majority of restoration projects in the Midwest focus on stream habitat and aim to improve its quality and connectivity through the construction of in-stream structures (Moerke and Lamberti, 2004; Alexander and Allan, 2006). The most common types of structures that aim to improve habitat quality include those that mimic natural stream features e.g. large wood and boulders, but also various kinds of artificial flow deflectors or J-hook vanes (Radspinner *et al.*, 2010). For example, recent restoration projects carried out by Trout Unlimited (TU) on Little Mainstee River, Poplar River, and other tributaries of Lake Michigan have used structures constructed using large wood. The common feature of all these diverse installations is that they substantially alter local flow characteristics and, consequently, hydraulic habitat for fish.

Unfortunately, the design of the in-stream habitat improvement structures is based on somewhat vague biological criteria. This situation stands in contrast to fish passage research, which has been relatively successful in incorporating understanding of fish swimming performance and behavior (Kemp, 2012). While guidelines implicitly assume that physical changes caused by structures will improve ecological function, few specifics are provided regarding biological advantages and disadvantages of various structure types and designs. Similarly, assessments of the ecological efficacy of restoration structures have been rare (Moerke and Lamberti, 2004; Alexander and Allan, 2006) and mixed ecological outcomes have been reported (Roni *et al.*, 2008; Whiteway *et al.*, 2010). Even if such an evaluation is carried out, it usually involves fish abundance as the main biological metric. Importantly, this lack of proper assessment leads to uncertainty whether increased fish density represents enhanced fish production or simply spatial aggregation of fish around the structure and whether the implementation of structures produces meaningful biological benefits. Current approaches fall short of establishing “measurable biological improvement” postulated by restoration science (Palmer *et al.*, 2005) as a criterion for restoration success.

Using physiological responses of fish offers a promising opportunity to develop a better, mechanistic and quantitative understanding of the causes and effects of environmental degradation or habitat fragmentation as well as the benefits of restoration activities (Cooke *et al.*, 2013; Rosenfeld *et al.*, 2013). Mechanistic models of fish habitat, coupled with 2D and 3D numerical hydrodynamic models, have become an increasingly popular tool to define relationships between hydraulic habitat and fish performance (Booker *et al.*, 2004; Cienciala and Hassan, 2016). Mechanistic models have been also applied to fish passage (Nestler *et al.*, 2012). All these models improve upon and complement older and often criticized approaches, based on pure correlation between hydraulic parameters and fish abundance (Lancaster and Downes, 2010).

Importantly, however, current field-based and modeling approaches rely overwhelmingly on simplified hydraulic metrics, which represent time-averaged characteristics of flow. In contrast, recent research has demonstrated that turbulent properties of flow may be at least as important for fish energetics (Enders *et al.*, 2005) and behavior (Cotel *et al.*, 2006). This area of research is still new, and conflicting reports of positive (Liao *et al.*, 2003) or negative (Enders *et al.*, 2005) effects of turbulence on energy use demonstrate the need for more research into this subject. Despite the ever-increasing computational capabilities, which enable direct simulation of the largest, most energetic eddies in relatively complex flows (e.g. Large Eddy Simulator; e.g. Xu and Liu (2017)), such an approach cannot be employed in numerical modeling because of the lack of relationships that would systematically link turbulent characteristics to fish physiology and behavior. Flow around in-stream structures and in fish passage facilities is inherently heterogeneous and turbulent (Uijttewaal, 2005; Koken and Constantinescu, 2008) therefore, fish-habitat relationships which take turbulent flow characteristics into account are critically needed for guiding scientifically-robust design of habitat restoration.

The overall aim of our research was to advance current understanding of the effects of turbulent flow on fish swimming behavior and energetics to support design of in-stream structures for restoration of Lake Michigan tributaries. Tributary habitat is essential for many fish species in the Great Lakes and our research informs watershed-scale management of these coupled freshwater ecosystems.

Our specific objectives for this project were:

(1) To identify key parameters of turbulent flow that influence the spatial utilization of habitat by fish and the energetic cost of swimming in complex flows.

(2) To develop and evaluate under realistic field conditions a quantitative model that links key parameters of turbulent flow identified in (1) to the energetic cost of swimming. Such a model will improve predictions of energy expenditure in bioenergetic models, providing valuable information for habitat restoration and management practices for Great Lakes fisheries.

To address, these objectives, research was conducted in three parts. First, small-scale laboratory experiments (Section 2.1) were conducted to provide new insights regarding the close-range, local interactions between fish and turbulent flow generated by turbulence-generating features (TGFs) simulating instream restoration structures. Second, large-scale laboratory experiments (Section 2.2) were conducted to allow for a detailed, mechanistic evaluation of the impact of turbulence generated by TGFs on fish energy use and position choice, as well as the development of models linking specific characteristics of turbulent flow to energy use. Finally, *in-situ* field experiments (Section 2.3) tested these models while allowing for greater environmental and structural complexity, as well as greater freedom for fish positional choices. Together, these three sections provide novel insights into the use of energy use as a means to assess the effectiveness of instream restoration structures, and serve to increase the success of restoration activities by identifying the characteristics of instream restoration structures that lead to flow conditions that are energetically beneficial for fish.

2. Project Narrative

2.1 Small-Scale Lab Experiments

Our first objective was to identify key parameters of turbulent flow that influence fish space use and the energetic cost of swimming in complex flows found around in-stream structures. To achieve this objective, it was first necessary to conduct 1.) small-scale laboratory experiments to relate data derived from accelerometers and oxygen consumption (energy use), so that the oxygen consumption of free-swimming fish could be estimated; and 2.) large-scale laboratory experiments with accelerometer-tagged fish to examine fish space use and energy use (estimated via accelerometer tags) around various simulated in-stream restoration structures.

We conducted our first small-scale lab experiment in Fall 2018. Following the completion of data collection, we discovered that the manufacturer of the accelerometer tags used had incorrectly programmed the tags. As a result, these tags reported the change in a fish's acceleration ("jerk"), rather than raw acceleration values. It was not possible to use these data to relate acceleration to fish energy use, and thus it was necessary to conduct a second round of small-scale lab experiments. However, we leveraged the data from this experiment to gain new insight into the close-range interactions between fish and flow conditions altered by TGFS and the effects of those interactions on fish energetics and swimming stability. The results from this study have since been published in *Canadian Journal of Fisheries and Aquatic Sciences* (Strailey et al., 2021; for details please see Section "Outputs"). The methodology and results from both rounds of small-scale experiments are presented below.

2.1.1 Small-Scale Lab Experiment #1

Methods:

This experiment focused on examining the impact of close-range interactions between smallmouth bass (*Micropterus dolomieu*) and turbulence-generating structures on fish energy use (hereafter referred to as oxygen consumption) and swimming stability. Smallmouth were acclimated to one of three temperatures (15, 18, and 21 ̊C) for a period of 65-70 days, and then were surgically implanted with an accelerometer tag that measured the rate of change in acceleration, also known as jerk. Fish were tested within a Brett-type intermittent flow respirometer. This piece of equipment essentially acts as a "fish treadmill", allowing fish to swim against a constant flow (determined and set by the researcher) (Fig. 1 [a-c]).

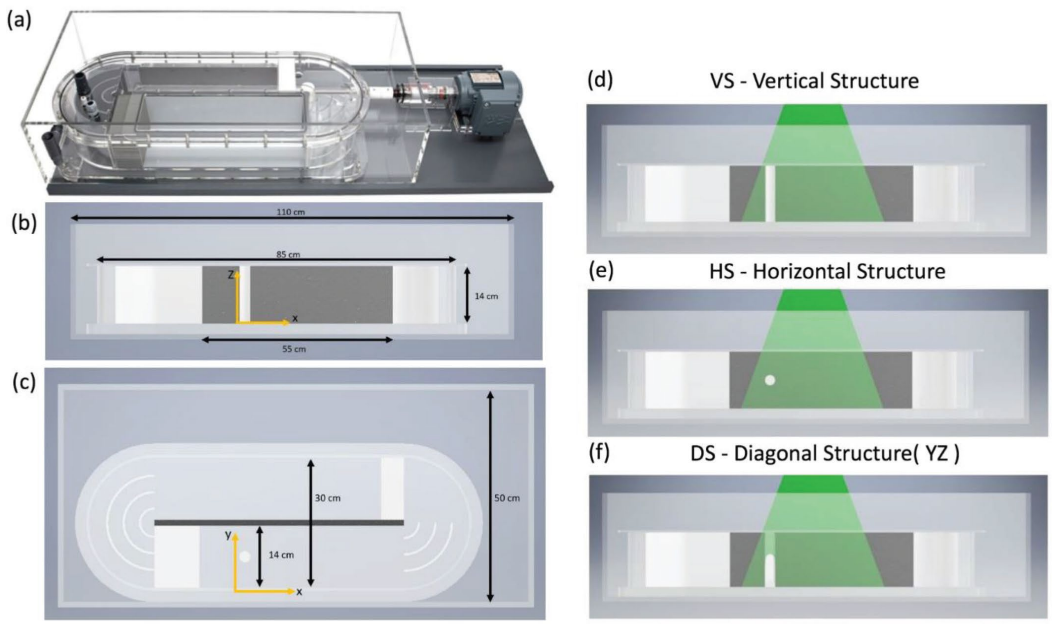

Figure 1. *Photo of a 30 L swimming respirometer (a) utilized for small-scale lab experiments, depicting the side (b) and top (c) view of the respirometer. For our initial experiments, three structures, a vertical structure (VS, d), a horizontal structure (HS, e), and a diagonal structure (DS, f) were tested.*

Fish were first introduced to the respirometer and allowed to acclimate at a flow rate of 0.5 body lengths per second (BL/s) for a period of 30 minutes. After this period, fish were tested over a range of mean flow velocities following a 'stair-step' design methodology similar to a critical swimming velocity test. Water velocity was increased by approximately 0.5 BL/s, and fish were allowed to swim at that velocity for a period of time. This period of time was adjusted as necessary to produce a high R^2, or coefficient of determination, of 0.9 or above. This value was targeted as it indicates that the oxygen consumption data are reliable and that any changes in the oxygen content of the water are indeed due to usage by the tested fish. After the desired R^2 was met, the water velocity was then increased by 0.5 BL/s, and velocity increases proceeded in this fashion until 3.0 BL/s or the fish was no longer willing to swim. One measurement of MO_2 was obtained at each of these five (1.0, 1.5, 2.0, 2.5, and 3.0 BL/s) velocities.

Experimental treatments with turbulent flow consisted of the addition of a single 2.54 cm diameter acrylic cylinder (referred to as a structure) securely mounted in the swimming chamber in one of three orientations: a vertical structure (VS), a horizontal structure (HS), and a diagonal structure (DS)

(Fig. 1 [d-f]). Our reference framed was defined such that X is the longitudinal coordinate in the direction of the mean flow, Y is the horizontal transverse coordinate perpendicular to the mean flow, and Z is vertical. The HS was aligned with the X axis and placed at half-depth; the VS was aligned with the Z axis and placed on the chamber centerline; and the DS was placed at a 45° angle, with the high end of the structure placed against the swim chamber's inner wall. Control trials were also conducted with no structure (NS) placed in the swim chamber. Individual fish were randomly assigned to one of these four flow conditions.

Particle image velocimetry (PIV) was used to measure flow characteristics within the respirometer. Measurements were taken on two two-dimensional (2D) planes within the test section: (i) a vertical plane oriented along the direction of the flow (XZ plane) at the tank centerline and (ii) a horizontal plane oriented along the direction of the flow (XY plane) at mid-depth. According to our reference frame, components of the velocity were defined as u in the longitudinal direction (X), v in the transverse direction(Y), and w in the vertical direction (Z). Lowercase symbols(u, v, w) were used to indicate instantaneous values and uppercase symbols were used to indicate time averages.

The accelerometer tags used for this experiment yielded data in the form of jerk, the change in acceleration between two successive measurement times. For a given data point at time t_x, a jerk value greater than zero corresponds to a change in acceleration relative to acceleration at time t_{x-1} (i.e., a "jerk" or change in swimming acceleration); a jerk value equal to zero at t_x indicates an unchanged acceleration relative to acceleration at time t_{x-1}. Thus, when quantified over time, periods of zero jerk indicate a consistent, smooth swimming gait, while nonzero values of jerk indicate that fish are changing gait and not swimming in a consistent fashion. The quantity of jerk data generated varied across individual fish and between trials due to the varying lengths of time at which a given velocity was maintained. As a result, data were sorted as either zero (jerk measurements of 0, indicating no change in acceleration) or non-zero (jerk measurements greater than 0, indicating a change in acceleration). Counts of these data were used to generate a "jerk proportion".

Both jerk proportion and oxygen consumption data were analyzed via linear mixed effects models that accounted for the usage of individual fish across multiple flow velocities. A range of possible predictor variables, including water velocity, structure type, water temperature, fish mass, and interactions between these terms, were tested to determine which had the greatest impact on fish oxygen consumption and jerk proportion.

Results:

At the lowest flow velocities, the proportion of jerk measurements experienced by fish did not vary across structure orientation or structure presence (Fig. 2a). However, beginning at 1.5 BL/s, the proportion of jerk measurements increased significantly for fish swimming with NS and continued to increase with velocity. In contrast, at 2.0, 2.5, and 3.0 BL/s, fish swimming with any structure had a significantly lower proportion of jerk measurements, and it was only at the very highest velocities of 2.5 and 3.0 BL/s that fish swimming with a VS or HS experienced any significant increase in this proportion as compared to their proportion at lower velocities; fish swimming with a DS never experienced any real increase in their proportion of jerk measurements.

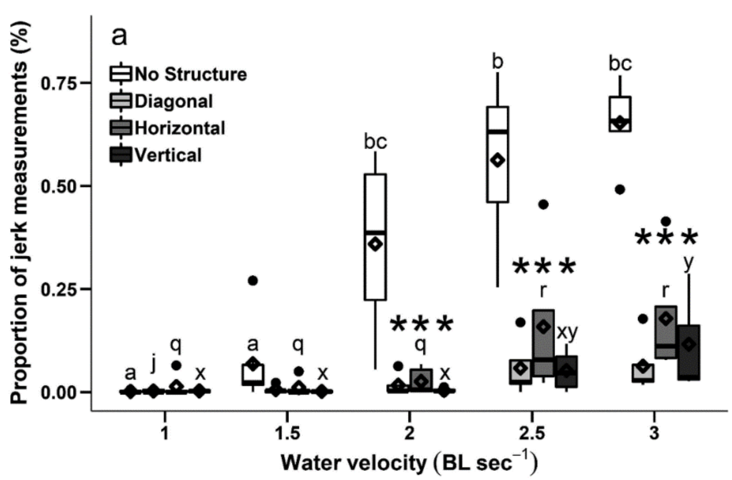

Figure 2a. *The proportion of jerk measurements, by structure treatment and swimming velocity, for smallmouth bass in our first small-scale lab experiment.*

A similar pattern was seen within the oxygen consumption data. The MO_2 of smallmouth bass swimming with structures did not differ across water velocities; even at the highest velocities of 2.5 and

3.0 BL s^{-1}, MO_2 did not differ significantly from MO_2 at 1.0 BL s^{-1} (Fig. 2b). Essentially, fish swimming with any structure were able to maintain about the same level of oxygen consumption at all times, even as water velocity increased. In contrast, fish swimming without a structure experienced an increase in MO_2 of about 20%, relative to MO_2 at 1.0 BL s^{-1}, at 2.5 and 3.0 BL s^{-1} (Fig. 2b). However, at a given water velocity, MO_2 did not differ significantly for fish swimming with or without a structure.

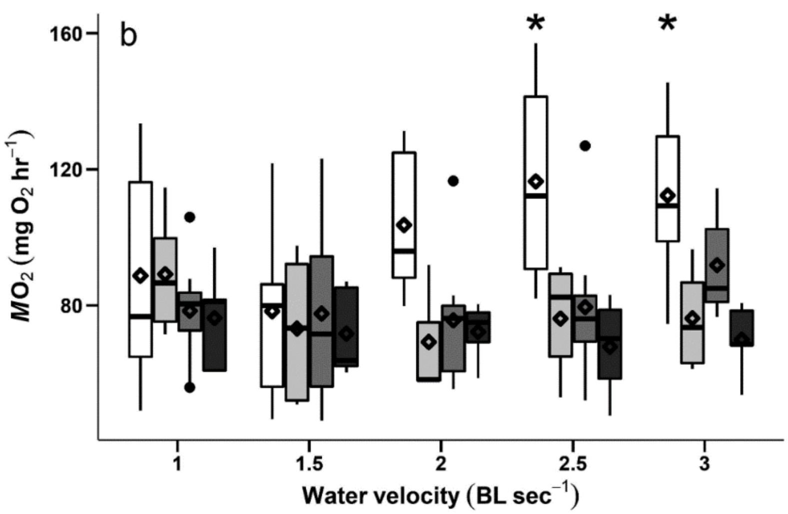

Figure 2b. *The oxygen consumption, by structure treatment and swimming velocity, for smallmouth bass in our first small-scale lab experiment.*

Water velocity was highest overall throughout the test section for tests without a simulated structure. Pockets of reduced velocity developed in the lee of all structures, which produced a wake effect in the corresponding plane of orientation (the XZ (vertical) plane for the HS and the XY (horizontal) plane for the VS. The DS produced a diagonal wake in both the XZ and XY planes. A clear zone of recirculating fluid existed behind all structures. High TKE values were present downstream of the structures, with a wake in the vertical plane formed in the lee of the HS, a wake in the horizontal plane generated behind the VS, and a diagonal wake formed behind the DS. The DS enhanced TKE, vorticity, and Reynolds stresses both in the horizontal and vertical planes, while the VS and HS enhanced these parameters only in the XY and XZ planes, respectively.

Conclusions:

The presence of simulated structures in the respirometer resulted in a smoother swimming gait (i.e., reduced jerk) for smallmouth bass. Fish swimming with structures experienced a significantly lower proportion of nonzero jerk measurements relative to fish in the control treatment, likely due to altered flow characteristics. Generally, the results indicate that structures confer benefits when fish are interacting with turbulent flow immediately downstream of these structures by improving swimming stability, especially for flows with high mean velocities within the ranges used in this study.

Smallmouth bass swimming with structures experienced a lower proportion of jerk measurements and were able to maintain a more stable swimming position (i.e., lower proportion of jerk measurements), particularly at swimming speeds above 2 BL·s–1, likely due to their utilization of the flow conditions generated by the structures. These fish were likely able to exploit pockets of reduced velocity from the relatively high velocity in other areas of the flow thereby resulting in a smooth swimming gait and a reduced proportion of jerk measurements at a given swimming speed compared with NS fish. Alternatively, smallmouth bass may also have coordinated their swimming mechanics with characteristics of coherent turbulent structures generated by simulated structures. The ability to exploit turbulence has been well-documented in a number of fish species. Smallmouth bass may potentially be capable of exploiting turbulent vortices as well and may have utilized such a swimming strategy in this experiment.

While the zones of reduced velocity behind each structure can be beneficial regardless of orientation, the orientation of a vortex affects whether it can be exploited by fish, and the effects of this were demonstrated within this experiment. Flow analyses characterizing flow on vertical and horizontal planes for three structure orientations (HS, VS, and DS) demonstrated the similarities of generated wakes in their respective planes, allowing for the assessment of a broad range of Re and TKE levels. Horizontally oriented vortices, such as those generated by the VS, can be exploited by fish (Liao et al. 2003; Taguchi and Liao 2011), such that they do not need to use as much energy to swim, while vertically oriented vortices, such as those generated by the HS, may destabilize fish. These documented relations may explain why smallmouth bass in the DS treatment, which included both the development of a zone of low velocity behind the structure and horizontally oriented vortices, experienced no increases in jerk across water velocities. On the other hand, HS fish, which were exposed to potentially destabilizing vertically oriented vortices, experienced a higher number of jerk at high velocities than either DS or VS fish.

The presence of simulated structures provided an energetic advantage for smallmouth bass relative to fish in the control (NS treatment), particularly once fish reached the two highest water velocities of 2.5 and 3.0 BL s^{-1}. Fish swimming with structures, regardless of orientation, never experienced any significant increases in their MO_2, even as water velocity increased. Smallmouth bass species may have some ability to exploit turbulent flow, similar to rainbow trout. Such behavior may account for the lack of an increase in MO_2 values, despite an increase in water velocity. Alternatively, smallmouth bass in the structure treatments may have simply positioned themselves in the low-velocity pockets behind each simulated structure, thereby reducing swimming oxygen costs. Regardless of the underlying cause, the results confirm that smallmouth bass swimming in the presence of simulated restoration structures maintained a consistent MO_2 across water velocities in comparison with fish swimming without simulated structures, which experienced pronounced increases in MO_2 at high velocities.

2.1.2 Small-Scale Lab Experiment #2

Methods:

Laboratory studies were conducted in Fall 2019 to identify the relationship between data derived from accelerometers and oxygen consumption (energy use). Two species, smallmouth bass (*Micropterus dolomieu*) and rainbow trout (*Oncorhynchus mykiss*), were used for these experiments. Fish were first acclimated to one of two ecologically-relevant temperatures for a minimum of 30 days. After this point, fish were internally outfitted with a tri-axial accelerometry tag that quantifies acceleration in three dimensions and then placed within an intermittent-flow respirometer to measure fish MO_2. After an acclimation period, fish were tested over a range of mean flow velocities, following a ‘stair-step’ design methodology similar to a critical swimming velocity test. After acclimation at 0.5 body lengths per second (BL s^{-1}), water velocity was increased by approximately 0.5 BL s^{-1}, and fish were allowed to swim at that velocity for a period of time, with velocities ranging from 1.0 up to 3.0 BL s^{-1}. The change in oxygen concentration was measured to calculate the metabolic rate of the swimming fish. Accelerometer data was collected by external receivers every 2 seconds during swimming in order to link it with oxygen consumption. TGFS were not present in the respirometer during these experiments. Because fish on average were nearly a third of the length of the test section, in order to be able to accommodate the accelerometer tags, there was not sufficient space to have TGFs in place while allowing fish sufficient space to properly perform swimming tests.

All acceleration points for each individual fish at each velocity were averaged to produce a "representative acceleration" value. Linear mixed-effects models (LMEs) were then used to produce an equation relating oxygen consumption to swimming acceleration. This type of model was used because each individual fish swam across multiple velocities and thus yielded multiple oxygen consumption data points; this type of model accounts for this repeated use. Several candidate models were testing with various combinations of acceleration, water temperature, and fish mass tested as predictors of oxygen consumption. The best fitting candidate model was determined through several factors, included Akaike information criterion (AIC) score, model R^2 values, and biological sense, based on the relevant literature.

Results:

The selected model for each species included acceleration, acclimation temperature, and fish mass as fixed effects, with individual fish ID as a random effect. Both oxygen consumption and fish mass were log-transformed to account for the non-linear relationship between $\dot{M}O_2$ and mass. Below, the model for smallmouth bass and a figure showing the relationship between acceleration and oxygen consumption for this species are shown (Fig. 3).

$$\text{Log } (\dot{M}O_2\text{, in mg } O_2\text{/kg/hr}) = (0.76582 * \text{acceleration}) + (0.03730 * \text{acclimation temperature}) + (0.28196 * (\log (\text{fish mass}))) + 2.79461$$

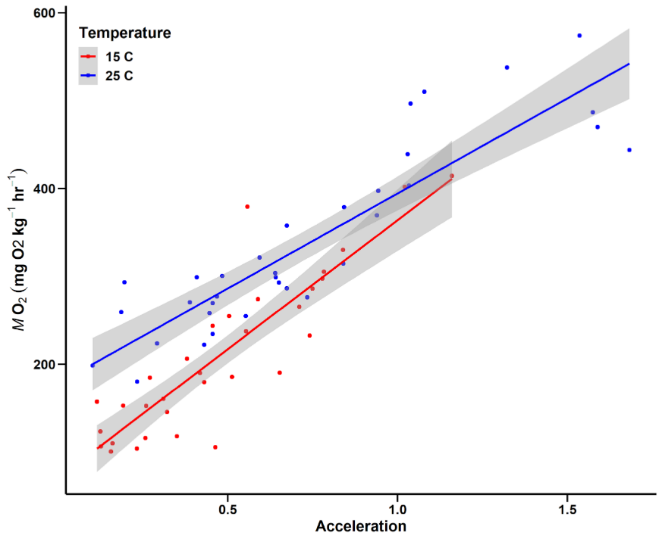

Figure 3. *The relationship between acceleration and oxygen consumption for smallmouth bass in small-scale lab experiments.*

2.2 Large-Scale Lab Experiments

Methods:

Large-scale laboratory experiments were conducted in an 11m long, 0.8m channel wide, 0.6m tall, racetrack flume at the Ecohydraulics and Ecomorphodynamics Laboratory (EEL) of the University of Illinois at Urbana-Champaign (Fig. 4). The flume's dimensions allowed for the testing of larger TGFS, and also enabled fish to maneuver and swim more freely, a significant improvement considering fish are known to exhibit different swimming patterns in small flow chambers (Boisclair and Tang, 1993; Tang and Boisclair, 1993).

Figure 4. *The flume utilized for large-scale lab experiments*

Smallmouth bass and rainbow trout were used. Separate test sections were established within the flume, and cylindrical PVC structures were placed within these to investigate interactions between fish and TGFs,. Three orientations (vertical, horizontal, diagonal in the YZ plane) and three diameters (2.56-cm, 5.08-cm, 7.62-cm) were tested, across three velocities (approximately equivalent to 1.0, 1.5, and 2.0 BL s^{-1}). A control, in which no TGF was placed, was also tested. Before each test, the TGF (if present), was placed, and fish then acclimated at 0.5 BL s^{-1} for one hour. Fish then swam for 15 minutes at each velocity. Six fish were used from each species, and every fish was tested with every combination of flow conditions. Accelerometer tags recorded acceleration data, and cameras recorded video.

As with small-scale lab experiments, the acceleration data resulting from large-scale lab experiments were processed to produce a “representative acceleration”. To do this, all acceleration points for each individual fish at each combination of structure and velocity were averaged. These representative acceleration values were then used to estimate oxygen consumption using the equations established in small-scale lab experiments. Fish positions during large-scale lab experiments were derived from video. Fish location data were used in combination with PIV data to extract the time-averaged values for various flow statistics at each of the locations a fish occupied. These location data were further used to examine two more position variables: the proportion of time fish spent upstream, and the standard deviation of a fish from its average position.

Results:

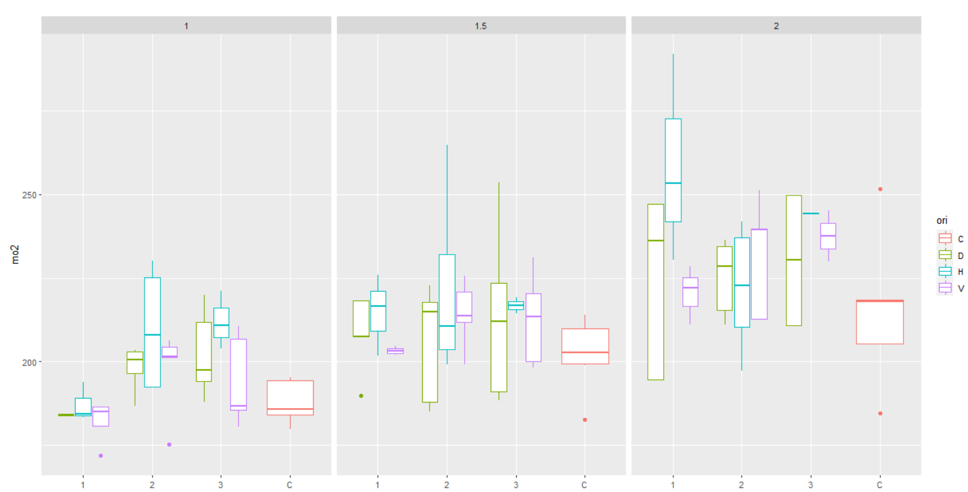

Figure 5. *The oxygen consumption of smallmouth bass, estimated via accelerometers. Structure diameter is shown on the x axis, and different colors indicate different structure orientations. Data are shown faceted by flow velocity.*

Counter to expectations, our preliminary results indicate that fish experienced higher acceleration when swimming with structures, regardless of diameter or orientation, than in comparison to when swimming without any structure (Fig. 5). This translated to higher estimations of oxygen consumption under such flow conditions, which was surprising as fish were exposed to much higher mean flow velocities when no structure was present to block part of the flow and provide pockets of reduced velocity as refugia. In contrast, when structures were present, fish chose to occupy locations with reduced mean velocity, but elevated turbulent kinetic energy as compared to the conditions they utilized when no structure was present (Fig. 6&7).

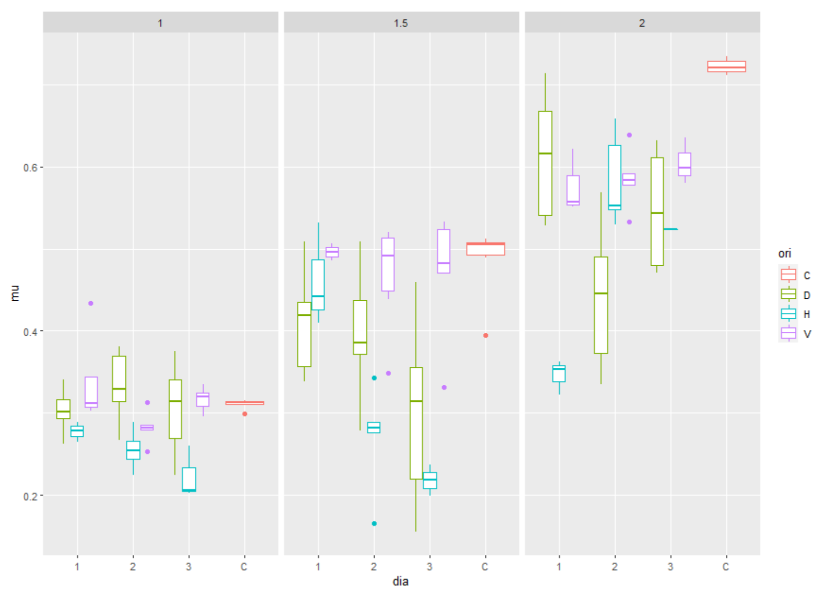

Figure 6. *The range of mean velocity (u) values experienced by smallmouth bass at selected swimming positions. Structure diameter is shown on the x axis, and different colors indicate different structure orientations. Data are shown faceted by flow velocity.*

Though the presence of structures lead to increased energetic costs for fish and exposed them to higher levels of turbulence, fish appeared to exhibit high fidelity to positions within the wake of structures, and additionally tended to choose to remain downstream of structures, while spending more time upstream of where structures would be when no structure was present. This indicates that fish were choosing to remain within the area of flow influenced by structures, despite experiencing higher energetics costs as a result, suggesting that fish are selecting locations based upon more than their potential impacts on the energetic costs of swimming. Further analyses of results for smallmouth bass large-scale lab experiments are in the process of being finalized and a new manuscript is being drafted. Moreover, analyses for rainbow trout data are underway.

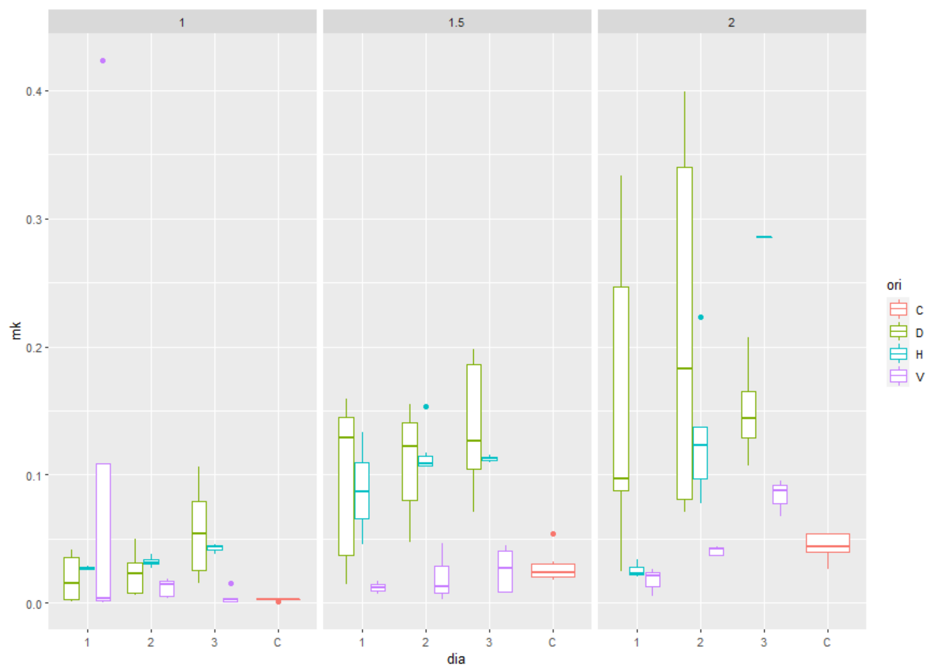

***Figure** 7. The range of mean turbulent kinetic energy (k) values experienced by smallmouth bass at selected swimming positions. Structure diameter is shown on the x axis, and different colors indicate different structure orientations. Data are shown faceted by flow velocity.*

2.3 Field Experiments

Methods:

Experiments were conducted near an established field site in the Kaskaskia River in west Champaign, IL. Two netted enclosures, approximately 5 m^2, were constructed along the same lateral transect to contain fish during experiments. The size of these enclosures was chosen to ensure that fish were likely to encounter and interact with structures, while simultaneously allowing sufficient space for turbulent wakes to develop downstream of each structures. Four flow conditions, one structureless flow and three with TGFS present, were tested. The three TGFS were composed of 10.16 cm-diameter PVC in arrangements of one single TGFS, a single longitudinally-oriented row of three equally-spaced TGFS, and two longitudinally-oriented rows of three TGFS, with equal spacing between TGFS.

For experiments, fish implanted with accelerometers were released into enclosures in same-species groups of 3. This was done to create conditions that are more realistic for a field environment- in a natural, unbounded stream environment, areas that have beneficial hydrodynamic conditions are attractive and will likely have multiple fish present at a time. Each trial (with one trial consisting of two groups of fish, released into separate enclosures, and exposed to all four flow conditions) took place over the course of a single day. Fish swam with each condition for a total of two hours. The first hour was treated as an acclimation period, and thus only acceleration measurements from the second hour were considered.

Acoustic doppler velocimetry (ADV) was used to characterize flow conditions. ADV measurements were taken following the completion of all fish trials, and were taken within each enclosure for each flow condition. Two ADVs were used together to take synchronous point measurements of the flow field at multiple depths and locations throughout each enclosure.

Fish acceleration data will be processed using the oxygen consumption-acceleration models developed during small-scale lab experiments. These will then be analyzed in a similar fashion to large-scale lab experiments, using linear mixed-effects models. The resulting models will then be compared against the models developed during large-scale lab experiments to evaluate how well the model performs in a field environment. ADV data will be analyzed using Matlab (MathWorks R2017a).

Results:

All data necessary for field experiments have been collected. Analyses from field experiments will begin once analyses are completed for large-scale lab experiments.

3. Potential Applications, Benefits, and Impacts

Our approach to studying fish-structure interactions opens the possibility of directly translating physical habitat properties, as well as their changes due to restoration, into the ecologically meaningful response of fish growth. For example, findings of this project regarding energetic cost of swimming can be applied within the framework of bioenergetic modeling (to predict cost of swimming) which also opens the possibility drawing connections to population-level response. An important advantage of mechanistic models is that they are not site- or context-specific (Kearney and Porter, 2009). Thus far, the dominant approach in the science and practice of river restoration is that of correlation-based models of fish-habitat relationships that lack a solid mechanistic basis (e.g. habitat suitability index). Our work complements empirical approaches and improve the predictive capabilities available in the restoration toolbox. Even among mechanistic models, only a few account for the effects of turbulence by introducing a multiplier to correct the energy expenditure estimates based on mean flow velocity (Rosenfeld and Taylor, 2009). However, the relationship between mean velocity and turbulence intensity may vary in different flows, thus, such a correction factor cannot provide accurate results. The models we generate can be linked directly to modeled or measured turbulent flow properties (e.g., physical model) and provide expectedestimates of energy expenditure by fish.

The significance of this work is twofold. First, through the development of a quantitative model, we generate a useful tool to explore appropriate restoration strategies under various scenarios of projected climate or land use change (e.g., increased flow velocities due to elevated precipitation or runoff). Effective restoration of fish habitat in tributaries of Lake Michigan and elsewhere must account for these future scenarios (Beechie *et al.*, 2013). How much more or how much less energy fish are expected to expand to swim around a given structure if a climate-driven decrease in discharge results in altered velocity and turbulence and water temperature increases by 1°C? How can one design engineered log jams for a given project to optimize fish growth under changing hydraulic and thermal conditions? The tool produced through our work is a first step in building an approach that enables such questions to be explored quantitatively. This type of tool is urgently needed in light of the climate projection of significant changes in hydrological (Arnell and Gosling, 2013) and thermal regimes in streams. Secondly, the construction of in-stream habitat improvement structures continues to be the dominant approach to stream restoration. A vital need exists to determine exactly how these structures provide ecological benefits to fish through the modification of flow characteristics, including turbulence.

Overall, this project directly addressed one of the four National Sea Grant Program's Focus Areas: "Sustainable Fisheries and Aquaculture". Specifically, it employed a novel research strategy to better understand fish-habitat relationships and inform management, restoration, and conservation of fish habitat. Therefore, our research addressed the theme "Innovative approaches to managing and capitalizing on environmental resources". Moreover, in the regional context of the Great Lakes (including Lake Michigan), this work supports the objective of improving restoration techniques and methods (Science Strategy for Improving Great Lakes Restoration, 2012) and directly contributes to meeting research priorities outlined by the Great Lakes Fisheries Commission, especially the questions articulated in the following passage: "What attributes of aquatic habitats are essential to achieve environmental and fish community goals and objectives? (…) What are appropriate methods and metrics for determining progress in implementing environmental objectives?" (GLCF, 2015; http://www.glfc.org/research/). Finally, our project addressed specifically in-stream restoration, one of five high priority actions identified in 2020 by Lake Michigan Committee, based on the guidance included in *Environmental Principles for Sustainable Fisheries in the Great Lakes Basin* (Council of Lake Committees 2016), as critically needed to address key ecological impairments (GLCF, 2020; http://www.glfc.org/pubs/lake_committees/michigan/Lake%20MIchigan%20Committee%20Environmental%20Priorities%20April%208%202020.pdf).

4. International applications

Considering the global nature of freshwater ecosystem degradation and the mechanistic (thus, non site-specific) nature of this research, our findings have a wide international relevance for restoration science.

5. Data Management Plan

Data generated by this project are being managed and integrated by the PIs (Cienciala, Suski, Tinoco, Rhoads) and their collaborators. The following types of data have been generated:

(1) PIV - raw images are saved in TIFF format. Post-processing using the Matlab-based package PIVLab yielded instantaneous velocity fields for each time step that were then processed into .mat files through the use of Matlab. This processing yielded 6 column matrices with columns for x, y, and z coordinates, followed by U, V, and W velocity components.

(2) ADV - output from each point measurement of the ADVs comes in two files: a .hdr with th configuration details of each sample and a .dat file, in a csv format containing u, v, and w velocities, a well as correlation, SNR and amplitude data. Synthesized results after post-processing the data will be stored in MATLAB's .mat format files

(3) Accelerometers – raw data will be stored along with post-processed data in .csv format.

(4) Dissolved oxygen from respirometry experiments – raw data will be stored along with post-processed data in .csv.

(5) Videos of fish – raw videos are stored in a .mp4 format. Videos were rectified to remove fish-eye distortions and were then processed in MATLAB to yield fish location data. Due to the sheer amount of video recorded during experiments, it will not be possible for these videos to be stored on a public repository, but derived fish location data will be available through such a medium. Rectified videos will be stored and made available according to IACUC guidelines regulating the distribution of videos collected in animal facilities.

(6) Fish data – species, body length, body weight, etc. will be recorded and stored in .csv format. Metadata files will be included to explain labels of data columns and include any other critical information (comments regarding data quality issues/errors or missing data)

Data will be made accessible at no charge, per NOAA guidelines, within 2 years of completion of this project. Given the large volume of data generated, data access and sharing will be achieved via published manuscripts and upon request to any of the PIs. Data archiving on external hard will remain a shared responsibility of the four PIs.

Section C. Outputs

1. Media Coverage

Project progress and results were communicated at various points via the social media. In particular, this was done through the Twitter accounts of project personnel:

- @Piotr_Cienciala (Piotr Cienciala)
- @rafaeltinoco (Rafael Tinoco)
- @FishFizz (Katherine Strailey)
- Information tweeted by IISG @ILINSeaGrant in connection with this project was further retweeted by those listed above.

Katherine Strailey gave an interview with Carolyn Foley of IISG in 2021; to the best of our understanding, this interview has not yet been published.

2. Publications, Theses, Dissertations:

Publications:

- **Strailey, K.K**, Osborn, R.T., Tinoco, R.O., Cienciala, P., Rhoads, B.L., and C.D. Suski. 2021. Simulated instream restoration structures offer smallmouth bass (*Micropterus dolomieu*) swimming and energetic advantages at high flow velocities. Canadian Journal of Fisheries and Aquatic Sciences, 78(1): 40-56.
- **Strailey, K.K**., and C.D. Suski. Restoration physiology of fishes: Frontiers old and new for aquatic restoration. *In* Fish Physiology Vol. 39B – Conservation Physiology of Fishes. [under review]

Another manuscript is currently in preparation. We also anticipate that the collected data will result in further publications.

Katherine Strailey, a PhD student supported by this grant, is currently working towards completing her doctoral dissertation, which is based on the research completed in this project.

Oral Presentations:

- **Strailey, K.K**, Tinoco, R.O., Cienciala, P. Rhoads, B.L., and C.D. Suski. 2021. These turbulent times: interactions between fish and turbulence-generating simulated instream restoration structures and their implications for stream restoration. American Fisheries Society Annual Meeting, Baltimore, MD. November 2021.
- **Strailey, K.**, Tinoco, R.O., Cienciala, P. Rhoads, B.L., and C.D. Suski. 2020. Simulated instream restoration structures offer smallmouth bass (*Micropterus dolomieu*) swimming and energetic advantages at high flow velocities. 2020 Upper Midwest Stream Restoration Symposium, Stillwater, MN. February 2020.
- **Strailey, K**., Tinoco, R.O., Cienciala, P. Rhoads, B.L., and C.D. Suski. 2020. Simulated instream restoration structures offer swimming and energetic advantages at high flow velocities. 80th Midwest Fish and Wildlife Conference, Springfield, IL. January 2020.
- **Strailey, K.**, Tinoco, R.O., Cienciala, P. Rhoads, B.L., and C.D. Suski. 2020. Energetics and swim behavior of fish swimming in turbulent flows. 20th International Conference on Fluid Flow Problems. Chicago, IL, April 2019.

Poster Presentations:

- **Strailey, K.K**, Tinoco, R.O., Cienciala, P. Rhoads, B.L., and C.D. Suski. 2021. These turbulent times: interactions between fish and turbulence-generating simulated instream restoration structures and their implications for stream restoration. AGU Fall 2021 Meeting (virtual), December 2021.
- **Strailey, K.K**, Tinoco, R.O, Cienciala, P., Rhoads, B.L., and C.D. Suski. Incorporating Fish Physiology in Stream Restoration: The Influences of Turbulence on Fish Energetics and Positional Choice. AGU Fall 2020 Meeting (virtual), December 2020

3. Undergraduate/Graduate Names and Degrees:

All students are/were from the University of Illinois. Conferral semester is presented for graduated students; if available, expected conferral semester is presented.

- Katherine Strailey*: current PhD student, expected 2022
- Ryan Osborn*: former BS student, Spring 2019
- John Bieber*: current MS student
- Alec Fojtik*: former MS student, Spring 2019
- Toniann Keiling: former MS student, Spring 2019
- Qihong Dai: current PhD student, expected 2022
- Emily Allen: current MS student, expected Spring 2022
- Hojung You: current PhD student
- Vindhyawasini Prasad: current PhD student
- Haley Capone: former BS student, Spring 2020
- Chelsy Salas: current PhD student
- Tanya Shukla: current PhD student
- Sydney Curts: current BS student

4. Other Outputs:

Project personnel engaged in a range of outreach events in which IISG-derived research and findings were shared.

- DREAAM outreach event: Underserved 3rd and 4th grade students from the DREAAM (Driven to Reach Excellence and Academic Achievement for Males) program came to an associated laboratory space (the Ecohydraulics and Ecomorphodynamics Laboratory to learn about flow. Specific activities involved a hands-on activity where students were able to feel turbulence, then take the knowledge from their experience to figure out how turbulence affects what types of habitat fish choose, relating the topic back to restoration and other habitat changes. Students also participated in a rubber duck obstacle course, where they were further able to see how different types of turbulent flows affect movement.

- RAP research demonstrations: Two separate groups of high-school students, as part of UIUC's RAP (Research Apprentice Program) came to see and engage in demonstrations of fish research at the associated Illinois Natural History Survey Aquatic Research Facility; all students were young women, primarily rising juniors or seniors. Discussion focused on how fish energy expenses are changed by different environmental conditions, and students were able to see aspects of both laboratory and fieldwork related to this project.
- Walnut Point Stewardship Day: As part of a large educational day for 100+ 5th graders regarding environmental stewardship and science, students learned about different aspects of fish physiology, such as energetics. Specimens remaining from prior experiments associated with this project were used to show how fishes' bodies help them perform in their environments.
- General Teaching: In Fall of 2020 and 2021, Katherine Strailey incorporated her IISG-funded research into 100-level course lesson plans to demonstrate to undergraduate students how research questions are developed, how studies are designed, and how data can be analyzed to yield new scientific findings

5. Patents/licenses: N/A

6. Project partnerships: N/A

7. Related Projects:

- "Metabolic recovery of fish in turbulent flow following exhaustive exercise"
- "Turbulence training: the effect of repeated exposure to turbulent flow on fish swimming performance"

8. Awards:

- 2019 PEEC Conference Travel Award – Received by Katherine Strailey*
- "Best Poster" Award at Midwest Fish and Wildlife Conference 2020 – Received by Haley Capone and Katherine Strailey*

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