# Juvenile Coho Salmonid Energy Expenditure in a Turbulent Flow Field

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**Abstract:**

Currently, there is no consistent, predictable relationship between turbulence in the flow field and energy expended by fish in the flow. This is due to a divergence in fish behavioral response to turbulent flows; fish are either able to harness the energy in the flow and reduce their expenditure, or for the fish swim against the full amount of energy at the given location in the channel and expend a higher amount of energy (Liao 2013). The widely accepted "standard" model for calculating energy expenditure uses the velocity of the stream in the downstream (x) direction as the representation of a fish swimming speed. For this study, energy expenditure was calculated using the velocity from the x, y and z velocity components which were recorded and combined to create a high-resolution velocity measurement to represent fish swimming speed. The three dimensional swimming speed measurements were computed with day length, stream temperature and fish size to generate the output of energy expenditure (InSTREAM, 2009). Comparisons were made of the influence of turbulent kinetic energy (TKE) on energy expenditure and on the influence of strain on energy expenditure. The results were separated by fish size, which plays the greatest influence on fish energy expenditure. Strong relationships between TKE and fish energy expenditure were determined once fish were separated by size, however due to the velocity input to energy expenditure and TKE, the relationship is easily understood and is somewhat predictable. The relationship between strain and energy expenditure displays less predictability, but is expected from the methods used to compute strain. The "standard" method used to calculate fish swimming speed assume that the fish is maintaining position in the stream. To evaluate the precision of this model, two other methods of calculating swimming speed were developed and used to calculate energy expenditure. One method, using vectors to model fish motion helps quantify the fish motion in the channel as well as the water velocity. The second model is a water velocity independent measurement of the fish swimming speed that uses a measured tail-beat frequency as a proxy for swimming. These two methods have been compared to the "standard" model to evaluate the precision and to try and understand how fish swim in a turbulent flow.

**Introduction:**

Turbulent Kinetic Energy quantification of the velocity flux in the flow over time due to turbulent waters. Strain is the special gradient of velocity across the flow field. It is difficult to predict the relationship between TKE and energy expenditure of fish in a turbulent flow field due to difference in swimming mechanisms that can either raise or lower the energetic cost of swimming in turbulence. There are two distinct

possibilities of fish-turbulence interactions: the fish is able to harness the turbulent energy by exploiting the energy in vortices, or a fish must expend more energy because due to the turbulent energy in the flow. (Liao 2013) This relationship has been explored by monitoring hydraulic conditions at fish locations to analyze the energy expended at a given location for a given fish. The energy expended at a location has been plotted with the TKE values at the fish location and displays a possible lower boundary of fish harnessing the energy in the flow. My hypothesis is that there will be a clear, linear boundary of lowest values of energy expenditure for each TKE value, which would indicate the lowest energy expended for a given turbulent value. This boundary could represent the fish observations where fish are harnessing the energy of turbulence. Above this boundary, there will be a range of higher values of energy expenditure at the same TKE value, which displays that fish that are expending larger amounts of energy due to turbulence. I hypothesize that the influence of body size will have a greater influence over energy expenditure than changes in TKE or strain. Concerning the precision of measuring fish swimming velocity, I hypothesize that the methods of tail-beat frequency and vectors will display lower velocities than the standard model for the same fish observation.

## Study Objectives:

One of the initial objectives of this study was to examine the question whether fish of different sizes inhabit different regions of different hydraulic variables in the channel. This study will also examine and explain several relationships between fish energetics and hydraulic variables. The questions of how do the variables TKE and strain in the channel effect fish energy expenditure will be addressed and relationships will be displayed. The secondary objective of this study is to examine the importance and effect of body size on energy expenditure in the flow field. The effect of body size on energy expenditure will be displayed and compared to the influence of hydraulic variables on energy expenditure.

In this study, the method used to evaluate the relationship between energy expenditure and hydraulic variables assumes that the fish maintain position in the channel and are moving at the speed of the velocity in the x, y and z - directions. However the "standard" method is to assume that the fish is swimming at the speed of the stream in the x-direction only (InSTREAM, 2009). The final objectives of this study will address the assumption that fish are maintaining position in the flow. Using new methods for calculating fish swimming speed, the standard method will be evaluated to determine the precision of the model. Is the standard method an true representation of the true fish swimming velocity, or can fish reduce their swimming speed by harnessing energy in the flow?

## Methods:

The observations of this study were collected from a constructed channel on Falls Creek, in West-Central Oregon. The hydraulic measurements were made with multiple Acoustic Doppler Velocimeters (ADV) throughout the channel (shown in

Figure 1 below) to create a 10cm x 10cm x 20cm grid of velocity measurements (shown in Figure 2 below). The ADV's collected water velocity in three dimensions, and the turbulent kinetic energy (TKE) and strain, the change in velocity over space, were computed from these measurements.



Figure 1: Looking upstream at the ADV devices collecting hydraulic data
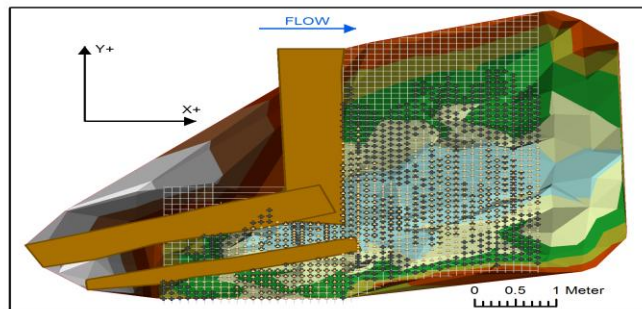Photo by Cara Walter



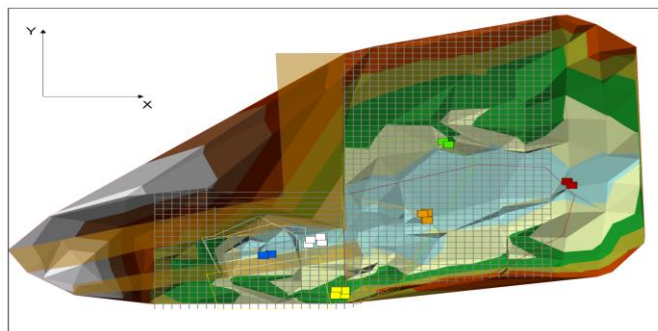Figure 2: Visualization of the 10x10x20cm grid
Graphic by Cara Walter



Figure 3: Locations of cameras in the channel (blue, orange, yellow, green, red, white)
Graphic by Cara Walter

On February 1, 19 and 20, Juvenile Coho Salmon were captured and placed into the channel at various times throughout the day. GoPro video cameras were used to observe fish behavior and location in the channel, camera locations displayed in Figure 3. As the fish moved about the channel their nose and tail location were tagged approximately every 20 seconds, shown in Figure 4 below. These precise fish coordinates were matched to the previously recorded hydraulic variables. This

generated a master data set of fish nose and tail locations (XYZ grid) with velocity (xyz components), strain, TKE, depth, distance to wood and height above the streambed as variables to analyze.

### High Resolution Velocity Measurements

The swimming speed of the fish was computed from the resultant of the x, y and z velocity vectors. This method of examining swimming speed has assumed that fish maintain position in the water column and at the speed of the stream in the x-direction. After watching the raw GoPro videos of the fish, this appeared to be a large assumption. Two alternative models were developed to attempt to quantify the fish energy expenditure without assuming a maintained position. These methods were developed and computed to evaluate the precision of the standard method of fish swimming speed measurements.

### Vector Model of Fish Swimming Velocity

The three dimensional velocity measurements were used to create a vector to represent the water flow at each point on the grid ($W_1$ and $W_2$, Figure 2 a.). To represent the velocity of the water between two points we assumed that an average of $W_1$ and $W_2$ would best approximate this value. This is how the vector of water velocity ($W_3$) was created. By using the three-dimensional coordinates of the individual fish locations, we created a vector that represented the fish motion between points 1 and 2 (Figure 2 b.). By taking the Euclidean distance between points 1 and 2 (Figure 2 b.), and dividing by the time between fish observations, measured approximately 20 seconds apart; we created a vector ($V_s$) to represent the fish motion. By subtracting $V_s$ (which is shown in a (-) direction compared to the flow) from vector $W_3$ (Figure 2, a.) the total swimming velocity of the fish ($V_e$) was calculated (Figure 2 c.). This method holds the assumption that a fish travels linearly between two points without deviating from the path.
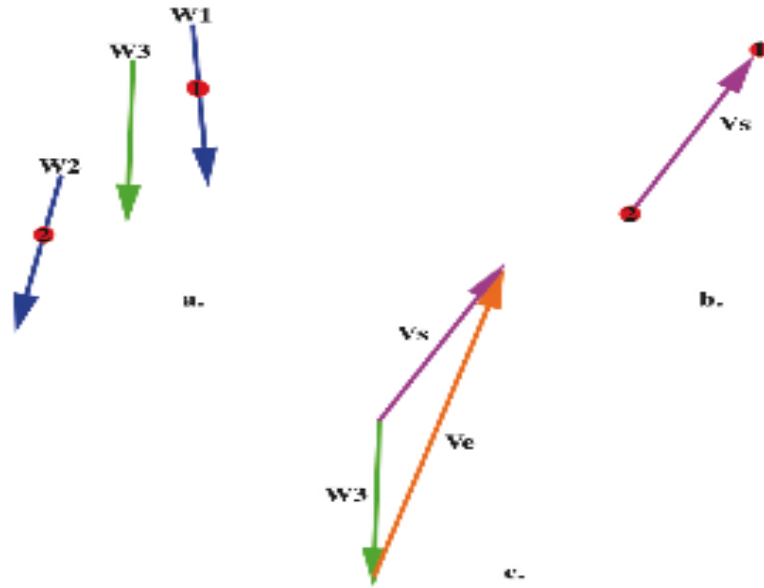
Figure 2: Representation of the methods used to calculate swimming speed with vectors. a. The averaging of water velocity vectors ($W_3$), b. The calculation of a fish motion vector ($V_s$), c. The calculation of the net fish swimming speed ($V_e$)

**Tail-beat Frequency Model of Swimming Speed:**

Turbulent kinetic energy (TKE) is a value computed from the standard deviations of the velocity measurements in three dimensions. TKE quantifies the flux of velocity in the flow over time due to turbulent waters. Strain is the special gradient of velocity across the flow field. Due to these variables being computed from velocity of the stream, there is a relationship between velocity and TKE, Figure 3, while the relationship between velocity and strain is less prescriptive, Figure 4. However, because velocity is an input for energy expenditure, there would be a pre-determined relationship between energy expenditure and TKE or strain. To effectively examine these relationships, the equation to model swimming speed should not depend on a water velocity measurement. A velocity-independent methodology to measure swimming speed will give an insight as to the efficiency of fish utilization of eddies and boundary areas as a refuge from high velocity flows and whether fish utilize the turbulence or expend more energy because of it. The method that we decided to use measured swimming speed via an equation that used fish length and fish tail-beat frequency as inputs. There is only a sixty-eight percent partial correlation between tail-beat frequency and swimming velocity due to the influence of amplitude, substrate, fork length and location (McLaughlin and Noakes, 1998). The tail-beat frequency of a fish is measured as two half-beats of the tail, or as a complete back and forth tail oscillation. For fifty-four fish observations the number of tail-beats was counted in eight seconds, and used this to find the beats per second (Webb 1984). This method of measuring swimming velocity will be able to show a difference between the previous methods that have been examined that assume that the fish is under the influence of the full velocity of the stream.
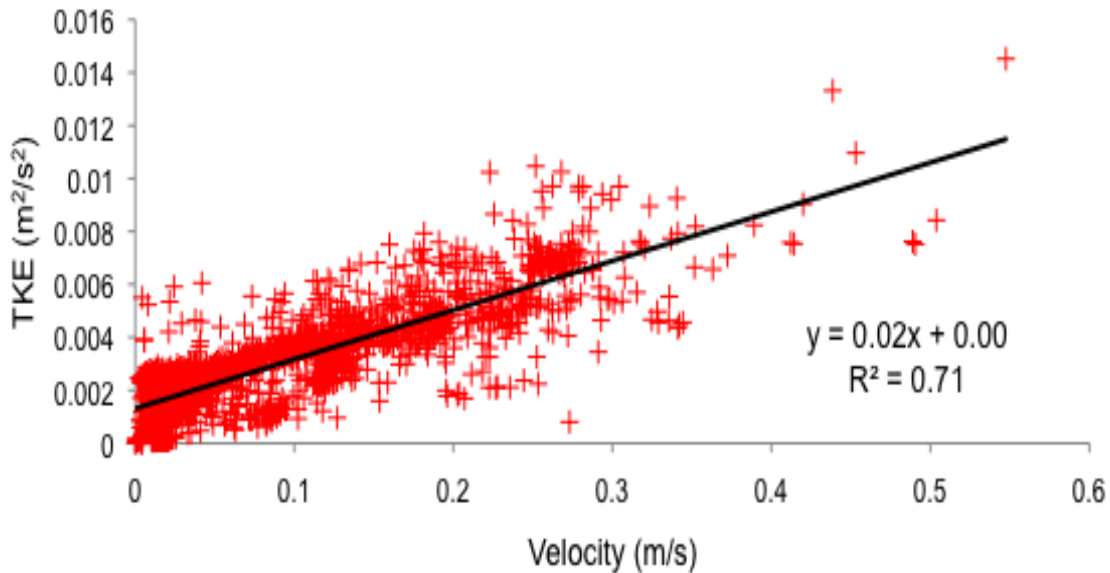
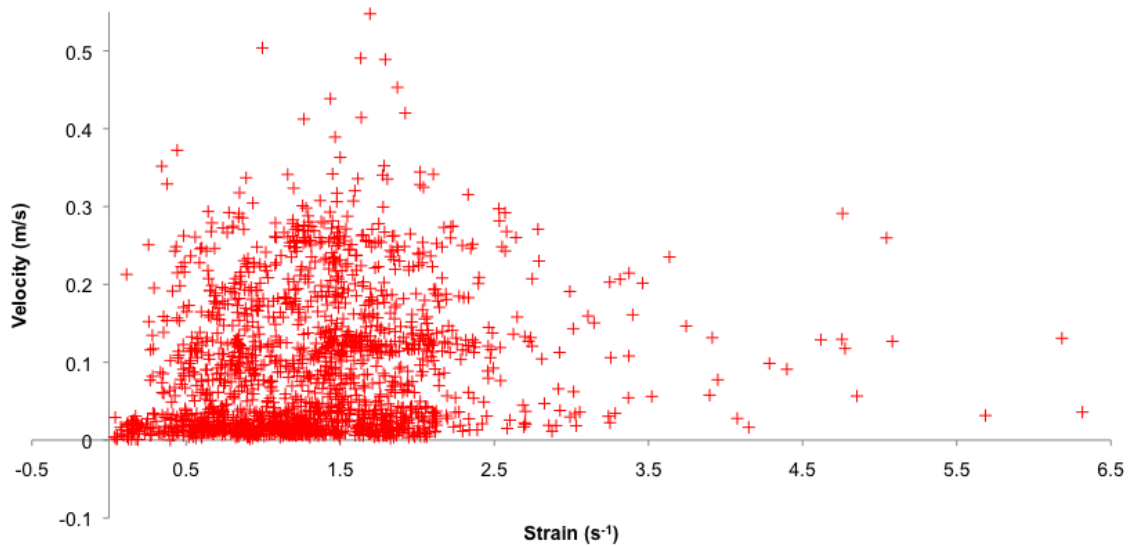Figure 3: The hydraulic relationship between TKE and stream velocity



Figure 4: The hydraulic relationship between strain and velocity

**Fish Length Measurements:**

The length of the fish in the channel was computed by using fish observations where the fish was perpendicular to the view of the camera. The nose and tail of the fish were documented on a three dimensional grid and the Euclidean distance was computed to generate the length of individual fish. Fish with more than one length measurement used an average of all calculated values. Fish without a length measurement were assigned a value equal to the average of all fish lengths.

**Modeling Energy Expenditure:**

**Equations:**

The journal, individual-based stream trout research and environmental assessment model (InSTREAM) provided equations to model the salmonid energy expenditure and mass. These models from this journal are a compilation of different studies on trout behavior, energetics and other aspects of biology and hydrology. The equations used in this research include equations to model energy expenditure and weight of the fish. The equation to compute swimming velocity from tail-beat frequency was taken from Webb (1984), which was a revision of a previous equation from Bainbridge (1958).

**Table 1: Equations used to compute energy expenditure, swimming speed and fish weight**

| # | Output | Equation | Source |
|---|--------|----------|--------|
| 1 | TKE ($m^2/s^2$) | TKE = 0.5 $(\sigma_x^2 + \sigma_y^2 + \sigma_z^2)$ <br> $\sigma$ is the standard deviation of the velocity in a given direction | Liao 2013 |
| 2 | Strain ($s^{-1}$) | $= \sqrt{\left(\dfrac{u_{i+1} - u_i}{x_{i+1} - x_i} + \dfrac{u_i - u_{i-1}}{x_i - x_{i-1}}\right)^2 + \left(\dfrac{v_{i+1} - v_i}{y_{i+1} - y_i} + \dfrac{v_i - v_{i-1}}{y_i - y_{i-1}}\right)^2 + \left(\dfrac{w_{i+1} - w_i}{z_{i+1} - z_i} + \dfrac{w_i - w_{i-1}}{z_i - z_{i-1}}\right)^2}$ | |
| 3 | Metabolism Total (Joules/Day) | $= Standard + Activity$ | InSTREAM |
| 4 | Standard Metabolism (Joules/Day) | $= (30*W^{0.784})*e^{(.0693*T)}$ | InSTREAM |
| 5 | Active Metabolism (Joules/Day) | $= (feedTime/24)*[e^{(.03*V)}-1]*Standard$ | InSTREAM |
| 6 | Feed Time (hours) | $= dayLength + 2$ | InSTREAM |
| 7 | Weight (grams) | $= .0134* L^{2.96}$ | InSTREAM Van Winkle et al. (1996) |
| L = Fish Length (cm)    W = Fish Weight (g)    T = Water Temperature (°C) <br> V = Swimming Velocity (cm/s) | | | |

All computations were conducted in Matlab (2012). By calculating the swimming speeds of fish at given locations in the channel and using the methods outlined in Table 1 (#3-7), energy expenditure of fish was computed. This involved separating the data by individual fish observation, calculating the water speed and direction, calculating the speed of the fish movement and calculating the length measurement of each fish.

Energy expenditure was calculated using four different methods of calculating swimming speed: velocity in the x-direction, three dimensional velocity measurements, tail-beat frequency and vectors were all used to effectively assess the relationship between energy, TKE, fish size and strain. Due to an apparent difference in outputs that depended on fish size, Figure 5, fish were grouped and separated by a determined size range. This allowed the results to be analyzed and a line of best fit to be created.
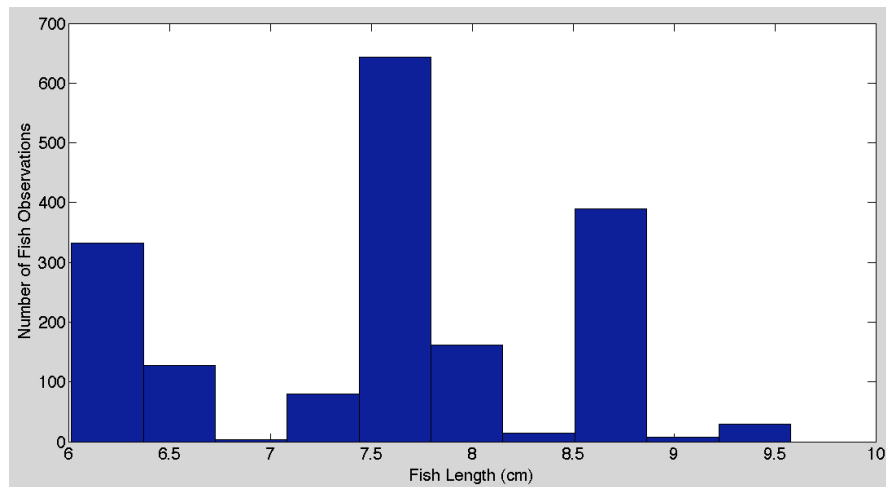


Figure 5: Histogram of the distribution of fish lengths (cm)

**Results:**

**Effect of TKE and Fish Size on Energy Expenditure**

Figures 6 – 8 display the effect of TKE on energy expenditure for a given fish size range. The observations were separated by fish size to increase the clarity and consistency of the relationship. Quadratic functions were used to form a line of best fit to the fish observations due to the high $R^2$ value that each exponential line of best fit held with the data.
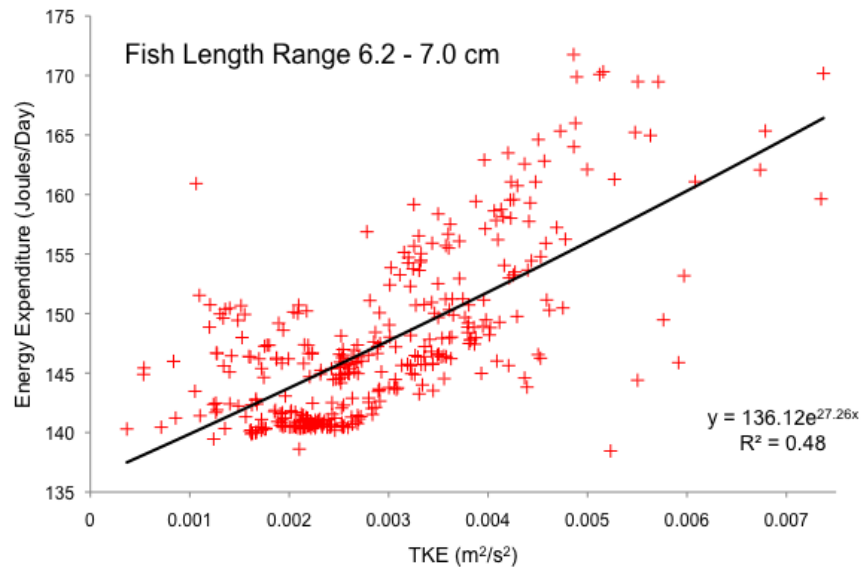
Figure 6: The effect of TKE on energy expenditure for Coho of 6.2 – 7.0 cm lengths
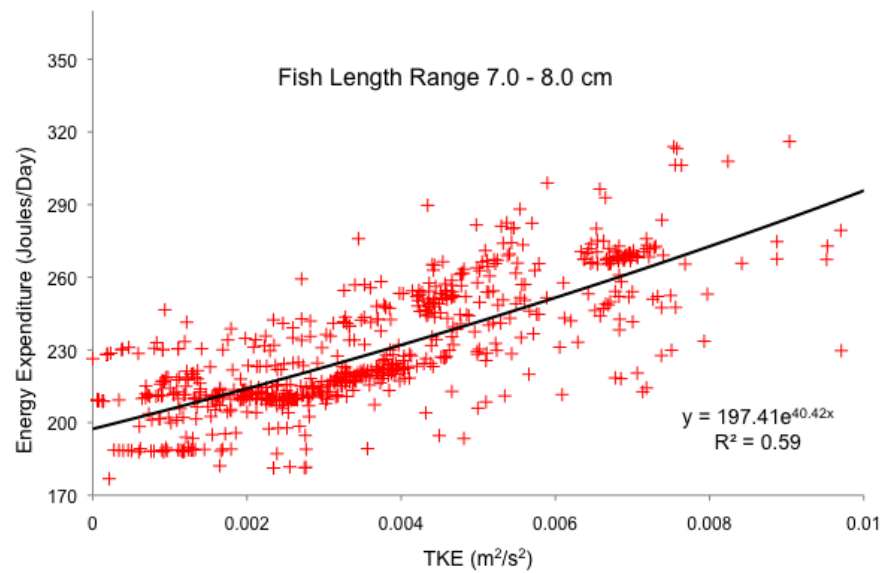


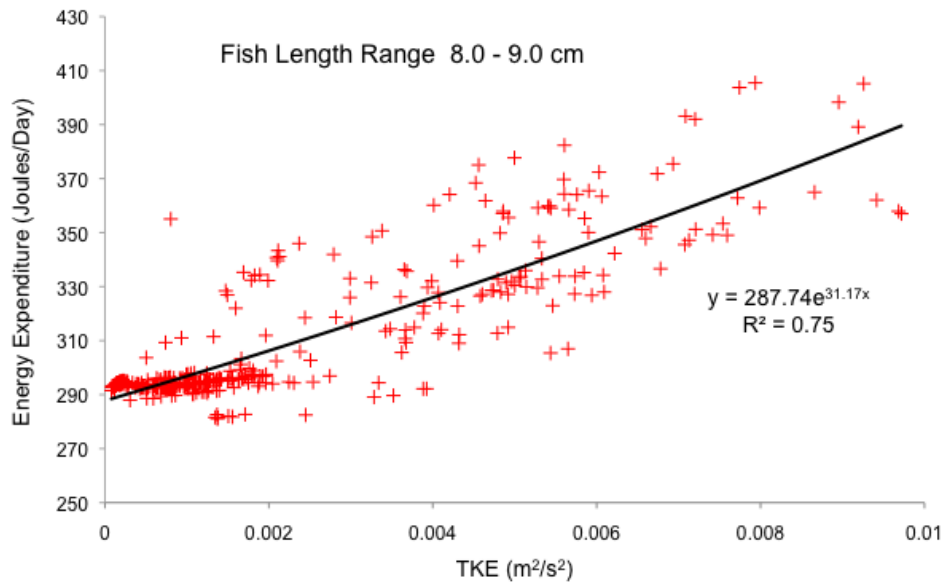Figure 7: The effect of TKE on energy expenditure for Coho of 7.0 – 8.0 cm lengths

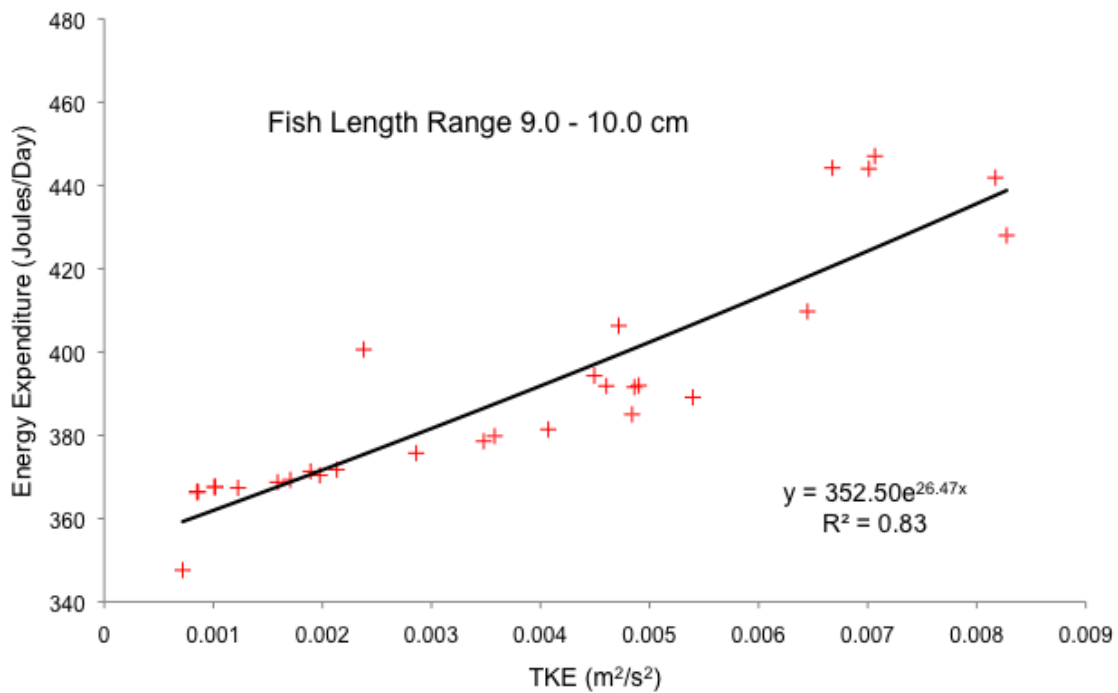Figure 8: The effect of TKE on energy expenditure for Coho of 8.0 - 9.0 cm lengths



Figure 9: The effect of TKE on energy expenditure for Coho of 9.0 – 10.0 cm lengths

The resulted line of best fit is unique to each fish size range (Table 2). Each size range has a line of best fit with a different intercept and slope that define the effect of TKE on energy expenditure. The intercept value increases with the fish size range; this indicates that there is a larger initial level of energy expenditure for fish of larger sizes than fish of smaller sizes at the same low TKE value.

**Table 2: The slope, intercept, and $R^2$ values for the relationship between TKE and energy expenditure for fish of different sizes**

| Fish Size Range (cm) | Equation Type | Slope | Intercept | $R^2$ |
|---|---|---|---|---|
| 6.2 – 7.0 | Exponential | 26.00 | 136.72 | .41 |
| 7.0 – 8.0 | Exponential | 41.27 | 196.95 | .61 |
| 8.0 – 9.0 | Exponential | 31.93 | 287.45 | .74 |
| 9.0 – 10.0 | Exponential | 27.38 | 353.40 | .68 |

**Individual Fish Model of the Effect of TKE on Energy Expenditure**

Grouping fish based on body size is an important technique to generate an equation to model the influence of TKE on energy expenditure. To examine the true effect of TKE on fish energy expenditure, individual fish were separated out from the dataset and the relationship between TKE and energy was graphed for four fish of varying lengths. Figures 11 – 12 display observations for single fish, yet due to an apparent piecewise regressional relationship, the data was divided into two significant trends represented by red plus signs and blue squares. These figured displayed two distinct relationships between energy expenditure and TKE, thus the lines of best fit were assigned accordingly. These figures display the difference in individual fish behavioral responses to changes in TKE in the flow field.
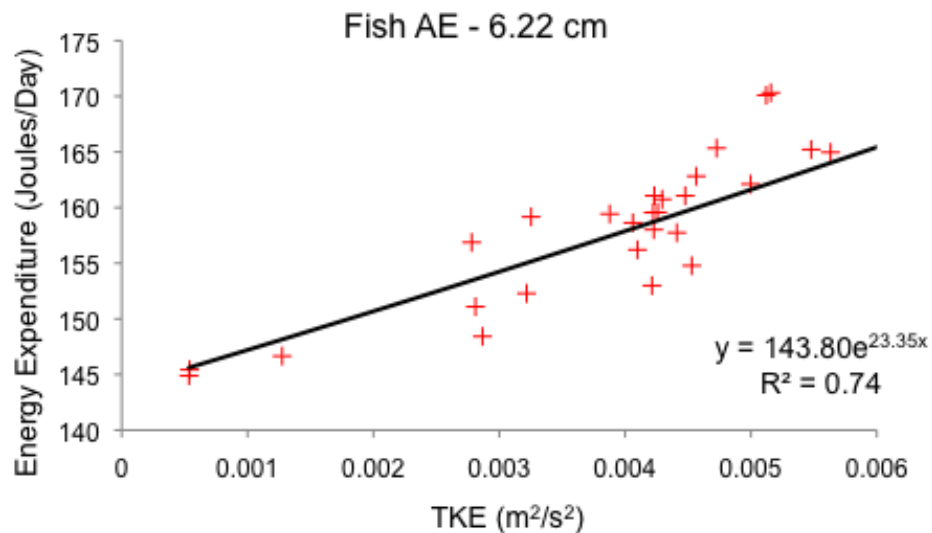


Figure 10: The effect of TKE on the energy expenditure of an individual 6.22 cm Coho "Fish AE"
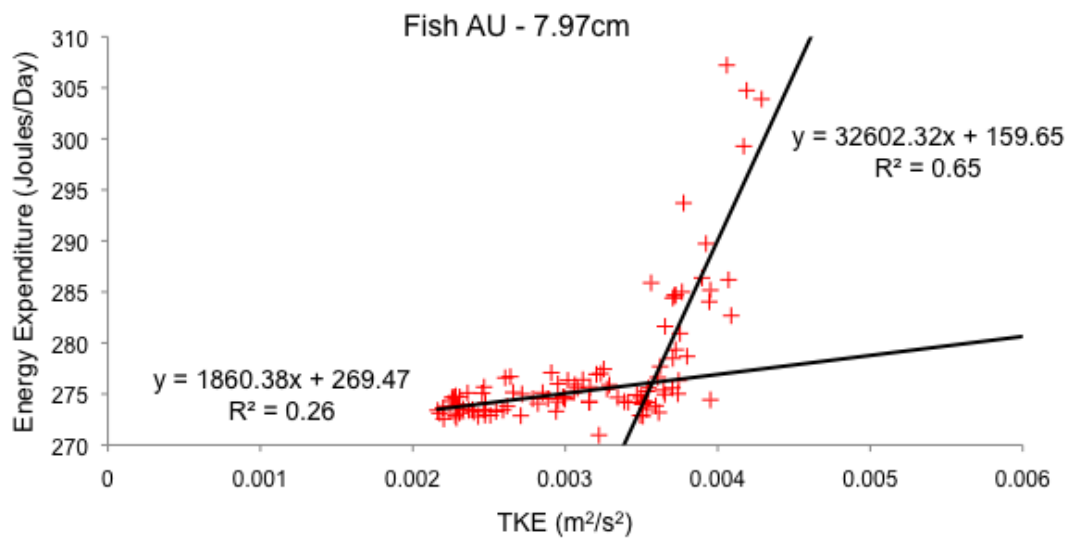
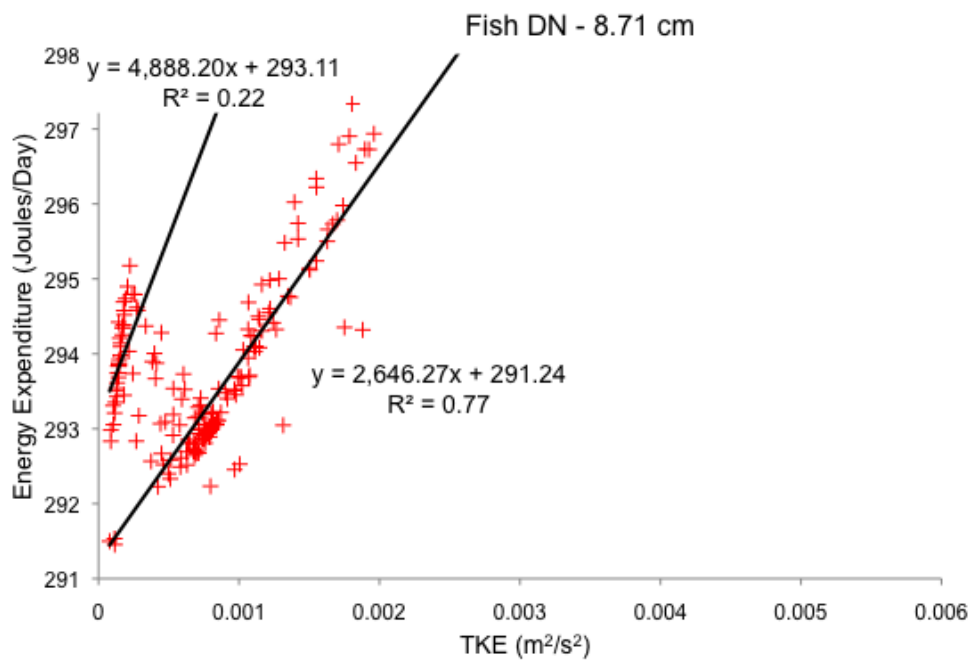Figure 11: The effect of TKE on the energy expenditure of an individual 7.97 cm
Coho "Fish AU"



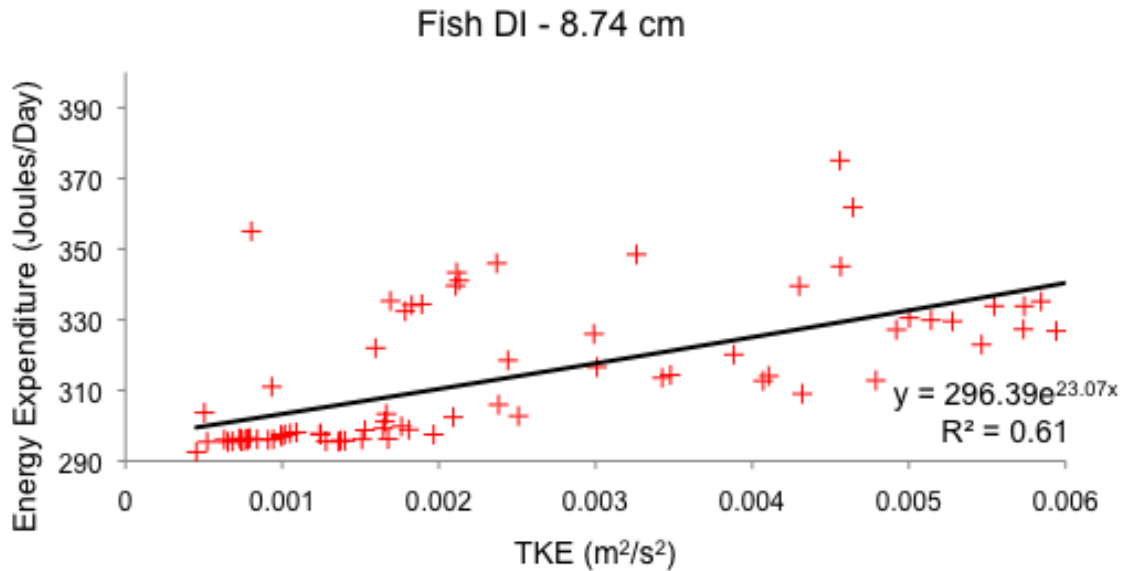Figure 12: The effect of TKE on the energy expenditure of an individual 8.71 cm
Coho "Fish DN"

Figure 13: The effect of TKE on the energy expenditure of an individual 8.74 cm
Coho "Fish DI"


**Comparing Methods for Measuring Swimming Speed**

The different methods for calculating swimming speed resulted in a difference in the
energy expenditure outputs for each given model. Using the method that assumes
the fish is swimming at the velocity of the stream in the x-direction as the standard, I
compared the methods from vector swimming speed and tail-beat frequency. The
tail-beat frequency method is compared to the standard method by using a q-q plot
in Figure 14; a q-q plot compares two measurements of the same variable around
the line y=x to observe differences in the measurement methods. There is a fairly
tight 1:1 relationship until a plateau of swimming speed from the tail-beat
frequency method around .15 m/s. The deviation from the black line, y=x, displays a
difference in the resulted swimming speed measurements between the two
methods. Below the line indicates that the standard method is over-estimating the
swimming speed.

The method of measuring swimming speed by using vectors to account for fish
motion in the stream is compared to the standard method in Figure 15. The values
follow the y=x relationship tightly, except for above 0.25 m/s there is a plateau of
energy expenditure from the method of using vectors. This indicated that at high
velocities, the standard method is over-measuring the velocity of the fish in the
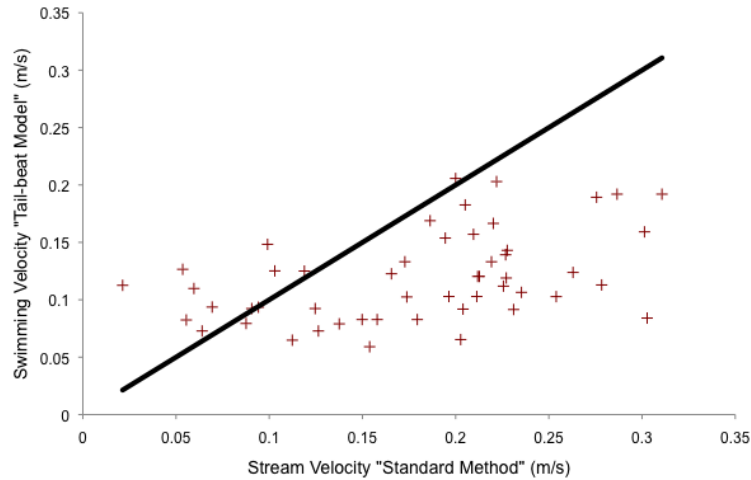stream.

Figure 14: q-q plot comparing the standard calculation of energy expenditure (InSTREAM) and a non-traditional method of using the tail-beat frequency to calculate swimming speed (Webb 1984)
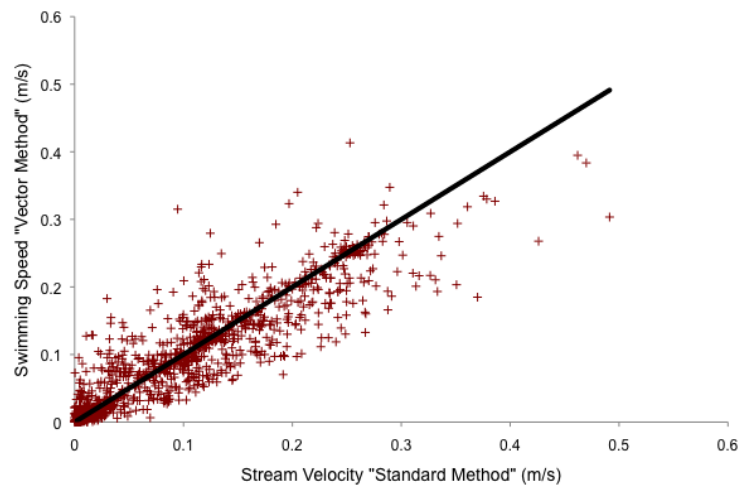


Figure 15: q-q plot comparing the standard calculation of energy expenditure (InSTREAM) and a method that we developed using vectors to represent fish motion and water velocity.

The relationship between strain and energy expenditure is less predictable than the previous correlation between TKE and energy expenditure. Strain is the measurement of the spatial velocity gradient, Table 1 (#2) higher strain indicates more velocity variance. Higher strain values indicate a greater range of velocity values, which also causes a higher range of energy expenditure rates. As strain increases, so does the range of energy expenditure rates, shown in Figures 16 – 19. This displays a consistent relationship across fish sizes.
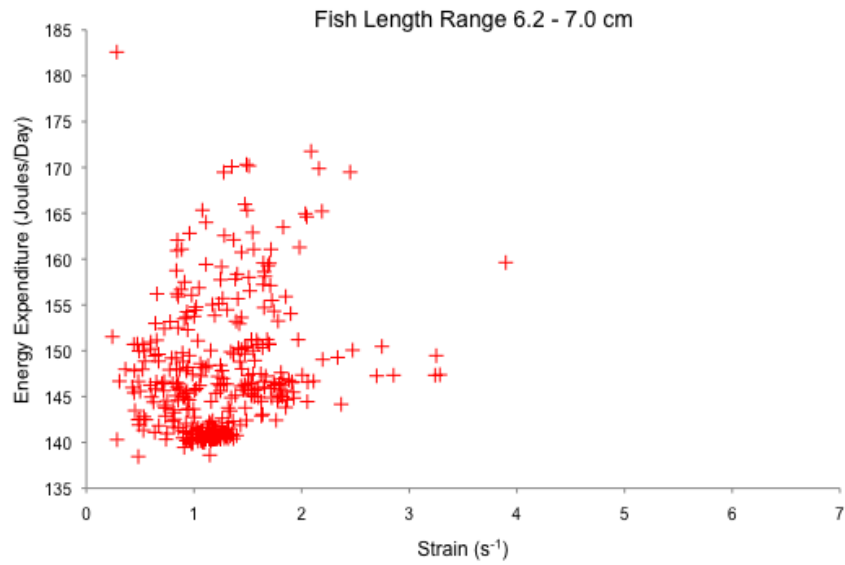
Figure 16: The effect of strain on energy expenditure for Coho of 6.2 – 7.0 cm lengths
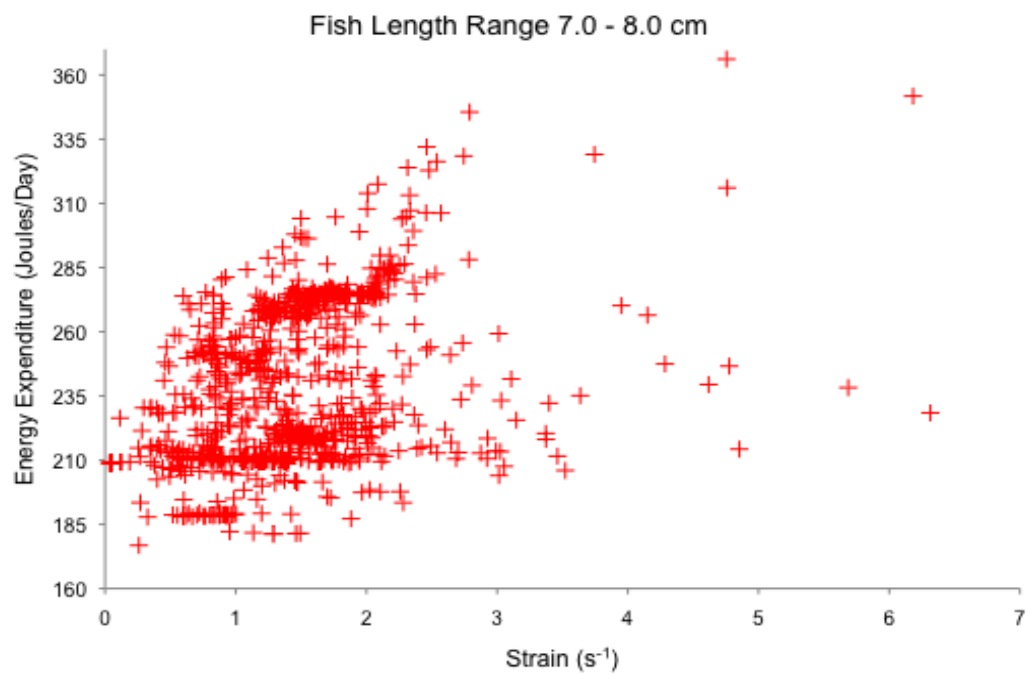


Figure 17: The effect of strain on energy expenditure for Coho of 7.0 – 8.0 cm lengths
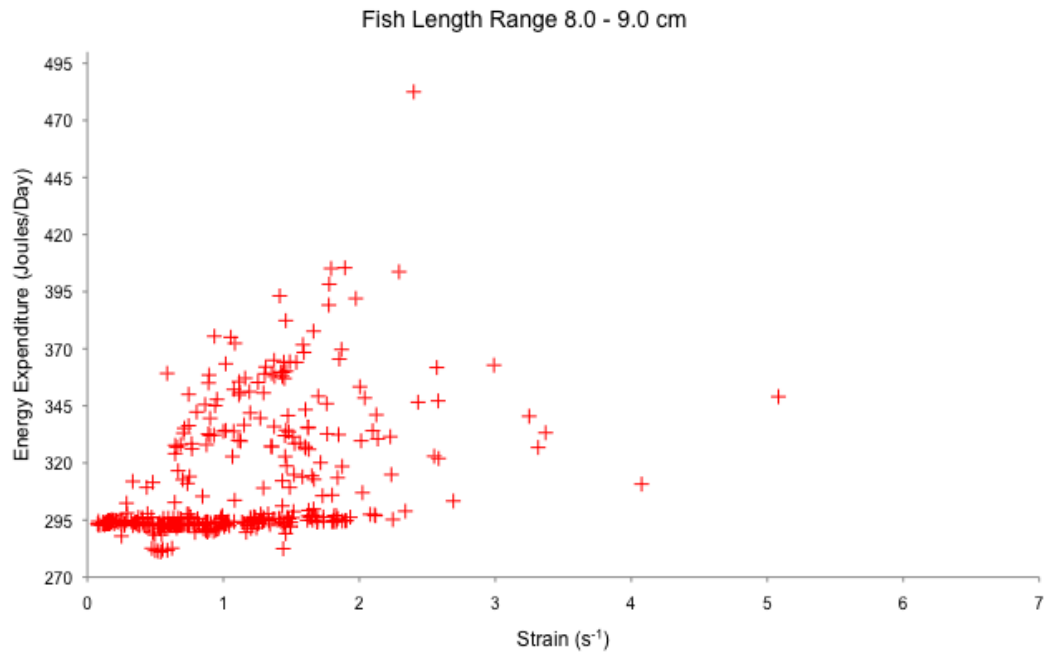
Figure 18: The effect of strain on energy expenditure for Coho of 8.0 – 9.0 cm lengths
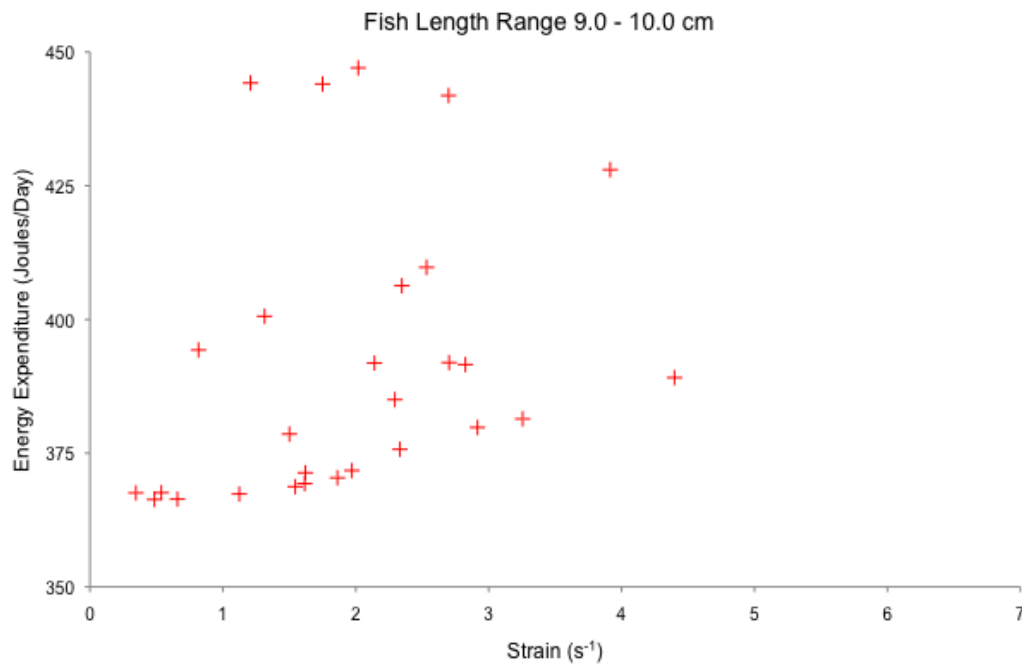


Figure 19: The effect of strain on energy expenditure for Coho of 9.0 – 10.0 cm lengths

## Discussion:

### Relationship Between TKE and Energy Expenditure

The link between metabolic cost and stream velocity has been studied, observed and quantified in two studies that used respirometry to measure oxygen consumption as a proxy for energy expenditure. The studies by Blazka et al. (1960) and Brett (1964) used a swim tunnel and respirometer to document the positive relationship between velocity and energy expenditure (Liao 2013). This relationship has continued to develop from different studies into the InSTREAM journal from 2009, developed by U.S. Department of Agriculture as the widely accepted methods from stream research. Yet, one of the topics unexplored in this journal is the relationship between TKE and energy expenditure.

One of the initial questions of this study was to examine whether fish of different sizes discriminate between turbulent habitats in the channel and use different areas of velocity and turbulence based on size. Initially, when processing the data, there was no clear relationship between TKE and energy expenditure, shown in Figure 20. When the ranges of fish lengths are highlighted in this graph, it is apparent that there is no discrimination between habitats within the flow field based off of TKE. There is a distinct change in the relationships between TKE and energy expenditure between fish of different body sizes. It is apparent that body size is a grater influence over fish energy expenditure than changes in hydraulic variables.
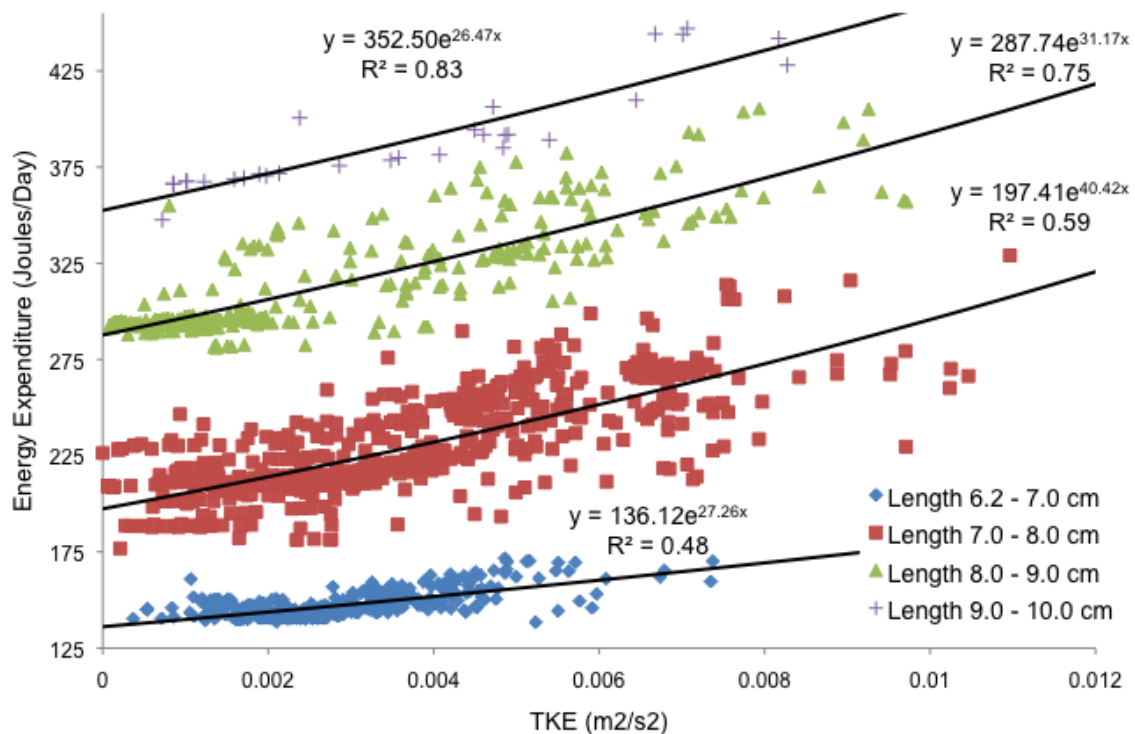


Figure 20: The influence of body size and TKE on energy expenditure for all fish

**The Effect of Body Size on Methods of Measuring Swimming Speed**

The variable with the greatest influence on fish energy expenditure is fish body size. The fish of lengths (9.0 – 10.0 cm) use approximately twice as much energy as the fish of (6.20 – 6.5 cm) for locations with identical TKE values in the stream, displayed by the intercept values in Table 2. It is clear that body size influences on fish energy expenditure, but how does body size influence on the ability of a fish to swim under a given TKE value and minimize the energy expended at that location?

While the relationship between velocity and energy expenditure has been fully examined and defined, the relationship of how turbulent kinetic energy in the flow field effects the energy expended by the fish is unclear. Fish have the ability to harness energy in the flow field through vortices and reduce their energy expenditure, or are subjected to higher turbulent kinetic energy and expend more energy to maintain position (Liao 2013). This relationship is documented and compared in Figures 6 – 9 and Table 2. The slopes from Table 2 display that the fish in the low length measurement range (6.2 – 7.0 cm) and fish in the high length range (9.0 – 10.0 cm) expend the least increase in energy expenditure for each increasing TKE value. The mid-range of fish lengths, (7.0 – 9.0 cm) display a higher increase in energy expenditure per increase in unit of TKE, displayed by the higher slope value. These results could indicate that the fish in the small length range are able to harness the energy of vortices in the flow and fish of a larger body size are less affected by changes in flow due to increased mass. Yet fish in the mid-length range are subject to high increases in energy expenditure for each TKE value. This could indicate that these fish are too large to harness the energy in vortices and too small to have the body mass to efficiently resist the increases in TKE.

For all of the middle and large fish ranges, energy expenditure is predictable at high TKE values. However, for the fish size range 6.2 – 6.5 cm (Figure 8) there is a highly varied response to high turbulence. This could be another indication of smaller fish being able to utilize the turbulent vortices to reduce their cost of swimming, while the larger fish are unable to do this due to a larger body size. This can change based on the relationship between vortex size and fish size. "When fish hold station in a vortex sheet behind a cylinder for several swimming cycles they can exploit the energy of vortices, a behavior called Kármán gaiting." (Liao 2013).

Figure 11 and Figure 12 show a highly variable relationship between TKE and energy expenditure. Juvenile Coho with a larger body size there is a highly variable relationship between TKE and energy expenditure. The different relationships of energy expenditure for Coho AU and DN displays that there is a threshold of TKE that a given body size can resist efficiently (red points) and after that threshold there is a high energetic cost to swim or maintain position in the flow field (black points). These trends are opposite between fish, which raises questions about how individual fish respond to changes in TKE across a turbulent flow field. The rapid changes in energy expenditure rates in Figure 11 and Figure 12 could represent the shift between the ability of fish to use this technique to reduce their energy and swimming against the full turbulent force of the water. This threshold is not present in all of the individual fish graphs.

Figure 10 and Figure 13 display two different relationships of TKE and energy expenditure. Fish AE and DI, Figures 11 & 13, display a more consistent relationship of the effect of TKE on energy expenditure. Across the individual fish figures there no consistent pattern that indicates a threshold of efficient TKE. This indicates that there should be more future research on the effect of hydraulic variables on individual fish.

**Velocity Measurement Comparisons**

During the 1980's, several studies came out from Donald M. Baltz and Peter B. Moyle that showed that the velocity of the stream at a specific location of a fish was related to, but less than the velocity at 2/3 the thalweg (InSTREAM, 2009). In Figure 14 and Figure 15 shown above, there is an effort to compare new methods of measuring fish swimming speed to the standard methodology derived from the x-velocity.

**Table 3: The equations used to calculate the swimming velocity of the fish**

| Name | Equation | Source |
|------|----------|--------|
| Standard | = velocity (x-direction) | InSTREAM, 2009 |
| High Resolution | = velocity (x, y, z-directions) | This Study |
| Vector | = Water velocity + fish velocity between locations | Figure 2 |
| Tail-beat | = (L * ($f$ - 2.0 L$^{-1/3}$)) ÷ 1.56 | Webb 1984 |
| $f$ = Tail-beat frequency (beats/s)    L = Fish length | | |

The first method of evaluating the fish swimming velocity uses vectors (Figure 2) to quantify the fish motion in addition to the water motion. This model is not assuming that fish are maintaining position in the stream, but it does assume that fish travel in a linear path from point to point. When this vector model is compared to the standard method of using the x-velocity, Figure 15, there appears to be a plateau of swimming speed at about 0.25 m/s. This is a definitive separation from the previous 1:1 relationship that is tracked by the black line in Figure 15. From Figure 20 it is apparent that larger fish expend the highest values of energy, especially when spending time areas of high velocity. The separation from the 1:1 relationship at 0.25 m/s displays that there is a different mechanism of swimming that reduces the fish swimming speed at higher velocities. This divergence displays that the standard method for estimating fish swimming speed is overestimating the true fish velocity for the larger size range at higher velocities. This raises the question of how do the fish of a larger body size swim more efficiently to decrease their energy expended in the flow field?

The methods to evaluate swimming speed in Figure 14 use a velocity independent measurement of fish tail-beat frequency, Table 3, to calculate the fish swimming speed. By removing the stream velocity from the equation of energy expenditure and replacing it with the fish swimming velocity, measured by tail-beats, there is no dependence of energy expenditure on stream velocity. This allows the true effect of

hydraulic variables on fish energy expenditure to be examined. This is a key method that should be used to determine how fish utilize the turbulent eddies in the flow to reduce the energy of swimming. With more observations of tail-beat frequency, this method will help determine whether fish are utilizing the energy of vortices to minimize energy expenditure in the flow. Even though there is only a 68% partial correlation between tail-beat frequency and swimming speed (McLaughlin and Noakes 1989), this equation is still useful to examine the hydraulic-biological interactions. In Figure 14, there is an apparent plateau of swimming speed at 0.15 m/s. This indicates that at higher values of velocity, the fish are finding a way to reduce their swimming speed to maintain position. This also indicates that the standard method is overestimating the swimming speed and thus energy expenditure of fish swimming in areas of higher velocity and turbulence.

The results from Figure 14 and Figure 15 display that for fish of larger body size, under higher velocities, the standard method of evaluating fish swimming speed is overestimating the velocity and therefore is overestimating the energy expenditure.

**Conclusion:**

The effect of TKE and body size on energy expenditure is clearly defined by Table 2 by comparing the slope and intercept values. Increasing TKE causes increased energy expenditure for all fish sizes, as predicted by the equations in Table 2. Despite this predictable relationship, the rates of these equations change by fish size range, displayed by the slope value in Table 2. This could indicate behavioral preferences of fish of different sizes because more preference at higher or lower velocity values would result in more observations at these locations. More or less observations at a given hydraulic environment would skew the regressional relationship in that direction. No concise conclusions can be drawn from this observation, but it would be interesting to look at in a future study.

In the data displayed in Figure 20, there appears to be a minimum energy expenditure "lower edge" that is observable for each fish size range. This lower edge the minimum amount of energy that a fish must use to maintain position in a turbulent flow. A future study examining this relationship using the tail-beat frequency method could help determine with a greater certainty the minimum energy a fish must expend to maintain position in the flow.

As strain increases, so does the variation of energy expended at a given location in the flow; this is understandable because strain is the measurement of the velocity gradient over space. More velocity variation causes more variation in the fish behavioral response and energy expenditure rate. This relationship is easily understandable, but does not offer insight to the behavioral patterns of fish swimming in a turbulent flow.

Concerning the precision of the standard method for calculating fish swimming speed, there appears to be a variation of the true swimming speed from the standard downstream velocity hypothesis for fish in areas of high velocity. In Figure 14 and Figure 15, there is

an apparent trend of the standard method overestimating the energy expenditure for fish at high velocities. This could be due to many different behavioral mechanisms including body morphology, swimming behavior or a combination of the two. More tail-beat frequency measurements will help explore and examine this relationship and quantify the true fish swimming speed and energy expenditure.

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