RESEARCH ARTICLE

Key Points:
- Coarsening the resolution of observation impacts perceived habitat selection and energy expenditure
- Coarse resolutions created biases toward lower selectivity by fish and for higher velocities
- Coarse observations may lead to overestimating energy expenditure and suitability of high velocities

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Does resolution of flow field observation influence apparent habitat use and energy expenditure in juvenile coho salmon?

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Abstract This study investigated how the resolution of observation influences interpretation of how fish, juvenile Coho Salmon (*Oncorhynchus kisutch*), exploit the hydraulic environment in streams. Our objectives were to evaluate how spatial resolution of the flow field observation influenced: (1) the velocities considered to be representative of habitat units; (2) patterns of use of the hydraulic environment by fish; and (3) estimates of energy expenditure. We addressed these objectives using observations within a 1:1 scale physical model of a full-channel log jam in an outdoor experimental stream. Velocities were measured with Acoustic Doppler Velocimetry at a 10 cm grid spacing, whereas fish locations and tailbeat frequencies were documented over time using underwater videogrammetry. Results highlighted that resolution of observation did impact perceived habitat use and energy expenditure, as did the location of measurement within habitat units and the use of averaging to summarize velocities within a habitat unit. In this experiment, the range of velocities and energy expenditure estimates increased with coarsening resolution (grid spacing from 10 to 100 cm), reducing the likelihood of measuring the velocities locally experienced by fish. In addition, the coarser resolutions contributed to fish appearing to select velocities that were higher than what was measured at finer resolutions. These findings indicate the need for careful attention to and communication of resolution of observation in investigating the hydraulic environment and in determining the habitat needs and bioenergetics of aquatic biota.

1. Introduction

Quantifying use of the hydraulic environment by stream-living biota is critical for understanding species habitat requirements and foraging ecology [*Statzner et al.*, 1988; *Piccolo et al.*, 2014], but quantifying both biotic and abiotic elements of ecosystems is subject to biases and errors associated with incomplete understanding on the effect of resolution [*Wiens*, 1989]. Measurement and modeling of hydraulic conditions in streams, although routine in practice, can be challenging to implement at resolutions that are relevant to biota. Accordingly, the resolutions most relevant to managing biota are not always clear [*Peterson and Dunham*, 2010]. This issue is not unique to the study and management of aquatic habitats. The spatial and temporal resolutions used to study a system has been shown to influence the density of landslides detected [*Miller et al.*, 2003], the degree of effect beaver dams produce on local hydraulics and temperature [*Majerova et al.*, 2015], and the perceived vulnerability of social-ecological systems to natural hazards [*Gardner*, 2015].

The issue of resolution has proven particularly important for advancing understanding of fish bioenergetics. A growing body of literature indicates that the hydraulic variability that generates turbulence at small spatial scales can impact fish swimming stability and speed [*Pavlov et al.*, 2000; *Cada and Odeh*, 2001; *Nikora et al.*, 2003; *Liao*, 2007; *Lupandin*, 2005; *Tritico and Cotel*, 2010], energy expenditure [*Boisclair and Tang*, 1993; *Krohn and Boisclair*, 1994; *McLaughlin and Noakes*, 1998; *Enders et al.*, 2003; *Liao et al.*, 2003; *Tritico and Cotel*, 2010], prey encounter rates [*Kiørboe and Mackenzie*, 1995], and habitat selection [*Smith et al.*, 2005]. However, discrepancies exist between studies regarding the impact of turbulence on fish swimming performance and foraging. *Lacey et al.* [2012] argue that these discrepancies are likely due to between-study differences in the size of eddies relative to the length of the fish. Regardless, these studies provide substantial evidence that resolutions well below the reach and cross-section dimensions are relevant to fish bioenergetics and habitat selection, indicating that the common coarse and averaged observations may not reflect the resolution of the flow experienced by the fish.

Figure 1. Experimental channel and ADV setup. Image is oriented looking upstream.

The issue of resolution is likely to be particularly problematic for the Instream Flow Incremental Methodology (IFIM), a commonly-applied approach to establishing the relationship between usable habitat and discharge [*Bovee*, 1978; *Stalnaker et al.*, 1995]. The area sampled for instream flow studies, intended to be representative of the fish's selected habitat, varies widely, from depth-averaged velocities measured at channel units [*Southern California Edison*, 2004] to narrower areas (~50 cm) around the area where fish were observed [*Boavida et al.*, 2013]. Velocity is often, but not always [e.g., *Booker et al.*, 2004; *Leclerc* et al., 2005], assumed to be one-dimensional and field measurements are spatially averaged across multiple depths and channel units [*Scott and Shirvell*, 1987]. Although recent advances in remote sensing may provide bathymetric resolutions at 1 or 4 m^2 [*Carnie et al.*, 2015; *McKean et al.*, 2009], the resolution of instream flow studies can be as coarse as 10 m^2 or larger [*Leclerc et al.*, 1995], which studies increasingly indicate [*Smith et al.*, 2005] are too coarse to accurately predict fish selection of habitat or energy expenditure. This resolution mismatch can misrepresent the suitability of fish habitat and bias estimates of fish's expenditure of energy in their hydraulic habitats.

These findings raise questions about the influence of observational spatial resolutions on perceptions of how stream-living fish use the hydraulic environment and the energetic consequences of hydraulic habitat selection. As increasingly large amounts of water and financial resources are being dedicated to environmental flows [*Richter and Thomas*, 2007] and restoration of aquatic habitats [*Bernhardt et al.*, 2005], there is a growing need to advance understanding on the spatial resolutions that are important to fish. Until recently it has been extremely challenging to address these questions outside of the confines of controlled laboratory settings, but recent advances in application of hydraulic instrumentation in the field setting [e.g., *Tullos and Walter*, 2015] and in situ observation of fish [e.g., *Myrick*, 2009] allow for very fine-grain quantification of abiotic conditions, and the biota within them, in more realistic settings.

By applying high-resolution velocimetry and underwater videogrammetry to map fish locations in outdoor experimental stream channels, we sought to evaluate if the spatial resolution of the flow field observation influences (1) the velocities considered to be representative of habitat units; (2) the patterns of use of the hydraulic environment by fish; and (3) estimates of energy expenditure. We predicted that: (1) as the spatial resolution of observation coarsened, the estimated velocity, and variability of the flow field would increase; (2) relative to available habitats, use of habitat by fish will appear less selective, and skewed towards higher values with coarser resolutions; and (3) a positive bias in energy expenditure would result with coarsening spatial resolution, resulting in overestimation of energy expenditure at coarser resolutions. These issues are relevant to understanding the bioenergetics of stream fishes, as well as attempts to apply this information for managing stream flows to benefit fish [e.g., *Bovee*, 1978; *Stalnaker et al.*, 1995].

2. Methods

2.1. Study System

This study was conducted in an outdoor experimental channel at the Oregon Hatchery Research Center (OHRC) [*Noakes and Corrarino*, 2010], located in the central Oregon Coast Range. We modified the channel to provide a 1:1 scale model (Figure 1) of a full channel log jam and associated channel topography. The stream channel bed consisted of gravel with water depths of 0.1–0.3 m and wetted widths of 1.3–4.7 m during base flow. We restricted observations of flow and fish to 4.6 m longitudinally to focus on the area

Figure 2. Example image from analysis of fish videos in VidSync.

immediately surrounding the full channel jam. The full channel jam consisted of three logs of 0.25–0.8 m in diameter. Flow for the experiments was diverted from the adjacent Fall Creek through a settling basin and kept at a constant discharge of 0.045 m^3 s^{-1}. Water temperature was measured with a digital logger (Onset Water Temperature Pro v2 Data Logger Model U22, Onset Computer Corporation, Bourne, MA) and ranged from 6 to 7.6°C during the experiments.

2.2. Observations and Data Processing
2.2.1. Fish

Wild juvenile coho salmon, *Oncorhynchus kisutch*, were collected from Fall Creek on 30 November 2012 using a seine. Lengths of studied fish ranged from 50 to 120 mm and fish mass ranged from 2.2 to 16.0 g. The fish were kept until the time of the experiments in a single, shaded, outdoor, 6' circular fiberglass tank with water from Fall Creek exchanged at a rate of 26 min. During the time they were held, fish were provided 1.5 mm pellets and salmon roe two to three times daily. Fish were placed in the channel in a group of 12 (0.6 fish m^{-2}) for trials on 1 February 2013, and in a group of five individuals (0.3 fish m^{-2}) for trials on 19 and 20 February 2013. These densities are consistent with observations of wild juvenile coho in the Oregon Coast Range [*Ebersole et al.*, 2006] and much lower than the densities that *Rosenfeld et al.* [2005] found to generate density-dependent selection of stream velocities. Fish were observed using underwater videogrammetry techniques (Figure 2). Three pairs of GoPro cameras (GoPro, Inc., San Mateo, CA) were used for the 1 February observations and six pairs of cameras were used on 19 and 20 February 2013. Observation periods were 2 h in the morning and 2 h in the afternoon of each day. After each of the trials, the fish were removed from the channel by electrofishing, euthanized using tricaine methanesulfonate (MS-222), and weighed and measured for fork length.

Coordinates for fish point locations were measured every 20 s from each of the 2 h paired videos using the 3-D videogrammetry software VidSync [*Neuswanger*, 2013, *Leitshuh et al.*, 2014]. The locations in the camera-based coordinate systems were transformed to the channel topographic coordinate system in
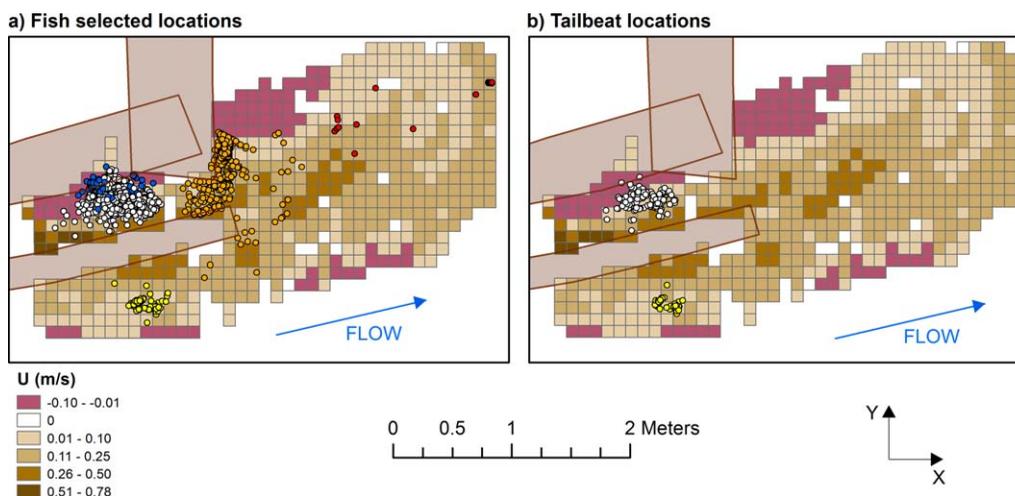

Figure 3. The locations of (a) all fish within the channel, and (b) fish locations for which tailbeat frequencies could be estimated. Point color corresponds to the camera pair used to make the fish observation. Flow moves from left to right of the figure.

Table 1. Hydraulic Characteristics at 10 cm Resolution

	Available Cells	Cells With Fish Selected Locations	Cells With Tailbeat Locations
Range (m/s)	−0.10 to 0.83	−0.10 to 0.58	−0.10 to 0.32
Mean (m/s)	0.12	0.13	0.10

Cyclone [*Leica Geosystems Inc.*, 2012] through points measured in both the underwater camera and channel topographic systems. For each grid resolution, the point locations of fish focal points were mapped to the velocity cells in which they were observed based on their coordinates using Matlab [*Mathworks*, 2015].

Fish did not use the entire flow field (Figure 3). They were observed in areas of the flow field that were adjacent to the large wood, both within and adjacent to the jet between logs, representing a range of high to low velocities. Tailbeat frequencies were assessed for a subset of all fish observations where fish were close enough and at appropriate orientations to observe tailbeats. We thus present observations in three data sets. Velocities measured across the entire study area reflect the full suite of velocities *available* to the fish [*Manly* et al., 2002]. The *selected* locations (Figure 3a) are where fish were observed and represent a subset of available velocities, whereas the *tailbeat* locations are where tailbeats were counted and thus reflect a subset of the locations where fish were observed (Figure 3b). The selected and tailbeat locations represent the limited parts of the flow field used by the fish, with velocities that have a narrower range than the available velocities (Table 1).

2.2.2. Flow Field

Following observations of fish, we measured velocities in the three orthogonal directions (longitudinal, transverse, and vertical) at a spacing (resolution) of 10 cm in all three dimensions to represent the temporal and spatial variability in velocities that represent the flow field. Velocity measurements were collected using an array (Figure 1) of four Acoustic Doppler Velocimeter (ADVs: Sontek 16 MHz MicroADV) operating at 50 Hz over 5 min for each location [*Tullos and Walter*, 2015]. Additional measurements were collected at irregularly spaced locations in regions around the wood for a total of over 1500 measured locations and nearly 17 million observations of velocities (Figure 4). The array of ADVs was suspended from an instrument platform that spanned the channel (Figure 1). Each ADV was oriented in the downstream direction based on the instrumentation frame, which was mounted on the concre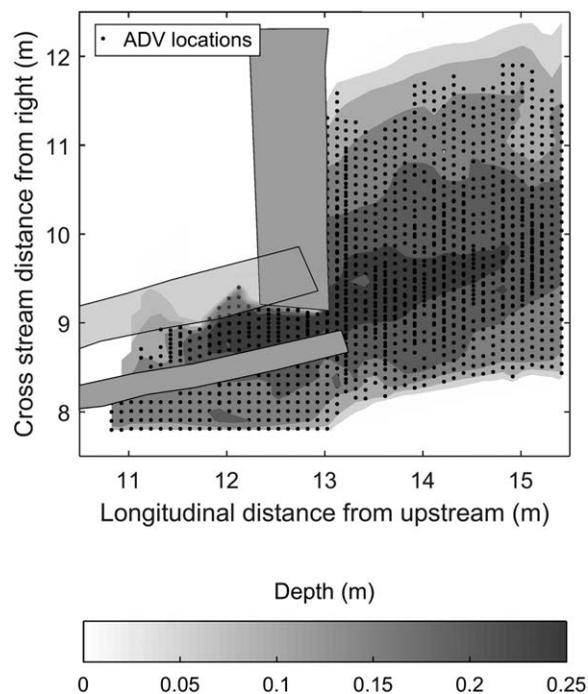te walls framing the experimental channels. The longitudinal velocities (u) reported are consistently oriented downstream based on the reference of the walls as the downstream direction, and are not rotated in any way to accommodate the change in downstream direction as flow moves through and around the wood. Velocity measurements were postprocessed in WinADV [*Wahl*, 2013] to derive summary statistics and remove observations with average correlations less than 70, average signal to noise ratio less than 15 dB, and spikes [*Wahl*, 2000; *SonTek/YSI*, 2001; *Goring and Nikora*, 2002; *Wahl*, 2003]. The values used in this analysis are the filtered average longitudinal velocities (U) for the 5 min observation period for each location from the WinADV postprocessing. The coordinates of each measurement were derived from measurements of distances between the fixed channel structures, probes, and instrument platform. Measurement coordinates were then converted to a universal coordinate system, which included the channel bathymetry surveyed using a total station (Nikon DTM 352).
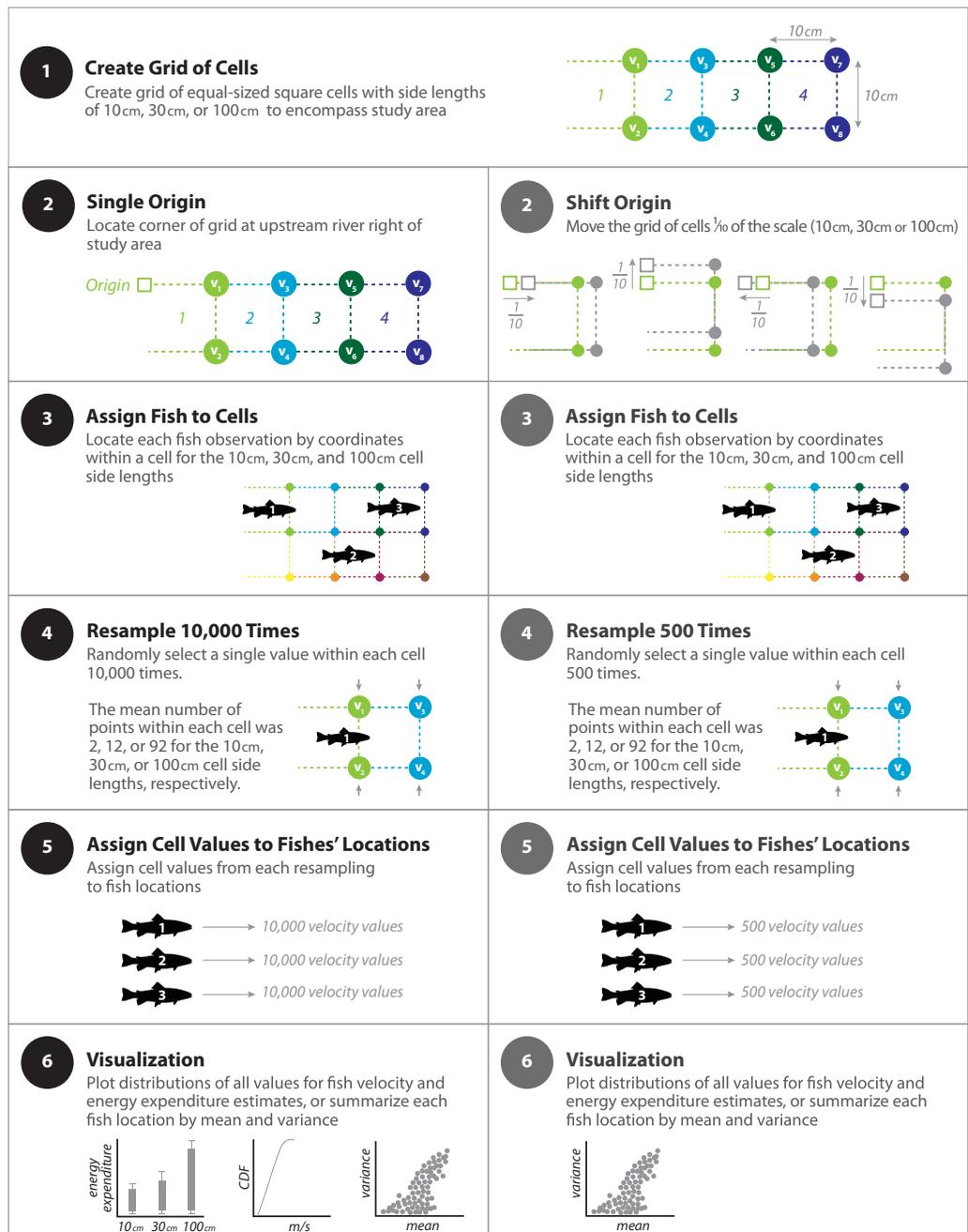

Figure 4. Channel topography, location and orientation of wood, and location of velocity observations. Flow moves from left to right in the figure.

Figure 5. Workflow of sampling algorithm for each resolution. The values at the available locations are assigned in the same way as the fish locations.

To most closely mimic how a field biologist might use a single value to represent the flow field used by fish, we aggregated longitudinal (U) velocity measurements made at the 10 cm grid spacing into increasingly larger 2-D horizontal grids consisting of square cells. This analysis focused on three grid sizes that represent the resolution of measurements often recorded by field biologists as habitat units. The 10 cm grid resolution reflects the approximate length of fish, which has been shown by some [*Pavlov et al.*, 2000; *Lupandin*, 2005] to be the resolution at which a fish's balance and the ability to maintain position are compromised, though some variability is reported in the exact ratio of body length to eddy length that impacts different aspects of fish swimming [see *Liao*, 2007; *Tritico and Cotel*, 2010 for review]. The 30 cm grid resolution is consistent with the depth of the channel in the location where fish were most commonly observed, which

is expected to generate the largest length of eddies in the flow [*Gioia and Bombardelli*, 2002]. Finally, the 100 cm grid resolution represents the width of the channel where fish were most commonly observed, consistent with the methodology often applied by field biologists where velocity for an entire cross section is represented by a single measurement or the mean of multiple measurements [*Scott and Shirvell*, 1987]. References to "resolution" or "resolutions of observation" herein refer to these three units as the grain or resolution of observation and not the spatial extent [sensu *Peterson and Dunham*, 2010].

The sampling algorithm to represent the effect of coarsening followed the following steps (see Figure 5 for details) for each resolution. First, we created a grid of cells as described in the previous paragraph. Second, we used either a single origin or multiple shifted origins, described below, to locate the grid relative to the study area. Third, we identified which cell each fish observation was located in. Fourth, we sampled a single value from the velocity measurements, where each velocity measurement is the filtered average value from the 5 min of data collected for each location, within each cell for the 10, 30, and 100 cm grids 10,000 times. Fifth, we used the 10,000 values for each cell to represent the velocity for the fish located in each cell. Sixth, we visualized the 10,000 values in multiple ways. We calculated the mean and variance for each fish location from all 10,000 values for each resolution. The effect of coarsening on the mean was investigated due to the sensitivity of means to extreme values. In addition, the full set of all values for all fish locations were used to characterize the distribution of velocities and the energy expenditure. To investigate the effect of sampling location relative to fish location within a certain grid resolution, we also shifted the origin of the grid by 1/10th of the resolution (e.g., 10 cm for the 100 cm resolution) for a total of 100 origins for each resolution. We then sampled a single value from the velocity measurements within each shifted cell 500 times.

Coarsening the grid resulted in fewer cells representing the study area, but more observations within each cell available to be sampled. The number of cells ranged from 570 cells at the 10 cm resolution to 11 cells at the 100 cm resolution. The number of measurements within each cell, from which values were resampled, increased from an average of 2 observations in the 10 cm grids to 92 observations within the 100 cm grids. The number of cells representing selected and tailbeat locations were even smaller. At the 100 cm resolution, 11 cells were required to represent the entire study area, whereas fish locations were contained within by eight cells and tailbeat locations were within only four cells.

2.2.3. Estimates of Energy Expenditure

We compared estimates of energy expenditure using a direct and indirect approach to estimate velocities experienced by the fish. Energy expenditure due to both standard and active respiration was then calculated using the same method, as described in further detail below.

The direct approach generated velocities, henceforth tailbeat (TB) velocities, based on observed tailbeat frequencies in the videos. Tailbeat velocities were estimated based on 8 s of observation of fish in the videos, with counts centered on 20 s intervals such that measurements were 12 s apart. We applied the Case II model of *Hunter and Zweifel* [1971] for rainbow trout to convert tail-beat frequency into swimming speed (equation (1)). This regression-based model was derived from video observations of fish swimming steadily in a fiberglass activity chamber over a range of 16 velocities, resulting in the model that describes how tailbeat frequency increases with swim speed and fish length [*Webb et al.*, 1984].

$$U = \frac{L}{156}\left(f - \frac{2}{L^{1/3}}\right) \tag{1}$$

where U = swim speed (m s^{-1}), L = fish length (cm), and f = tailbeat frequency (Hz). While the application of formulae developed for rainbow trout to juvenile coho salmon may lead to biases in the results, the biases were consistent among the comparisons made in this study.

For the indirect approach, the velocities measured in the cell that contained the fish (see section 2.2.2 for details), henceforth spatially matched velocities, were applied as the velocity in the energy expenditure formulae.

Finally, we estimated energy expenditure from TB and spatially matched velocities based on a modification of the models outlined in *Railsback et al.* [2009] for estimating energy expenditure from velocities. Their approach is based on the principles of energy expenditure due to both standard respiration and active respiration. The empirical model on which this analysis is based [*Van Winkle et al.*, 1996] separately calculates active respiration rates for time of active feeding (equation (2c)) versus standard respiration rates (equation (2a)) that occurs 24 h every day, and which does not include the effect of activity. Combined standard and
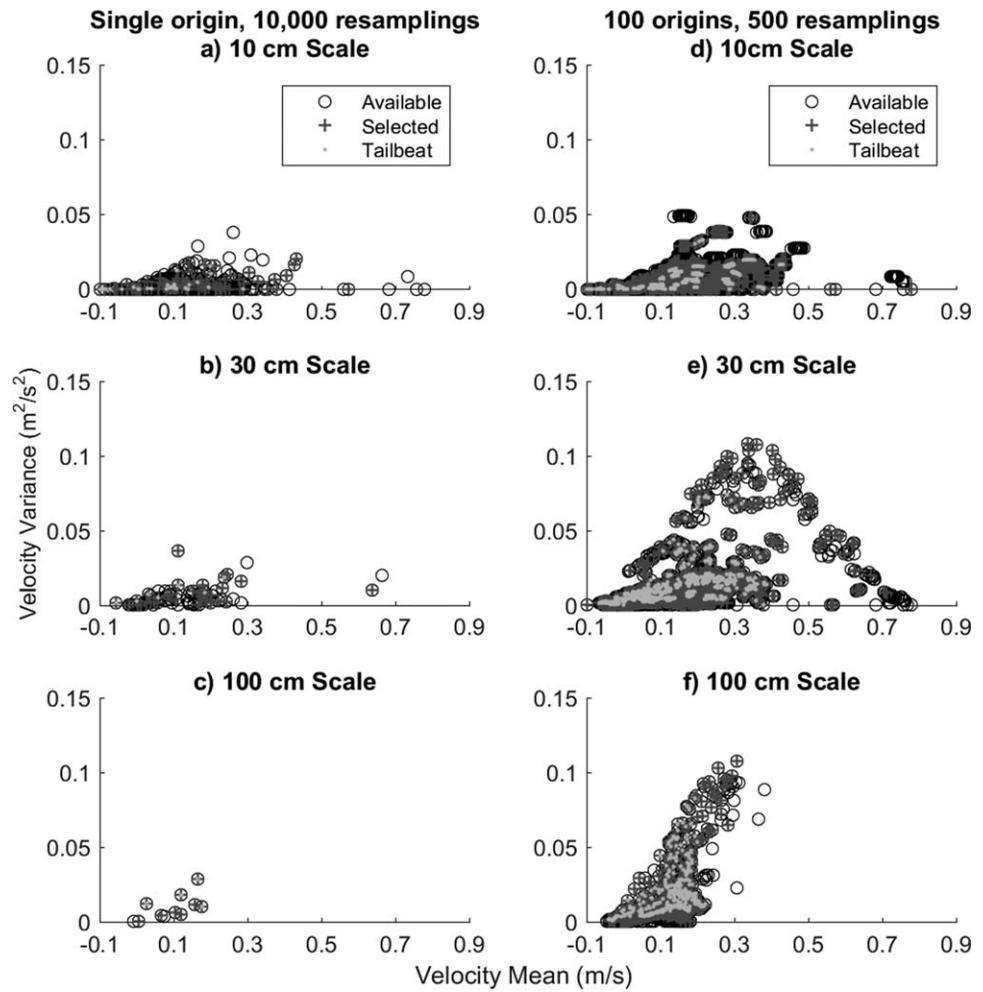
Figure 6. Mean and variance across cells for each location. Please see Figure 5 for methods on assigning velocities to fish locations.

active respiration are calculated (equation (2e)) by inserting parameters for standard respiration converted to Joules per second (equation (2b)) into the calculations for active respiration for the tailbeat observation time (equation (2d)).

$$\text{Resp}_{std}(J/day) = aW^b e^{c*T} \tag{2a}$$

$$\text{Resp}_{std}(J/s) = \frac{aW^b e^{c*T}}{24*60*60} \tag{2b}$$

$$\text{Resp}_{act}(J/day) = \frac{feedTime}{24}\left(e^{d*U}-1\right)\text{Resp}_{std} \tag{2c}$$

$$\text{Resp}_{act}(J) = obsTime\left(e^{d*U}-1\right)\text{Resp}_{std} \tag{2d}$$

$$\text{Resp}_{act}(J) = obsTime\left(e^{3*U}-1\right)\frac{\left(W^{0.784}e^{0.0693*T}\right)}{2880} \tag{2e}$$

Where W is fish weight (g), T is Temperature (°C), U is velocity (m s^{-1}), $Resp_{std}$ is standard respiration (Joules per second), $Resp_{act}$ is active respiration (Joules for the obsTime), feedTime (h/d)/24 (h/d) is the unitless portion of each day spent in active feeding, *obsTime* is observation time (s), a is an allometric constant (J/g) with a value of 30 developed for steelhead trout [*Rand et al.*, 1993], b is a unitless allometric exponent with a value of 0.784 developed for steelhead trout [*Rand et al.*, 1993], c is a temperature coefficient (1/°C) with a value of 0.0693 developed for steelhead trout [*Rand et al.*, 1993], and d is a velocity coefficient (s/m) with a
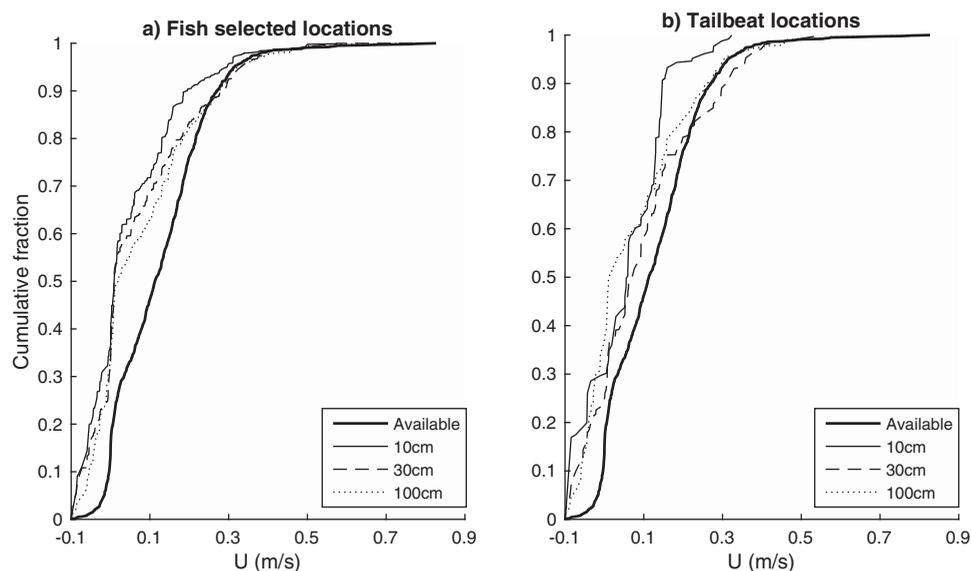
Figure 7. Cumulative density functions for (a) available (b) selected, and (c) tailbeat locations from all samples at all locations. Please see Figure 5 for methods on assigning velocities to fish locations. The distribution of available velocities did not change across resolutions because each cell was sampled evenly and therefore all values were represented regardless of resolution.

value of 3 developed for steelhead trout [*Rand et al.*, 1993]. Energy expenditure estimates are based on Joules across 8 s, rather than Joules across 24 h, as calculated by *Railsback et al.* [2009], to reflect the duration of observations from our direct observations of tailbeat frequencies.

3. Results

3.1. Effects of Coarsening on Accurately Representing Velocities

As expected, coarsening the grid cell resulted in a narrower range of values representing the hydraulic habitats (Figures 6a–6c). Since the mean is sensitive to extreme values, the reduction in mean velocity for all types of locations (i.e., available, selected, tailbeat) with coarsening resolution illustrated the impact of removing higher values that had greater representation in the finer grid cell resolution. As the resolution coarsened, the number of cells, and thus the number of possible values, decreased, resulting in fewer unique values assigned to the habitat units. However, while the range of mean velocities narrowed with coarsening resolution, only small decreases in the maximum variance was observed, shifting from 0.038 to 0.036 to 0.028 m^2/s^2 for the 10, 30, and 100 cm resolutions, respectively.

The effect of sampling location relative to fish location, illustrated by the shifting grid origin within each certain resolution (Figures 6d–6f), was to further widen the range of possible mean values and to increase the variance of those values. Variance of the flow field was particularly impacted by the moving origin, with a maximum variance for available and selected locations of 0.05 m^2/s^2 at the 10 cm resolution compared to 0.11 m^2/s^2 at both the 30 and 100 cm resolutions. With the larger spread of variance for the 30 and 100 cm resolutions, the shifting origin demonstrated how the effect of sampling location relative to fish location increases with coarsening resolution. The velocity at a fish's location could be represented by a value that is farther away for the 100 cm cell resolution than for the 10 cm cell resolution. In areas where velocity changes substantially in space, such as those around large wood and other roughness elements, where fish were most commonly found (Figure 3), this location effect is likely to result in substantial errors in velocities. Thus, this result further illustrates how one could observe a very different value to represent the flow field each time they make measurements in the coarser sample units.

3.2. Effects of Resolution of Observation on Apparent Habitat Use

Based on the mean values, fish generally utilized the lower range of velocities that were available to them (Figure 6), a relationship that did not appear to change across resolutions. In comparing the entire distribution of values (Figure 7) for each observation and resolution, the selected velocities were still lower than
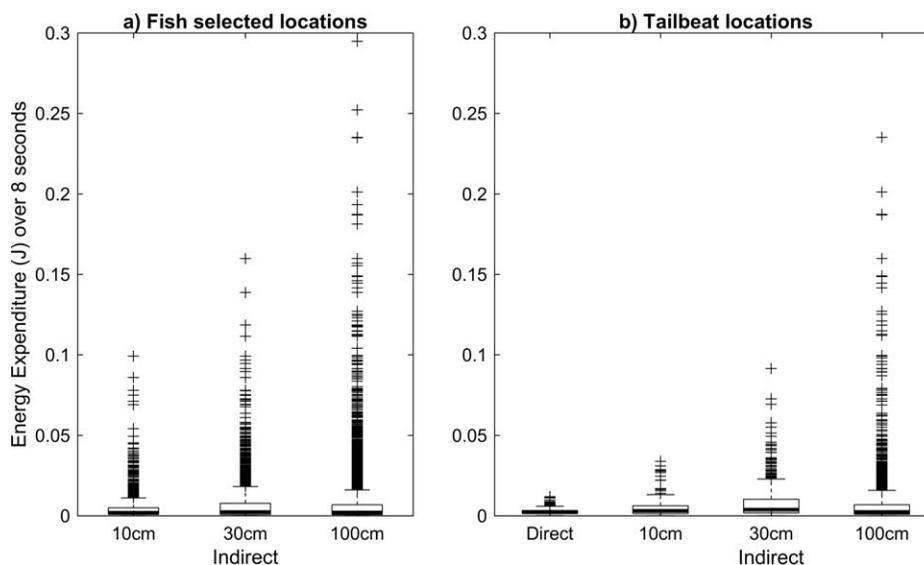
Figure 8. Box plots of energy expenditure for (a) selected, and (b) tailbeat locations. Please see Figure 5 for methods on assigning velocities to fish locations. The + symbols represent outliers, that are larger than 75th percentile + 1.5*(75th − 25th) or smaller than 25th percentile − 1.5*(75th − 25th).

those available, but an effect of resolution was evident. The cumulative fractions deviated consistently at approximately 50% and 60% for the 30 and 100 cm resolutions, respectively. The distributions with coarser resolutions indicated that higher velocities were used by fish in greater proportion than they were available for the 100 cm scale. In contrast, the finest resolution distribution indicated that the fish tended to avoid the highest velocities. This effect was most pronounced for the tailbeat locations, which represent a subset of the velocities with the lowest mean and range of values (Table 1).

Furthermore, interpreting the steepness of the distributions as selectivity, fish appeared to be most selective at the finest (10 cm) grid cell resolution. The differences across resolutions are largest for the tailbeat locations. There is a greater separation between the distributions for the tailbeat locations than for selected locations. The sensitivity of the tailbeat locations to coarsening resolution may be due to the high variability in the flow field adjacent to the tailbeat locations.

Thus, the effect of coarsening on apparently habitat use was multifaceted. Across all resolutions, it was evident that fish utilized velocities that were lower than what was available to them. However, coarser observations obscured this trend, based on the result that coarser observations indicated fish used higher velocities than what was observed at the finest resolution. The use of the mean to characterize these differences also obscured the resolution effect of coarsening.

3.3. Effects of Resolution on Estimates of Energy Expenditure

The effects of coarsening translated into impacts on the estimated energy expenditure by fish. At the locations selected by fish (Figure 8a), the effect of coarsening was to increase the range of values represented, but the median value did not appreciably change, ranging from 0.0018 J at the 10 cm resolution to 0.0020 J at the 100 cm resolution. Comparison of energy expenditure using velocities based on tailbeat frequencies (Figure 8b) to those based on spatial matched velocities illustrated that, across the entire distribution of values, the spatially matched estimates were far more variable than those based on tailbeat frequencies, and that the range of values again increased with coarsening resolution.

4. Discussion

Investigations of the hydraulic environment and bioenergetics of fish are important for sustainably managing rivers, recovering threatened and endangered species, and advancing fundamental knowledge on fish. This study demonstrated that apparent habitat use can vary with resolution of observation, location of measurement, and the statistical measure chosen to summarize the velocities. This finding is noteworthy

because modeling and measurements are generally conducted at coarse and varying resolutions, and IFIM approaches frequently rely on mean velocities, which are particularly susceptible to biases associated with extreme values.

4.1. Impacts of Resolution, Location, and Summary of Observations

The key findings relate to how we perceive the use of habitat by fish. As the resolution coarsened, there were more values possible within each cell that represented a fish's velocity since the fish's location was being associated with a larger area. Several practical impacts were observed. First, fish used lower velocities than that were available to them, but this effect was obscured by the impact of coarsening resolution, which created a bias that resulted in fish appearing to use higher velocities with coarser resolutions than for finer resolutions. Furthermore, the coarser resolutions suggested selectivity was lower than what was observed for the higher-resolution representations of the flow field. The wider distribution in coarser scales translated to a wider range of energy expenditure estimates. The results were also sensitive to the locations being sampled, with the widening range of means and variances, further illustrating how a very different value to represent the flow field can be observed each time measurements are made in the coarser sample units.

Results suggest several implications for the management of rivers and the fish that reside in them. First, the application of mean velocities in the study of biotic habitat needs is particularly problematic in studies where extreme or highly variable velocities are present, such as around large wood and other roughness elements. Second, applying a coarse resolution, and the resulting wider range of values, to instream flow studies may result in flow recommendations that are either too high or too low. The finding that coarser resolutions resulted in overrepresentation of larger values may vary across studies with physical and biological conditions, as discussed below. Third, a coarse-resolution analysis led to highly variable estimates of the energy expenditure by fish. Reliable estimates of energy expenditure have important implications for fish passage [*Fenkes et al.*, 2016] and identifying and modifying reaches to be more bioenergetically favorable to critical life stages of fish [*Hafs et al.*, 2014]. Finally, the results also highlighted the importance of selecting the location of fish within habitats, which is more pertinent in some critical life stages, when conducting instream flow and energy expenditure studies. It may be more accurate to discretize regions of the flow field based on how fish utilize them than to measure the entire flow field at high resolution, depending on whether one is interested in use (hydraulics associated with fish) or availability (what fish could use) or both (resource selection or use vs availability). For example, velocities used for foraging juveniles in energy expenditure estimates for active feeding (equation (2c)) are likely to be different than those applied in the estimation of standard respiration (equation (2a)).

4.2. Designing Robust Bioenergetics Studies

The study has a number of constraints that limit the degree of inference from the results, but these constraints are also consistent with general questions regarding the design of robust studies on fish bioenergetics. The experiments focused only on use versus availability, making no inferences or judgements regarding the quality of the habitat that was used or available or implying that lower energy expenditure was a preferred condition for fish. Fish may select a hydraulic environment that requires higher energy expenditure if it provides higher-quality and abundance of food resources that promotes net growth [*Fausch*, 1984]. Furthermore, the analysis does not consider the range of conditions that can vary across sites, such that the specific findings (e.g., coarser scales indicate higher velocities were used) may not be transferable as the nature of the biases are likely to vary with both biological and hydraulic conditions. Patterns of habitat use are known to be state-dependent [*Reinhardt and Healey*, 1999]. From the physical perspective, the appropriate resolution at which to observe a channel's dominant hydraulics changes with the size and roughness features across channels and with discharge within a channel [*Robert et al.*, 1996]. Biologically, it is likely that the biologically relevant resolution of the flow field varies with fish condition, size, and channel velocity, among other factors [*Hunter and Zweifel*, 1971; *Smith et al.*, 2005]. We expect that future investigations will find that the degree and direction of biases associated with coarsening will be associated with the spatial resolutions of turbulence perceived by the fish (biological effect) and the spatial resolutions of turbulence within the flow field (location effect) that are associated with channel geometry and obstructions (e.g., large wood).

The link to habitat suitability is methodological. These results indicated that estimates of suitability (e.g., for IFIM) or energy expenditure (e.g., for fitness based models) based on observations made at coarse or fine resolutions are likely to be different. This raises questions regarding the interpretation of individual studies, the transferability of suitability curves, and the validity of comparing across studies with observations made at different resolutions [*Lacey et al.*, 2012]. Results indicate that suitability curves could change with resolution of observation, and highlight the need to review the validity and communication of results from IFIM and bioenergetics studies that rely on velocity measurements.

Implementing robust studies on how fish exploit the hydraulic environment are nearly always difficult, and some limitations are inherent in this analysis, though none of them are expected to impact the key findings of this study. First, observations of fish do not represent independent, repeated samples. Markers on individual fish were not visible in the cameras and thus we could not identify individual fish in subsequent frames. In addition, the location of fish at time t is not independent of that fish's location at time t-1. Second, our direct estimates of energy expenditure are for an 8 s period in time and may not be consistent with estimates of net, resting, or burst expenditures reported in the literature for net energy intake models, which may be reported in Joules per day or Joules per second [e.g., *Jenkins and Keeley*, 2010]. Investigating the importance of time resolutions of observation were beyond the scope of this study. Finally, error may have been introduced in the spatially matched energy expenditure estimates from the use of relationships between fish length and weight in equations (2a) and (2c), given the sensitivity of energy expenditure to fish size [*Hunter and Zweifel*, 1971]. Because we were unsuccessful with tagging fish with unique identifiers in the experimental channels, a length-weight regression model ($R^2 = 0.75$), based on measurements collected on fish at the end of the experiment, was used to estimate length for calculating energy expenditure. However, the lengths of measured fish (mean = 84 mm, min = 76 mm, max = 94 mm) were comparable to those observed in Vidsync (mean = 76 mm, min = 50 mm, max = 120 mm) and thus were unlikely to generate a strong bias in the energy expenditure estimates.

5. Conclusions

Managing suitable habitats and flows for fish in rivers is hampered by the coarse and varied resolution of measuring and modeling the use and availability of hydraulic habitats. Despite the prevalence of research and management centered around fishes' utilization of aquatic habitats, the impact of resolutions of observation has not been thoroughly considered. This project employed high-resolution data collection to better understand the consequences of coarsening resolutions of observation on an understanding of habitat selection and bioenergetics. Results highlighted that resolution of observation did impact perceived habitat use and energy expenditure, as did the location of measurement within habitat units and the averaging of velocities to represent a unit's hydraulics. In this experiment, the range of velocities and energy expenditure estimates increased with coarsening resolution, reducing the likelihood of measuring the velocities locally experienced by fish. In addition, the coarser resolutions contributed to fish appearing to select velocities that were higher than what was measured at finer resolutions, which could, in practice, lead to overestimating the magnitude and range of velocities selected by fish and overestimating their energy expenditure. Results highlight the need for further investigation and communication around resolutions of observation, particularly under a range of physical and biological conditions.

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