Effects of water velocity and fish length on the shape and size of the foraging areas of juvenile salmonids

Tom Glass
Department of Biology, Whitman College, Walla Walla, WA 99362

ABSTRACT

The foraging areas of focal point holding juvenile salmonids typically vary widely in size and shape. Both the distance traveled to prey items (measured in three dimensions) and the resultant shape of the foraging area vary in response to extrinsic (eg. water depth and velocity) and intrinsic (eg. fish length and species) variables. Identifying the character of the relationship between these variables and foraging behavior is critical for creating robust foraging models and implementing effective stream habitat remediation strategies. Though heavily studied, the effects of water velocity on such behavior remain uncertain. Using 3D-videogrammetry techniques, I explored the effects of water velocity on the size and shape of the foraging areas of juvenile coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*) occupying streams in western Oregon. Though the low sample size and high quantity of analyses precludes any interpretation more than conjecture, vertical range of foraging areas appeared to become compressed as current velocity increased. Largely, this study highlights the necessity of further exploration of these topics.

INTRODUCTION

Stream-dwelling juvenile salmonids typically employ a sit-and-wait foraging strategy (Grant *et al.* 1989; Nielsen 1992). In this paradigm, a central position ("focal point") is held, to which a fish consistently returns following foraging and aggression forays into the surrounding water. This basic behavioral strategy has served as the theoretical foundation for a variety of in-stream space-use models (*eg.* Hughes *et al.* 2003), and as such is useful for determining effective stream habitat remediation strategies (Nislow *et al.* 1999). However, there is a large degree of variability within this focal point strategy. For example, prey detection distance increases with water depth (Piccolo *et al.* 2007), water velocity selection at night increases with light intensity (Metcalfe *et al.* 1997), and foraging efficiency varies with season (Nislow *et al.*1999). A correct understanding of the parameters that affect the various aspects of this foraging behavior is therefore paramount to creating robust models and accurately identifying habitat requirements.

Current velocity is among the most studied determinants of foraging behavior for juvenile salmonids. Aggressiveness (Grant and Noakes 1988), foraging rate (Grant and Noakes 1988), and focal point depth (Hazelton and Grossman 2009) all increase with current velocity, while response distance, (Godin and Rangeley 1989; O'Brien and Showalter 1993; Piccolo *et al.*2008), search window size (O'Brien and Showalter 1993), and prey location efficiency (O'Brien *et al*. 2001) all decrease. Interestingly, Flore *et al.* (2000) found velocity to be a positive predictor of mean prey capture distance (the distance traveled from focal point to foraging point), while Godin and Rangeley (1989) found the two to be negatively correlated, though the velocities sampled in the two studies differ considerably.

In addition to these effects, current velocity appears to have a variety of impacts on the location of prey capture points and the shape of the foraging area. Higher current velocities push mean foraging points farther downstream (Piccolo *et al.* 2008; Grant *et al.* 1989; but contradicted in Hughes *et al.* 2003), and compress the vertical range of foraging points (*ie.* fewer prey capture points at the stream surface and benthos, McLaughlin and Grant 1994). While the first of these effects makes sense (at higher velocities, a food particle will travel a greater distance in the time it takes a fish to recognize and reach it), the second is less intuitive. McLaughlin and Grant (1994) suggest that this decrease in surface and benthos capture points may reflect a shift in prey composition, which they speculate could be affected by current velocity. Hughes *et al.* (2003)

described the shape of the foraging area in the horizontal plane as a crescent, with the ends of the crescent being swept farther downstream as velocity increased. In general, mean juvenile salmonid foraging points are downstream of the focal point (Hughes *et al.* 2003; Grant *et al.* 1989), and single-central-place territories tend to be more elongated along the stream width than the length (Steringrimsson and Grant 2011). Steringrimsson and Grant (2011) described fish foraging areas in terms of eccentricity (the extent to which a shape deviates from a circle), but did so only in the horizontal plane.

This study investigates the shape of the foraging areas of focal-point holding juvenile salmonids in three dimensions, analyzing especially how current velocity affects that shape. In addition, in light of the inconsistent results regarding the relationship between current velocity and mean prey capture distance, this study revisits the effect of velocity on the position of individual prey capture points with respect to the focal point. To do so, 3D videogrammetry analysis was conducted on two species of salmonid (*O. kisutch* and *O.* mykiss) in third order streams of western Oregon.

METHODS

Field methods

I collected video footage between July 11 and August 21, 2012 on three tributaries to the Alsea River (Crooked Creek, Canal Creek, and Fall Creek), as well as one location on the Alsea itself, all near Waldport, OR. I selected sites based on known locations of focal-point-holding fish in an attempt to maximize the range of velocities represented. At each site, a snorkeler placed two GoPro HD (HERO2: Outdoor Edition) cameras on the streambed, both housed in a single side-by-side waterproof case (Eye-of-Mine 3D Flat Lens Housing), which was attached using adhesive feet to rocks.

Prior to placing the camera, the snorkeler observed each site for a minimum of five minutes to determine approximate locations of fish. Following this, s/he placed the cameras on the stream bed in a position that optimized visibility (facing across the stream), making any needed adjustments to the position of the camera within the first three minutes of filming. Recordings at each site lasted 15-30 minutes.

Figure 1 Survey site locations. Note that the Alsea River flows from east to west through the map, roughly along highway 34. The label "Alsea River" refers only to the survey location on the Alsea.

All procedure regarding 3D analysis is described in Neuswanger *et al.* (2010). In brief, the field component of this process consisted of capturing footage of a transparent box ("quadrat"), enabling the creation of the 3D coordinate system, and of a large plastic checkerboard, used to correct for lens distortion. Snorkelers filmed the quadrat once at the beginning of the season (7/11/2012), and the checkerboard twice during the season (7/11/2012 and 8/20/2012).

Analytical methods

I conducted all video analysis using the 3D videogrammetry software VidSync, described in detail in Neuswanger *et al.* (2010). VidSync enables the user to place any object that lies in the field of view of both cameras simultaneously on a 3D coordinate system, relative to the position of the cameras. Output data can be processed in spreadsheets containing the x, y, and z coordinates, as well as a timecode (and a variety of other fields) for each point.

Data collection

Collecting fish foraging data necessitated first identifying fish that were holding focal points, which was accomplished by a preliminary scan of each clip. For each target fish, I collected two datasets: forage points and focal points. Forage points were taken at the location of each feeding attempt (identified as a distinct directed movement away from the focal point, followed by the opening and closing of the mouth), and focal points were taken at the fish's location every 10 seconds, provided the fish was not moving to or from a food particle or point of aggression. I took all foraging points immediately following the closure of the mouth, and I defined all fish locations as the fish's eye facing the camera. If a fish turned completely around to catch a food particle, I waited until the original point-eye was again visible following the feeding attempt.

For each fish, I collected foraging data for five minutes, or until I had recorded 50 foraging attempts. I used no fewer than 12 foraging attempts for analysis of any fish.

Velocity calculations

I determined current velocity at each site within Vidsync by tracing suspended particles through the field of view, under the assumption that the rate of motion of the particles approximated that of the water. At each site, I collected between two and four velocity tracers. I calculated velocities manually (which represent 3D movement in the stream) from output data. As current velocity can vary greatly across small spatial extents in streams, I took care to sample particles at a variety of depths and distances from the camera, although in many cases the sparsity of particles precluded a completely representative sampling.

Fish foraging analysis

I rotated all foraging points, such that the direction of flow was oriented along the y-axis (Figure 2). I also standardized all foraging points, such that the mean focal point (calculated by averaging all focal points for each fish) fell on the origin. Such standardization allowed foraging points to be analyzed independently along each of the three axes

I analyzed the shape and size of foraging areas in terms of a variety of different representations. (See "Response Variables" in Table 2). I ran regression tests between each of these variables and both water
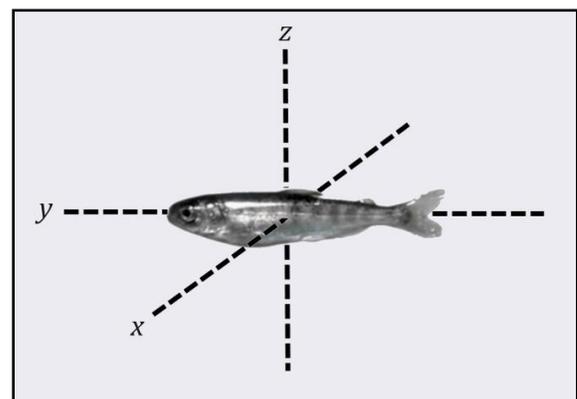

Figure 2 Orientation of axes with regard to an individual fish. Water flow is directed along the y-axis.

velocity and fish length.

Among the response variables analyzed was foraging volume. This was defined as the volume of water within which an individual fish captures prey items, and was calculated using the convhulln function in the geometry package of R (http://geometry.r-forge.r-project.org/).

To assess the shape of foraging areas, I also assessed them in terms of eccentricity. I did this for each of the three planes. Following Steringrimsson and Grant (2011), I defined eccentricity (the extent to which a foraging area deviates from a circle) as $\sqrt{a/b}$, where a = the mean distance travelled along the major axis, and b = the mean distance travelled along the minor axis. In all cases, I defined the major axis arbitrarily as the first axis in the notation for the coordinate plane, and the minor as the second (eg. in the x/y plane, the major and minor axes are x and y, respectively).

RESULTS

Table 1. Single-variable regression tests between current velocity or fish length and a variety of foraging behavior descriptors.

Predictor variable	Response Variable	Slope	Slope S.E.	R-Square	F (test statistic)	Significance F (p-value)
Current Velocity	% Captures upstream	-34.5	76.0	0.03	0.2	0.66
Current Velocity	x/z eccentricity**	1.37	0.7	0.4	3.9	0.09
Current Velocity	x/y eccentricity*	0.87	0.5	0.3	2.7	0.15
Current Velocity	y/z eccentricity	0.52	0.8	0.1	0.4	0.56
Current Velocity	Capture volume	-0.01	0.02	0.1	0.4	0.54
Current Velocity	Focal point volume	-0.001	0.01	0.002	0.01	0.92
Current Velocity	Mean capture distance*	-0.27	0.2	0.3	3.4	0.11
Current Velocity	Median capture dist.	-0.25	0.2	0.2	1.4	0.29
Current Velocity	Max capture distance**	-0.42	0.2	0.4	3.9	0.09
Current Velocity	Mean X capture dist	-0.12	0.1	0.2	1.3	0.29
Current Velocity	Mean Y capture dist	-0.14	0.1	0.3	2.4	0.17
Current Velocity	Mean Z capture dist***	-0.16	0.04	0.7	17.7	0.004
Length	Capture volume	-0.03	0.2	0.003	0.02	0.90
Length	Focal point volume	-0.05	0.1	0.03	0.2	0.68
Length	Mean capture distance	-2.20	1.6	0.2	1.9	0.21
Length	Median capture dist	-2.74	2.1	0.2	1.7	0.23
Length	Max capture dist	-0.70	2.6	0.01	0.1	0.80

I analyzed nine fish total, for each of which I collected a minimum of 12 foraging points (range: 12-52, mean: 31.2) and 23 focal points (range: 23-32, mean: 30.1). Site velocities ranged from 0.059 m·s^{-1} – 0.287 m·s^{-1}. Fish lengths ranged from 41 mm – 65 mm.

All but one of the 17 linear regressions performed yielded p-values of greater than 0.05 (Table 1), which is approximately what would be expected to be found by chance. Current velocity correlated positively with mean capture distance in the Z (vertical) direction (Table 1, Figure 3), indicating that the vertical range of fish foraging points becomes compressed as velocity increases. Current velocity also holds noteworthy positive relationships with X/Y foraging eccentricity (Table 1, Figure 4a) and X/Z foraging eccentricity (Table 1, Figure 4b), as well as negative relationships with mean capture distance (Table 1, Figure 5a), and maximum capture distance (Table 1, Figure 5b).
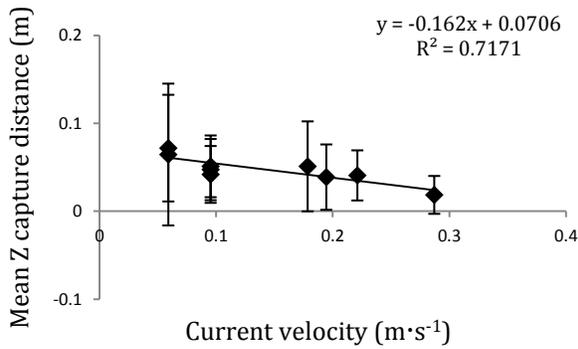
$y = -0.162x + 0.0706$
$R^2 = 0.7171$

Figure 3. Mean capture distance in the Z (vertical) direction, plotted against current velocity. Error bars represent one standard deviation.

(a)
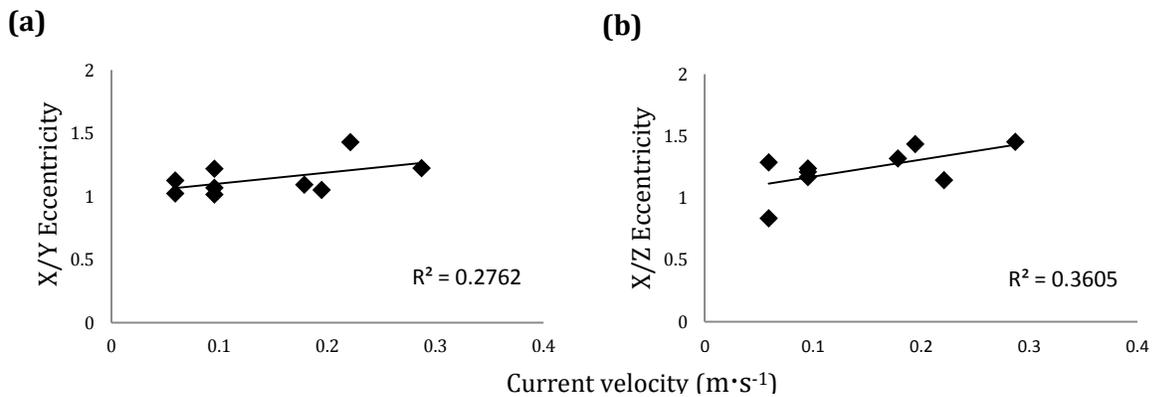
(b)

$R^2 = 0.2762$

$R^2 = 0.3605$

Current velocity (m·s⁻¹)

Figure 4. Foraging area eccentricity plotted against current velocity in the (a) X/Y plane, and (b) X/Z plane.

(a)

(b)

$R^2 = 0.3284$
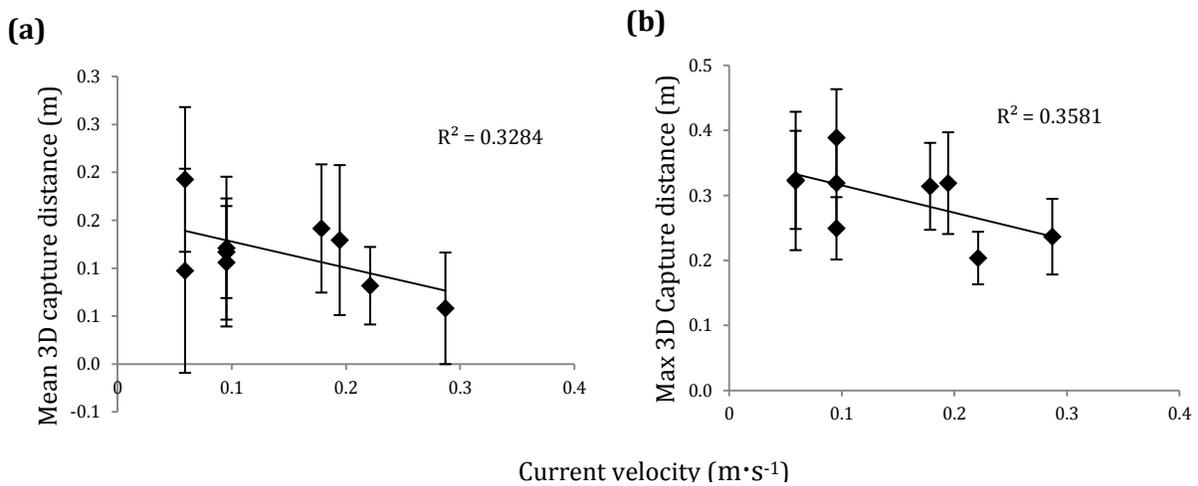
$R^2 = 0.3581$

Current velocity (m·s⁻¹)

Figure 5. Mean (a) and maximum (b) 3D capture distance plotted with current velocity. Error bars represent one standard deviation.

DISCUSSION

The quantity of analyses performed in this study severely limits the credibility of the results. In addition, the low sample size increases the probability of finding high correlation coefficients by chance. With this in mind, interpretation of the data is largely conjectural. That said, the relationships found between current velocity and mean z capture distance, x/y and x/z eccentricity, and mean and maximum 3D capture distance all warrant a call for further study. In such studies a larger sample size is needed to generate any significant correlative results.

My data suggest that the vertical range of a foraging area becomes compressed as the current velocity increases, which is consistent with one previous study (McLaughlin and Grant 1994). However, the survey protocols, as well as the site and fish characteristics differ considerably between the two studies. McLaughlin and Grant (1994) assessed vertical position in terms of the proportion of feeding attempts that took place in each of three zones: the benthos, midwater, and at the surface. The proportion in the midwater zone varied widely (from 0-1.0) at lower velocities, but approached 1.0 as the current velocity increased. Conversely, the proportion at the benthos and surface both decreased. This categorical approach may have obscured any finer relationship between vertical position and water velocity, and as such does not provide an ideal point of comparison for my study. The current velocities and fish lengths sampled both differ considerably between the present study and that of McLaughlin and Grant (1994) (present study: fork length range: 41-65 mm, velocity range: 0.06-0.29 m·s⁻¹; McLaughlin and Grant [1994]: fork length range: 16-27 mm, velocity range: 0-0.14 m·s⁻¹). In addition, my data do not suggest any such wide variation at lower velocities as found by McLaughlin and Grant (1994), but rather a more strict linear clustering. This could be attributable to the lower range of velocities sampled by McLaughlin and Grant (1994), and perhaps simply suggests that the vertical capture distance of fish occupying near-zero velocities is less likely to be affected by velocity than that of those fish occupying moving water. To the best of my knowledge, this study is the only which has assessed this relationship within these particular distributions of velocity and fish length, and it suggests that, as fish grow and move into regions of higher current velocities, their vertical movement becomes more restricted by the current velocity itself.

This effect is intriguing for a variety of reasons. First, the same effect is not seen for either of the other two axes, suggesting that the fish are not simply travelling shorter distances at higher velocities, but actually uniquely experiencing a vertical compression. Possible explanations for this include: (a) A reduced vertical search window at higher velocities. O'Brien and Showalter (1993) found a negative correlation between search window width and velocity, but did not assess search window height. (b) More severe effects of vertically-variable turbulence at higher velocities. Fish occupying higher velocities may have to cross a wider range of turbulence intensities when moving vertically through water than when moving horizontally, and this effect may be stronger at higher velocities. It should also be noted that water depth inevitably affects vertical movement, a factor not accounted for in this study. In general, fish utilized the complete range of available water in the vertical direction, indicating that the effect of depth could be significant. Moreover, depth and velocity are likely correlated, in which case velocity could simply exist as a measure of depth.

X/y and x/z eccentricity also yielded tentative positive relationships with current velocity. Steringrimsson and Grant (2011) found the territories of juvenile salmonids to be more elongated along the x-axis than the y-axis, but did not assess how this elongation is affected by current velocity. In the x/z plane, this loose relationship correlates with the absolute compression of mean vertical capture distance discussed above. Interestingly, no such absolute compression is seen in the y direction (neither is there seen an expansion in the x direction), but x/y eccentricity shows a nearly-significant relationship with water velocity. This suggests that juvenile salmonids may rely

primarily on other (non-velocity) factors as determinants of foraging area size (as has been found in this study), but that the foraging area shape itself may be determined by water velocity.

Mean and maximum 3D capture distance showed a loose negative relationship with water velocity. An economic framework of fish foraging locomotion suggests that fish travel shorter distances to capture food as the energetic costs associated with swimming in higher current velocities increase. Godin and Rangeley (1989) found this to be supported by experimental observation. Interestingly, by tethering food items in place and varying current velocity, Godin and Rangeley (1989) also determined that this reduced capture distance is not a result of differential prey drifting speed, but an impact of the swimming costs associated with the water velocity itself. The results of my study are consistent with such findings. Though Godin and Rangeley (1989) assessed the capture distance only in the streamwise (y) direction, the underlying principle makes intuitive sense in three dimensions as well. It is likely that this response is characterized by a threshold distance (which may increase with the size of the prey item), above which a fish foregoes an attack due to higher energetic costs, as is suggested by central-place foraging theory (Stevens and Krebs 1986).

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