

Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*)

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Abstract: We examined the effects of water velocity on prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) in laboratory experiments. We used repeated-measures analysis of variance to test the effects of velocity, species, and the velocity \times species interaction on prey capture probability, prey detection distance, and swimming speeds during prey capture. We used 3D video analysis to assess the spatial and temporal characteristics of prey detection and capture. Coho and steelhead showed significant, velocity-dependent decreases in capture probability (~65% to 10%, with an increase of velocity from 0.29 to 0.61 m·s⁻¹) and prey detection distance, with no effect of species and no velocity \times species interaction. Neither velocity nor species affected prey interception speed; fish intercepted prey at their predicted maximum sustainable swimming speed (V_{max}) at all velocities. Speed of return to the focal point increased significantly with increasing velocity, with no effect of species. At faster velocities, return speeds were faster than V_{max} , indicating potential increases in energetic cost because of anaerobic swimming. The 3D analysis suggests that the reduction in capture probability was due to both reduced prey detection distance and a uniform decline in detection probability within the prey capture area.

Résumé : Nous examinons lors d'expériences en laboratoire l'effet de la vitesse du courant sur la détection et la capture des proies chez de jeunes saumons coho (*Oncorhynchus kisutch*) et truites arc-en-ciel anadromes (*Oncorhynchus mykiss irideus*) qui se nourrissent dans la dérive. Une analyse de variance à mesures répétées a permis de tester les effets de la vitesse du courant, de l'espèce et de l'interaction vitesse \times espèce sur la probabilité de capture des proies, la distance de détection des proies et la vitesse de nage durant la capture des proies. Une analyse vidéo 3D a servi à déterminer les caractéristiques spatiales et temporelles de la détection et de la capture des proies. Les saumons et les truites connaissent des diminutions significatives des probabilités de capture (~65 % à 10 % lors d'une augmentation de vitesse de 0,29 à 0,61 m·s⁻¹) et de la distance de détection des proies en fonction de la vitesse de courant; l'espèce et l'interaction vitesse \times espèce restent sans effet. Ni la vitesse du courant, ni l'espèce n'affectent la vitesse d'interception des proies; les poissons interceptent les proies à leur vitesse maximale prédite de nage soutenue (V_{max}) à toutes les vitesses du courant. La vitesse de retour au point focal augmente significativement en fonction de la vitesse du courant, mais sans effet de l'espèce. Aux vitesses du courant les plus grandes, la vitesse de retour dépasse V_{max} , ce qui indique un accroissement potentiel du coût énergétique à cause de la nage anaérobie. L'analyse 3D laisse croire que la réduction de la probabilité de capture peut être due autant à la diminution de la distance de détection de la proie qu'à un déclin uniforme de la probabilité de détection dans la zone de capture des proies.

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Introduction

Stream salmonids often drift-feed, maintaining a position in the stream channel and capturing invertebrate prey as it is delivered by the current (Bachman 1984; Fausch 1984;

Hughes and Dill 1990). For drift feeders, selecting a position in faster water is assumed to be a trade-off between the benefit of encountering more prey (i.e., encounter rate) and the energetic cost of foraging in faster water (Fausch 1984; Hill and Grossman 1993). Ecologists have incorporated drift

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feeding into energetics-based models that predict stream salmonid distribution (Hughes and Dill 1990; Hughes 1992; Guensch et al. 2001), energy intake (Hill and Grossman 1993; Hughes et al. 2003), and growth (Hughes 1998; Hayes et al. 2000; Nislow et al. 2000). Water velocity plays an important role in these models because it determines the prey encounter rate, the probability that a fish will capture a prey (i.e., capture probability), and the swimming costs for a fish at a given stream position (Fausch 1984; Hill and Grossman 1993; Hughes et al. 2003). To date, researchers have found that drift-foraging models are more sensitive to changes in benefits (e.g., prey encounter rate) than they are to changes in costs (Hughes and Dill 1990; Hill and Grossman 1993, but see Hughes et al. 2003 for a discussion of prey capture costs). This underscores the importance of identifying how water velocity affects the fish's ability to detect (i.e., observe) and capture prey. Hughes et al. (2003) noted that developing models to more accurately predict energy intake rates of drift feeders will require a better understanding of how habitat factors such as water velocity influence a prey detection and capture probability.

Despite the importance of water velocity in drift-foraging models, few studies have addressed how velocity influences capture probability in drift-feeding salmonids. Increasing velocity may reduce the distance at which prey are detected or captured (i.e., detection and capture distance) (Godin and Rangeley 1989; Hill and Grossman 1993; O'Brien and Showalter 1993). O'Brien et al. (2001) found that increasing water velocity decreased capture probability and capture distance for Arctic grayling (*Thymallus arcticus*), but they did not find an expected increase in foraging rate (number of prey captured per unit time). They suggested this may be due to a trade-off between increasing encounter rate and decreased prey detection ability as water velocity increases. They also found that the amount of time searching for prey (search time) and the time it took to intercept prey (interception time) were not affected by water velocity. This is important because drift-foraging models rely on estimates of these times (Hayes et al. 2000; Guensch et al. 2001; Hughes et al. 2003), but to date little is known about how water velocity influences these times.

Although drift-foraging models have been used to predict habitat selection for two or more sympatric species (Hill and Grossman 1993; Braaten et al. 1997; Guensch et al. 2001), there have been no comparisons of the effects of water velocity on two sympatric drift feeders. This represents a gap in our understanding of habitat selection, because velocity-based habitat segregation has been documented for a number of sympatric pairs of salmonids (Hartman 1965; Everest and Chapman 1972; Bremset and Berg 1999). If fish segregate habitat based on their potential to maximize net energy intake (energetic gains minus energetic costs) at their respective positions (e.g., Fausch 1984; Hill and Grossman 1993), it ought to be possible to identify the mechanism that allows them to do so at different velocities. Werner and Hall (1979), for example, showed that differences in body morphology among three species of sunfish facilitated habitat segregation based on foraging efficiency. Differences in body morphology have been suggested as one explanation for habitat segregation in stream salmonids (Bisson et al. 1988), but no experimental tests have confirmed this.

Juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) occur sympatrically in freshwater streams (Groot and Margolis 1991; Behnke 1992; Nakano and Kaeriyama 1995), where they often drift-feed (Everest and Chapman 1972; Nielsen 1992). Although they are found within the same stream reaches, they have been documented to segregate microhabitat, with coho using pools and steelhead using riffles (Hartman 1965; Bisson et al. 1988; Bugert and Bjornn 1991). Bisson et al. (1988) proposed that coho may be better adapted to forage in pools because they have a laterally compressed body form with long median fins, which facilitates rapid turning and acceleration. Steelhead may be better adapted to foraging in riffles because they have a more cylindrical body form with shorter median fins, which minimizes drag during foraging maneuvers.

Our objective was to assess the influence of water velocity on prey detection and capture by juvenile coho and steelhead. We used three-dimensional (3D) video analysis of stream tank foraging experiments to test these hypotheses: (i) capture probability declines with increasing water velocity, and (ii) there are species-specific differences in capture probability, prey detection distance, prey interception speed, and speed of return to the focal point that might facilitate foraging in their respective preferred habitats.

Materials and methods

Stream tank

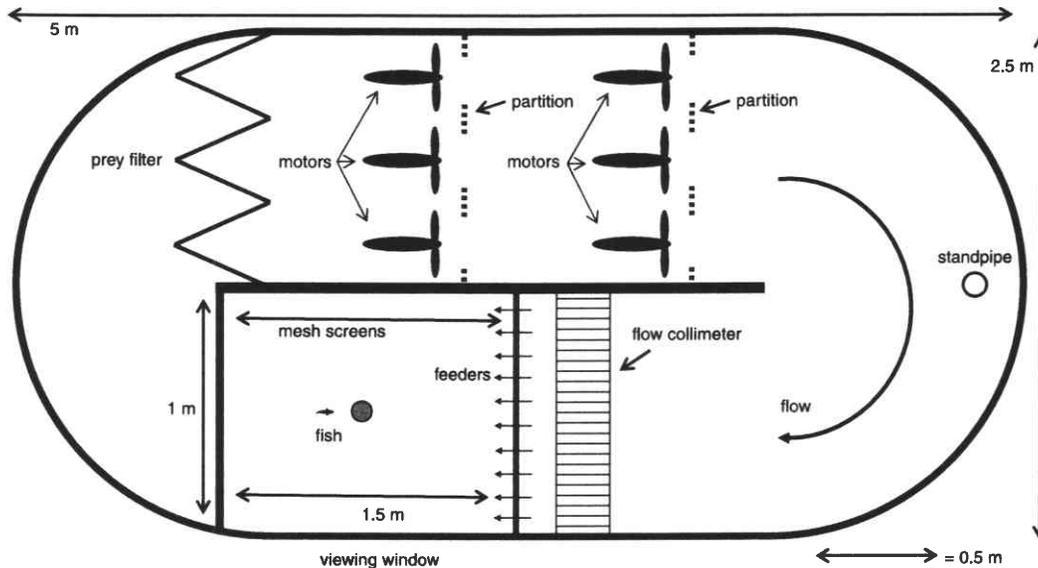
We constructed a variable-depth and -velocity stream tank to allow precise adjustment of water velocity (Fig. 1). The experimental arena measured 1.5 m long \times 1 m wide \times 0.3 m deep, enclosed at each end with mesh screens. A Plexiglas window on one side allowed us to videotape the experiments. The remainder of the arena was painted a light blue-green color. A 0.10 m \times 0.10 m grid of dots were drawn on the viewing window and the back wall to allow 3D analysis of video data (see below). The substrate was \sim 0.01 m diameter gravel. One flat, \sim 0.1 m diameter rock was placed near the center of the tank to serve as a focal point. Prey were delivered through the upstream screen via any one of 20 plastic feeder tubes (6.25 mm diameter) arranged in two layers of 10 each, equally spaced, at layers 0.1 and 0.2 m deep. Uneaten prey were filtered out by a 0.625 mm mesh stainless steel screen so they could not recirculate.

Experimental protocol

Nineteen wild fish of each species were collected from the West Fork of the Situk River near Yakutat, Alaska, in June 2001. Fish measured 70–80 mm fork length, which are presumed to be age 1+ based on length–frequency data (Lohr and Bryant 1999). All fish were collected from the same stream reach. Fish were shipped via air to Juneau, Alaska, and held in flow-through circular tanks. They were fed maintenance rations of frozen brine shrimp.

We conducted our experiments in a covered outdoor lab facility at the NOAA National Marine Fisheries Service Auke Bay Laboratory (Juneau, Alaska) in September–October 2001. Fresh water was supplied by a subsurface line from Auke Lake (mean water temperature was 10.46 °C (standard

Fig. 1. Top-view diagram of the stream tank, drawn to approximate scale. Water velocity was provided by six Minn Kota EM44 electric trolling motors powered by 120 V AC to 12 V DC transformers. The motors raised the water pressure head on the downstream side of the partitions, pushing water through the flow collimeter (0.04 m diameter PVC pipe), providing relatively uniform velocity across the tank. Filtered water was added continuously to maintain water quality, and it drained through the standpipe, maintaining a depth of 0.30 m. Overhead light was provided by a 150 W full spectrum bulb, shaded to reduce glare. Light intensity was 500 lux at the water surface above the focal point.



deviation, $SD = 0.84$); mean dissolved oxygen was $7.78 \text{ mg}\cdot\text{L}^{-1}$ ($SD = 0.66$); mean pH was 7.9 ($SD = 0.21$); mean turbidity was 0.36 nephelometric turbidity units (NTU; $SD = 0.16$). Photoperiod was maintained at 18 h day and 6 h night.

We selected five water velocity treatments, ranging from the minimum at which fish would hold station and drift-feed to near the maximum published value for 75 mm juvenile coho and steelhead (Everest and Chapman 1972; Beecher et al. 1993). Treatments were 0.29, 0.39, 0.48, 0.54, and $0.61 \text{ m}\cdot\text{s}^{-1}$ mean water column velocity (measured at a point 0.20 m upstream from the focal point). At each treatment level, we made a detailed map of water velocity in the experimental arena by measuring velocity in $0.10 \text{ m} \times 0.10 \text{ m}$ grids at three cross-sections, used for calculations of prey and fish speed (see Data analysis section below).

We randomly selected five fish of each species, ranging from 75 to 80 mm fork length, and paired by size between species. Experimental fish were held individually in $1 \text{ m} \times 0.3 \text{ m} \times 0.3 \text{ m}$ flow-through raceways during the experimental period. Each fish was tested individually at each velocity, assigned in a random order with 2 days rest between treatments. Two species pairs of fish were tested each day, and the entire series of feeding trials was completed in as few days as possible to minimize any effects of time or growth (fish grew an average of 3.4 mm during experimental period). Fish were not fed for 24 h prior to a feeding trial to ensure they would be motivated to feed.

Before we began the entire series of experiments, each fish received a 15 min "warm-up" feeding trial to acclimate them to the experimental arena. Fish acclimated well to the experimental protocol, usually selecting a position behind the focal point rock and feeding within 1 min of being intro-

duced to the tank. For each feeding trial, a fish was netted from its individual raceway and quickly released into the experimental arena at the slowest velocity. Velocity was stepped up gradually to the treatment level. A fish was observed to feed on at least one prey before the velocity was increased to the next level. When the test velocity was reached and the fish was observed to be actively feeding, the trial began. A feeding trial consisted of 100 individual prey being fed to a fish over a 25 min period ($4 \text{ prey}\cdot\text{min}^{-1}$). Prey were adult brine shrimp cut to 2 mm length to ensure that the fish's reaction distance to the prey (i.e., the furthest distance at which they react to and presumably detect prey) would be less than half of the tank width (Dunbrack and Dill 1984). Prey were randomly assigned to one of the 20 feeder locations and were fed at random times within each 15 s interval. At the conclusion of the experiment, fish were fed extra prey to be sure that they had not become satiated, and they were always observed to eat more prey.

We recorded our feeding trials on miniDV cassettes using two Sony GVD900 tape recorders and two Sony EVI 334 video cameras. Cameras were positioned at $\sim 90^\circ$ from each other relative to the fish focal point to facilitate 3D analysis.

Data analysis

During the course of a 25 min experiment, each fish made a number of prey capture maneuvers. A maneuver consisted of a fish (i) detecting a prey, (ii) leaving the focal point and swimming to intercept the prey, and (iii) swimming to return to the focal point. All prey capture maneuvers for each fish were digitized using custom-designed computer software (Hughes and Kelly 1996). This allowed us to count the number of prey captured to calculate prey capture probability (the number of prey captured divided by 100, the total num-

Table 1. Results of repeated measures analysis of variance (ANOVA) for the effects of water velocity, species, and the velocity \times species interaction on prey capture characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) ($N = 5$ of each species).

Dependent variable	Source of variation	df	F	p
Prey capture probability	Water velocity	4	117.71	<0.0001
	Species	1	0.10	0.76
	Velocity \times species interaction	4	1.23	0.32
Prey detection distance	Water velocity	4	17.60	<0.0001
	Species	1	2.33	0.17
	Velocity \times species interaction	4	2.24	0.09
Interception speed	Water velocity	4	1.31	0.29
	Species	1	1.46	0.26
	Velocity \times species interaction	4	0.27	0.89
Return speed	Water velocity	4	247.05	<0.0001
	Species	1	0.56	0.48
	Velocity \times species interaction	4	0.39	0.82

ber of prey). It also provided the videotape timecode and the 3D coordinates (x = upstream–downstream, y = across-stream, and z = vertical) for the nose and tail of the fish at the start, capture, and return point of each maneuver. To obtain the x,y,z coordinates and times for each prey capture maneuver, we followed the following procedure: (i) Identify a prey capture maneuver on the tape and obtain the x,y,z coordinates and time for the focal point location. (ii) Forward the tape to obtain the x,y,z coordinates and time of the capture location when the fish closed its mouth on the prey. (iii) Define the difference of these times as the prey interception time. (iv) Estimate interception distance by assuming that the fish initiated a maneuver as soon as it detected a prey and that it swam in straight line to capture it. Once the fish leaves its focal point and enters the water column, it is displaced downstream at the same rate as is the prey; therefore, interception distance = detection distance. (v) Estimate the x,y,z coordinates of the detection location by back-calculating the distance the prey had traveled along the x axis from the capture location during the interception time and assuming the y and z positions did not change. (vi) Calculate the detection distance as the distance between the focal point coordinates (i.e., x_1, y_1, z_1) and the detection coordinates (i.e., x_2, y_2, z_2) using Pythagoras' theorem as follows:

$$\text{Distance} = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2}$$

(vii) Define return time as the time taken from interception until the fish returned to the focal point. (viii) Estimate the return distance by adding the amount of downstream (x axis) displacement the fish experienced during the return time to the focal point location and calculating the distance between the capture location coordinates and this upstream point using Pythagoras' theorem. (ix) Calculate interception and return speeds by dividing distances by times. Front-, side-, and top-view figures of prey detection and capture locations were created by plotting the appropriate coordinates (front, y,z ; side, x,z ; top, x,y) after normalizing all focal point locations to the median and pooling by species ($N = 5$).

We tested for the effects of water velocity, fish species, and the velocity \times species interaction on (i) prey capture probability, (ii) mean prey interception distance, (iii) mean

prey interception swimming speed, and (iv) mean swimming speed of return to the focal point (return speed). We used separate repeated measures analyses of variance (ANOVAs) for each of these (S-Plus 6 for Windows, Insightful Corporation, Seattle, Washington). This procedure treats subjects as blocks to account for variation among individuals. If coho and steelhead differed in their responses as velocity increased, we would expect to see a significant velocity \times species interaction. Because the relationships between velocity and the dependent variables tested are of ecological interest, we also plot these data for each fish and provide separate regression equations for coho and steelhead for each of the factors.

Results

Prey capture probability

The effect of water velocity on prey capture probability was highly significant, but the effects of species and the interaction of velocity \times species were not significant ($p = 0.05$) (Table 1). Overall prey capture probability for both species was reduced from 65% to 25% with a water velocity increase from 29 to 55 $\text{cm}\cdot\text{s}^{-1}$, with both species averaging nearly identical probabilities at these velocities (Fig. 2). The lack of a significant effect of species or of the velocity \times species interaction suggests that neither the elevation nor the slope of the regression lines for coho and steelhead differ (Table 2, Fig. 2).

3D analysis: prey detection, prey interception, return to the focal point

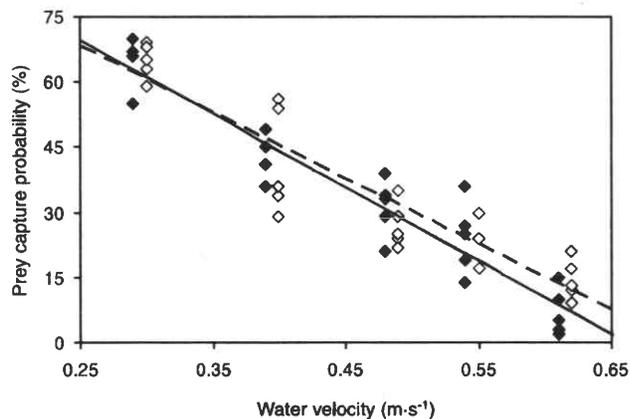
The effect of water velocity on prey detection distance was also highly significant, but again the effects of species and velocity \times species interaction were not significant (Table 1). Again the slopes and elevation of the regression lines did not differ (Table 2, Fig. 3a). Prey were detected throughout the detection volume rather than on the surface (i.e., at the reaction distance), and mean detection bearing increased with increasing velocity (Fig. 4). The reduction in detection distance was largely due to a reduction in the mean upstream (x axis) distance rather than in the lateral (y axis) or vertical (z axis) distances (Fig. 5).

Table 2. Regression equations and r^2 values for prey capture characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) ($N = 5$ of each species).

Regression y variable	Species	Regression equation	r^2
No. of prey captures	Coho	$y = -169.2x + 112.0$	0.90
	Steelhead	$y = -151.9x + 104.8$	0.85
Prey detection distance (m)	Coho	$y = -0.25x + 0.38$	0.44
	Steelhead	$y = -0.30x + 0.42$	0.69
Interception speed ($\text{m}\cdot\text{s}^{-1}$)	Coho	$y = -0.07x + 0.41$	0.02
	Steelhead	$y = -0.11x + 0.45$	0.09
Return speed ($\text{m}\cdot\text{s}^{-1}$)	Coho	$y = 1.37x - 0.11$	0.93
	Steelhead	$y = 1.39x - 0.13$	0.95

Note: Regression variable x in all equations is water velocity ($\text{m}\cdot\text{s}^{-1}$).

Fig. 2. Prey capture probability vs. water velocity for coho salmon (*Oncorhynchus kisutch*) (solid diamonds, solid line) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (open diamonds, broken line). Each data point represents the capture probability for one fish for a 25 min feeding trial ($N = 5$ of each species). Each fish was tested at each velocity, assigned in a random order. Steelhead data points are offset by $+0.01 \text{ m}\cdot\text{s}^{-1}$ for visual clarity. Regression equations are found in Table 2.



Neither water velocity, species, nor the velocity \times species interaction significantly effected prey interception speed (Table 1), again suggesting no difference between species (Table 2, Fig. 3b). At all velocities, coho and steelhead intercepted prey at close to their predicted maximum sustainable swimming speeds ($V_{\max} = 0.41 \text{ m}\cdot\text{s}^{-1}$), as calculated using equations for juvenile sockeye salmon (*Oncorhynchus nerka*) of the same size (Brett and Glass 1973) (Fig. 3b). The mean x coordinates for prey capture location were located further downstream with increasing velocity (Fig. 5) At the slowest velocity, fish of both species intercepted about an equal percentage of prey both upstream and downstream of the focal point; at faster velocities, nearly all prey were intercepted downstream of the focal point (Fig. 5). Capture probabilities declined nearly uniformly within the capture area (Fig. 6).

The effect of water velocity on return speed was highly significant, but the effects of species and the interaction of velocity \times species were not significant (Table 1); again there was no difference between species in either the slope or elevation of the regression lines (Table 2, Fig. 3c). Fish re-

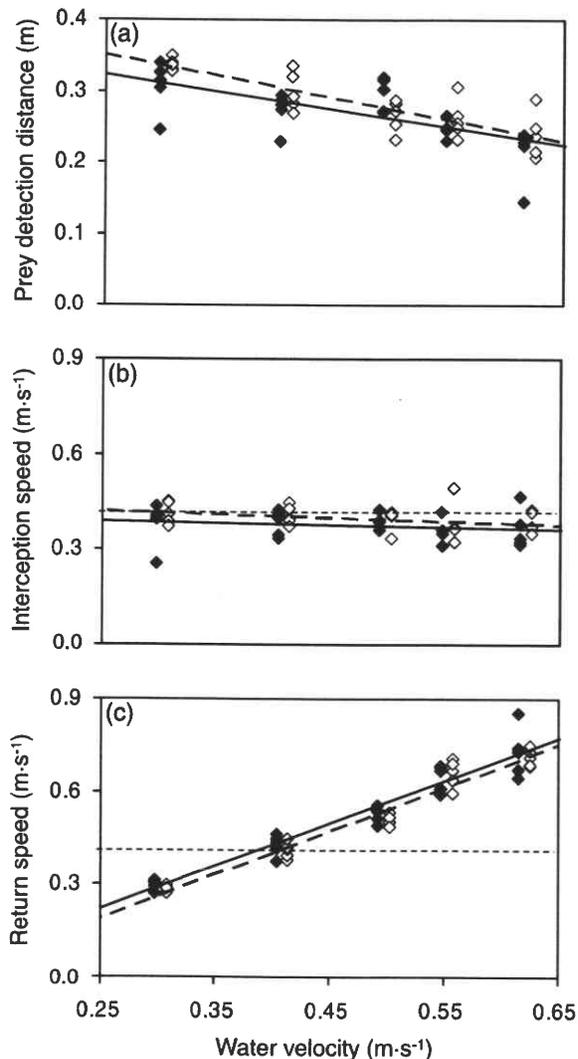
turned to the focal point at approximately the same speed as the current until it exceeded their V_{\max} , after which they exceeded current speed. At the faster velocities, fish tended to swim quickly to the substrate after a prey capture and then swim along the bottom back to the focal point.

Discussion

Drift-feeding coho and steelhead appear to differ little in their response to increasing water velocity. Nearly equal prey capture probabilities, combined with similar detection distances and swimming speeds, suggest that both species use very similar search and capture methods while drift feeding. In a related series of experiments, we also found that juvenile coho and steelhead differ little in their responses to increases in water depth (Piccolo et al. 2007). It seems possible, therefore, that differential prey capture ability cannot explain velocity or depth selection by juvenile coho and steelhead. Other factors, either physical (e.g., temperature, light intensity) or biological (e.g., competition, prey capture costs, prey selectivity), may be responsible for habitat segregation between the species. This has been shown for other pairs of sympatric stream salmonids (Everest and Chapman 1972; Nakano et al. 1999), but field studies identifying the underlying mechanism for habitat selection by sympatric coho and steelhead is lacking. Because water velocity appears to have similar effects on prey detection and capture by both species, we focus the remainder of this discussion on the effects of velocity in general, which we anticipate may be similar for other species of juvenile drift-feeding salmonids.

The inverse relationship between water velocity and prey capture probability appears to be due to two factors: (i) a decrease in prey detection distance (i.e., faster-moving prey are detected closer to the fish) and (ii) a decrease in detection probability for any given prey within the potential detection area. The first of these has been reported for drift-feeding salmonids (Hill and Grossman 1993; O'Brien and Showalter 1993) and also for drift-feeding coral reef fish (Kiflawi and Genin 1997). In our experiments, detection distance decreased more in the upstream direction, whereas O'Brien and Showalter (1993) and Kiflawi and Genin (1997) reported a decrease in the lateral detection distance. The prey detection area has been described as a pie-shaped wedge projecting forward from the fish's focal point, delimited upstream by their detection distance and across-stream by the

Fig. 3. Mean (a) prey detection distance, (b) interception speed, and (c) return speed vs. water velocity for coho (*Oncorhynchus kisutch*) (solid diamonds, solid lines) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (open diamonds, broken lines). Each data point represents the mean value of the y variable for one fish for a 25 min feeding trial ($N = 5$ of each species). The finely dashed horizontal lines in panels b and c are the predicted maximum sustainable swimming speeds for coho and steelhead. Steelhead data points are offset by $+0.01 \text{ m}\cdot\text{s}^{-1}$ for visual clarity. Regression equations are found in Table 2.



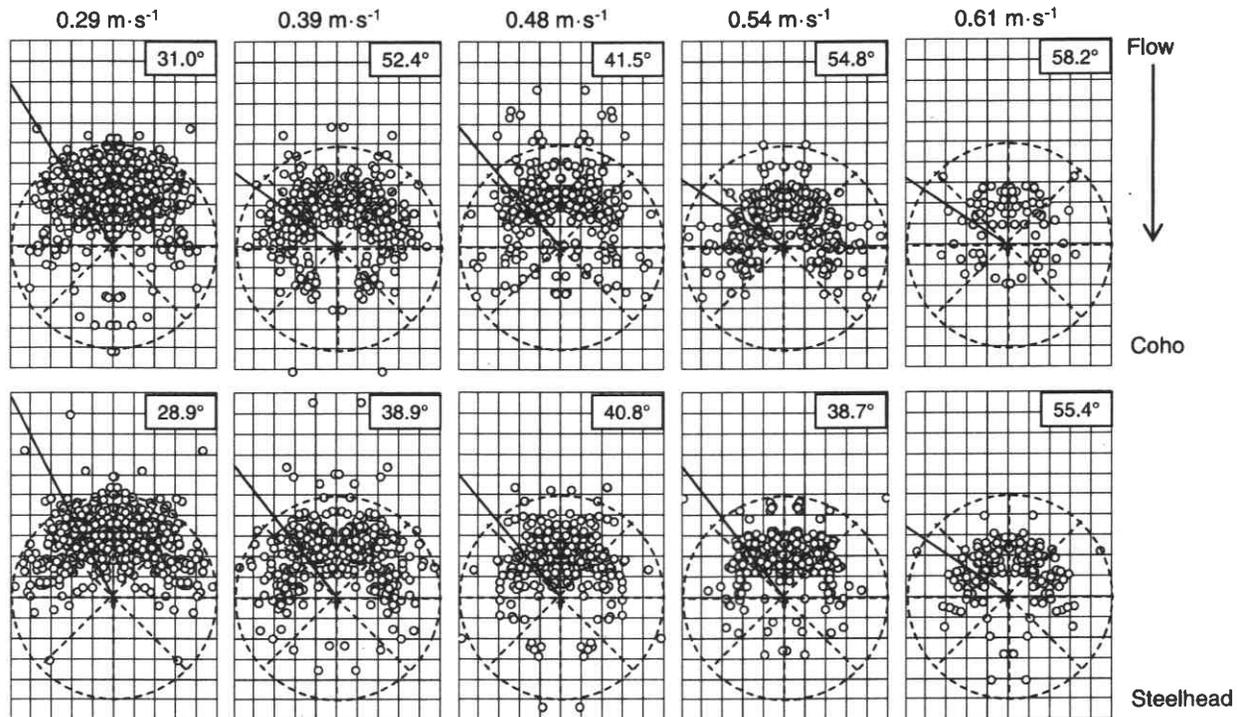
search angle (Hughes and Dill 1990; O'Brien and Showalter 1993; Kiflawi and Genin 1997). Our results show that the detection area may be reduced in an upstream rather than an across-stream direction, resulting in a shorter, not narrower, piece of pie. Whether the differences between our findings and those of O'Brien and Showalter (1993) and Kiflawi and Genin (1997) are due to fish species or size or to differences in experimental conditions is unknown. If fish are able to adjust the size and shape of their search area, they may be better able to adjust to changing environmental (e.g., stream

discharge) or biological (e.g., presence of competitors) conditions.

Decreased prey detection probability within the capture area appears to be an important factor that limits prey capture success. Hughes et al. (2003) proposed that velocity-dependent prey detection limitations might be one explanation for their model's over-prediction of foraging rate in adult brown trout (*Salmo trutta*). Similarly, Kiflawi and Genin (1997) proposed that a velocity-dependent decline in prey detectability and (or) capture success within the foraging area (the area in which prey are both detected and captured) might be responsible for their model's over-prediction of foraging rates of drift-feeding coral reef fish at faster velocities. Our results — a lack of velocity-dependent narrowing of the detection area; prey detections throughout, rather than on the surface of, the detection area; and a uniform reduction in detections within this area — support this idea of velocity-dependent prey detection limitations. Because our fish searched an area of similar height and width at all velocities (i.e., the maximum detection distance declined little), the volume of water searched (i.e., search volume) increased nearly proportionally to water velocity. Searching a larger volume of water for faster-moving prey would almost certainly decrease the probability of detection if information-processing ability was limiting. Hughes et al. (2003) note that no existing model of prey detection can explain spatial variability in prey detection; our results show that search volume and prey speed need to be incorporated into such models. Our experimental design, with known prey introduction locations and rates and variable water velocities, offers an effective means of testing prey detection models.

A velocity-dependent narrowing of the prey detection area has been an essential part of drift foraging models, used to predict the effects of water velocity on energy intake and consequently for predicting an optimum feeding velocity (Hughes and Dill 1990; Kiflawi and Genin 1997). To explain this narrowing, these models have assumed (i) that prey are detected at the fish's reaction distance, (ii) that prey are captured upstream of a line perpendicular to the fish's focal point, and (iii) a 100% capture probability on all energetically favorable prey. Our results and those of O'Brien and Showalter (1993) and Hughes et al. (2003) have shown this first assumption to be false. Although our maximum detection distance corresponds closely to the distance for coho of this size, as reported by Dunbrack and Dill (1984), the mean detection distance was less than the reaction distance, and it decreased with increasing water velocity. Our results also corroborate research that shows the second assumption to be false (Hughes et al. 2003), and further, they demonstrate that the downstream distance and the proportion of prey captured downstream of the focal point is velocity-dependent. Lastly, our results show the third assumption to be false, because prey capture probability within the foraging area never exceeded 70%. This, coupled with the fact that we did not find a velocity-dependent narrowing of the foraging area as previously reported (O'Brien and Showalter 1993; Kiflawi and Genin 1997), may lend insight into why foraging models have successfully predicted habitat selection despite incorporating these false assumptions. It is possible that the additional prey detected and captured both more laterally and further downstream than the models allow represent an

Fig. 4. Top view of prey detection locations (x,y coordinates) for coho (*Oncorhynchus kisutch*) (top) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (bottom) at five water velocities, listed at the top of the figure. Data are pooled for all fish ($N = 5$ of each species) tested at each velocity. Each circle represents one prey capture. Water flow is from top to bottom of figure. Solid lines to the left of the fish are mean prey detection angles (bearings in box) with 0° upstream and 180° downstream of fish. Detection locations have been rotated into the horizontal plane, retaining distance and bearing.



approximate trade-off for those prey within the foraging area that the models wrongly assume are captured.

Fish of both species intercepted prey at close to their predicted V_{max} at all velocities. One explanation for this is that at V_{max} fish should minimize their handling time while not acquiring oxygen debt as they would by swimming at burst speed (Puckett and Dill 1984). These results agree with Hughes et al.'s (2003) model assumption that fish should intercept prey at V_{max} . They differ from their results for adult brown trout, however, which tend to intercept prey at the same speed at which the prey drift (i.e., the same as water velocity). Because our fish did not increase interception speed at faster velocities, downstream displacement for prey captures increased as water velocities increased. Although this is mitigated somewhat by decreased prey detection distance at faster velocities, the net effect is a greater return distance as velocity increases.

Unlike interception speeds, return speeds were velocity dependent, with fish swimming at increasingly faster speeds at faster water velocities (again with no difference between species). At velocities less than V_{max} , fish returned to the focal point at the same speed as water velocity. At velocities faster than V_{max} , they swam faster than water velocity, thereby possibly incurring oxygen debt by burst swimming (Puckett and Dill 1984). There were velocity-dependent behavioural differences as well, with fish at slow velocities apparently searching for prey while returning to the focal point and fish at fast velocities burst-swimming

towards the substrate and returning the remainder of the distance to the focal point along the velocity shelter of the substrate. Models of drift feeding have often disregarded the costs of prey capture as relatively unimportant (e.g., Hughes and Dill 1990; Hill and Grossman 1993). Our results suggest that return costs may be considerable if fish are foraging in areas of velocity greater than their V_{max} .

One important factor that we did not consider in this study is prey density (number of prey per unit volume of water) and its influence on prey encounter rate. In our experiments, we held prey encounter rate constant ($4 \text{ prey} \cdot \text{min}^{-1}$) to reduce the effects of increasing encounter rate on measurements of prey detection and capture probability. This has the effect of reducing prey density, because as velocity increases, the volume of water that passes the fish's focal point increases while prey encounter rate remains constant. In natural streams, however, prey encounter rate is expected to increase proportionally to water velocity (Everest and Chapman 1972), and fish are expected to increase their capture rate until the time it takes to detect and capture one prey limits their ability to capture the next prey (termed the functional response; O'Brien et al. 2001). The prey encounter rate we used was well within the published foraging rates for drift-feeding salmonids (Biro et al. 1996; O'Brien et al. 2001), so it is unlikely that encounter rate limited capture probability even at our highest prey densities (i.e., the slowest velocities). Whether or not the benefits of the expected increase in prey encounter rate in faster water can

Fig. 5. Front and side views of prey detection and prey capture locations for coho (*Oncorhynchus kisutch*) (left) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (right). Grid squares are 0.10 m × 0.10 m. Front view is the same for detection and capture locations; top side view in each panel is detection and bottom is capture. Arrows indicate mean x, y, z axes detection and capture distances. Data are pooled for five of each species tested at each velocity. Each circle represents one prey capture.

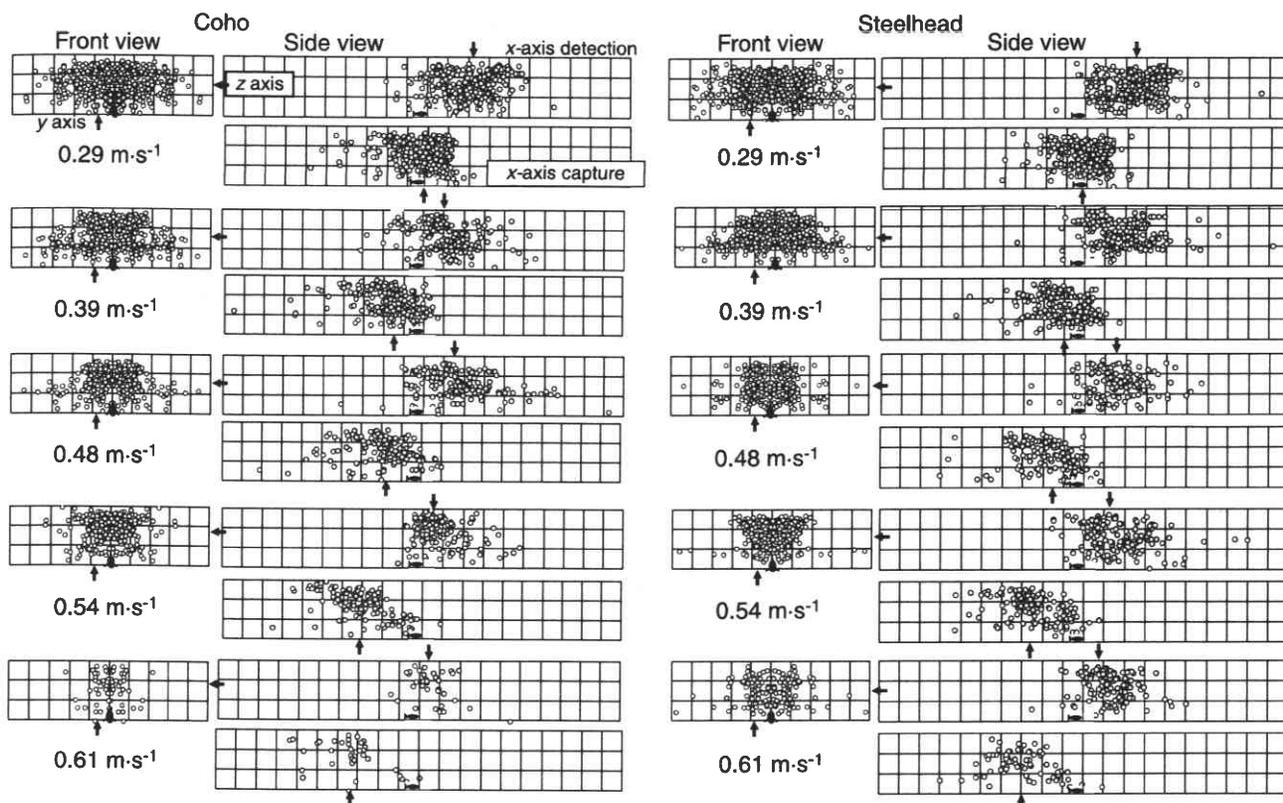
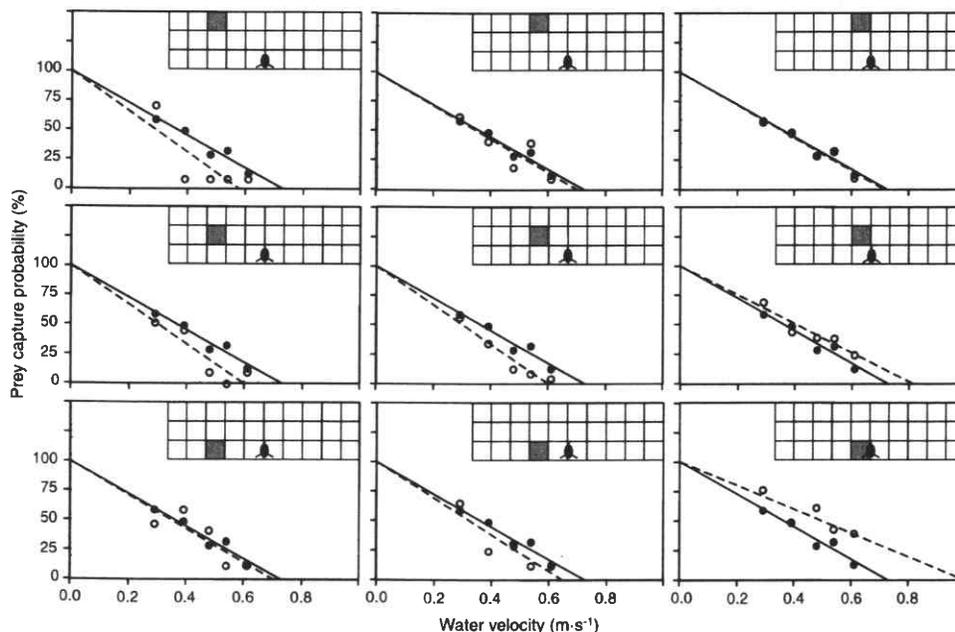


Fig. 6. Capture probability vs. water velocity for coho (*Oncorhynchus kisutch*) (solid circles, solid lines) and steelhead (sea-run rainbow trout, *Oncorhynchus mykiss irideus*) (open circles, broken lines) for each 0.10 m × 0.10 m square of the capture area shown by gray shading in the front view figure. Each data point represents the mean capture probability of five fish.



outweigh the demonstrated reduction in capture probability remains to be tested.

Our experiments were designed to isolate the effects of water velocity on drift-feeding salmonids. Our results corroborate and extend the findings of earlier research that suggested a negative relationship between water velocity and prey capture probability for drift-feeding salmonids (Hill and Grossman 1993; O'Brien and Showalter 1993). We conducted our experiments over a wider range of velocities and with a greater number of replicates, and our 3D analyses are the first to clearly demonstrate both a decreased prey detection distance and a decline in capture probability within the detection area. Although we attempted to simulate natural conditions in our stream tank, there are a number of factors that we did not address, but that are likely to influence prey detection and capture probabilities in natural streams. These include both physical (e.g., light intensity, temperature, water depth) and biological (e.g., competition, predation risk, prey size or density) factors. The interaction of these factors with water velocity should be considered if our results are to be incorporated into foraging models or applied to field studies.

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