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The effects of water depth on prey detection and capture by juvenile coho salmon and steelhead

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Abstract – We used three-dimensional video analysis of feeding experiments to determine the effects of water depth on prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*). Depth treatments were 0.15, 0.30, 0.45 and 0.60 m. Mean prey capture probabilities for both species were constant across all treatments (coho = 0.51, steelhead = 0.39), and did not differ significantly between species. In deeper treatments, capture probabilities were lower nearer the surface than they were nearer the substrate, particularly at the lateral edges of the foraging area. In deeper treatments coho had greater capture probabilities nearer the surface than did steelhead. It is unclear if this was a species difference, or one based on the relative amount of foraging experience the fish had in the wild prior to capture. Prey capture manoeuver characteristics were very similar for both species, including positive relationships between water depth and both prey detection distance and prey interception swimming speed, and no relationship between depth and speed of return to the focal point. Because prey encounter rate is expected to increase with increasing water depth, we used capture probabilities to predict capture rates for coho and steelhead, which increased linearly with water depth. We conclude that any benefit of foraging in deeper water is more likely due to increased encounter rate rather than to increased capture probability.

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Introduction

Juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss irideus*) have been shown to segregate stream habitat at both the stream reach (Hartman 1965; Bugert *et al.* 1991) and microhabitat (Fraser 1969; Johnston 1970; Allee 1981) scales. Within a stream reach, coho are often found in slower-velocity, deeper pools, whereas steelhead are often found in shallower riffles or runs (Hartman 1965; Bugert *et al.* 1991). Within microhabitats, coho have been shown to forage nearer the surface, and steelhead nearer the substrate (Fraser 1969; Johnston 1970; Allee 1981). Both species have also been shown to segregate along the water depth axis with other species of salmonids (Bravender & Shirvell 1990; Dolloff & Reeves 1990) or intraspecifically by fish size (Nielsen 1992; Harvey & Nakamoto 1997). Water depth is an important niche axis for segregation in other species of stream fish as well, both salmonid (Gibson & Power 1975; Bagliniere & Arribe-Moutounet 1985; Heggenes *et al.* 1999), and nonsalmonid (Greenberg 1991; Reyjol *et al.* 2001; Jowett 2002; Hesthagen *et al.* 2004). Although depth is a commonly measured feature of stream habitat (e.g. Bovee 1978), there has been little research on how it influences the relative foraging abilities of sympatric stream salmonids.

Bisson *et al.* (1988) proposed that coho are better adapted to forage in pools because their laterally compressed body form and long median fins facilitate rapid turning and acceleration, whereas steelhead are better adapted to forage in riffles because their more cylindrical body form and shorter median fins minimize drag during foraging maneuvers. If this is true, the species might be expected to differ in prey capture success or in energetic costs in relation to water depth

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or velocity. Piccolo (2005) developed models of net energy intake (NEI) that suggest that velocity-dependent differences in foraging abilities or in energetic costs are not likely to explain habitat segregation by coho and steelhead. In this paper we extend these results with experiments designed to test the effects of water depth on prey capture success by juvenile coho and steelhead.

For drift feeders, foraging in deeper, slower, versus shallower, faster water should represent a tradeoff in prey encounter rate, assuming equal stream channel width and equal prey density (number of prey m^{-3}) throughout the water column. This is illustrated by the following: assume that the prey encounter rate in a slower, deeper section is 1.0 prey s^{-1}, calculated as:

$$[1.0\ \text{prey m}^{-3}] \times [1 - \text{m wide} \times 1 - \text{m deep} \times 0.5 - \text{m s}^{-1}] = 1.0\ \text{prey s}^{-1}.$$

Prey encounter rate would be equal in a faster, shallower section, calculated as:

$$[1.0\ \text{prey m}^{-3}] \times [1 - \text{m wide} \times 0.5 - \text{m deep} \times 1 - \text{m s}^{-1}] = 1.0\ \text{prey s}^{-1}.$$

The two habitats may differ, however, in the way in which they influence a fish's ability to detect and capture prey. Faster water velocity, for example, has been shown to reduce the prey detection area and capture probabilities within this area, and it may increase the energetic costs of prey capture (Godin & Rangeley 1989; Hill & Grossman 1993; O'Brien & Showalter 1993; Piccolo 2005). In theory, foraging in the deeper water ought to increase a fish's prey encounter rate, if water velocity and prey density remain constant. Prey encounter rate should increase with increasing water depth until depth reaches the fish's maximum prey detection distance, after which it should asymptote. The effects of deeper water on prey detection and capture probabilities, however, have never been investigated, nor have there been comparisons of the effects of depth on two sympatric species.

Our objective was to assess the effects of water depth on prey detection and capture by juvenile coho and steelhead. We used three-dimensional video analysis of stream-tank foraging experiments to test these hypotheses: (i) prey capture probability increases with increasing water depth, 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. We also used the relationship between water depth and capture probability to predict the effect of depth on prey capture rates for coho and steelhead.

Methods

Stream tank

We modified the variable-depth and -velocity stream tank for these experiments (see Piccolo 2005). The experimental arena measured 1.5-m long × 0.6-m-wide, and depth treatments were 0.15, 0.30, 0.45 and 0.60 m. Prey were delivered through the upstream screen via any one of 20 plastic feeder tubes (6.25-mm diameter) arranged in four layers of five each, equally spaced in rows at depths 0.15, 0.30, 0.45 and 0.60 m. A series of ten 1000-W aquarium heaters was used to maintain constant water temperature (mean = 8.5 °C, SD: 1.03). Light intensity was 500 lux at the water surface above the focal point.

Experimental protocol

Ten wild fish of each species (50–60 mm fork length) were collected from Peterson Creek, near Juneau, Alaska, in October 2002. All fish were collected from the same stream reach. We conducted our experiments at the Douglas Island Pink and Chum Macaulay Hatchery in Juneau, AK, USA. Fish were held in flow-through 40-l circular tanks and fed maintenance rations of frozen brine shrimp. Filtered freshwater was supplied by a subsurface line from Salmon Creek Reservoir, near Juneau, Alaska. Photoperiod was maintained at 18 h day and 6 h night.

We selected four water depth treatments (0.15, 0.30, 0.45 and 0.60 m) that spanned the published range of depth preferences for juvenile coho and steelhead ~60 mm fork length (Everest & Chapman 1972; Sheppard & Johnson 1985; Beecher *et al.* 2002). Water velocity was held constant at 0.30 m s^{-1}mean column velocity, measured 0.20 m upstream from the fish's focal point. We randomly selected four fish of each species, ranging from 53 to 65 mm fork length, and species-paired by size. Each fish was tested individually at each depth, assigned in a random order with two days rest between treatments. Two pairs of fish were tested each day and the entire series of feeding trials was completed in 8 days to minimize any effects of time or growth. Fish were not fed for 24 h prior to a feeding trial to ensure they would be motivated to feed.

Each fish received a 15-min 'warm-up' feeding trial to acclimate them to the experimental arena. For each feeding trial a fish was netted from its individual raceway and quickly released into the experimental arena. When the fish was observed to be feeding actively, the trial began. A feeding trial consisted of 100 individual prey being fed to a fish over a 25-min period (four prey min^{-1}). Prey were adult brine shrimp cut to 2-mm length to ensure that the fish's reaction distance to the prey would be less than half of the tank width (Dunbrack & Dill 1984). Prey were randomly assigned to one of the 20 feeder locations, and were fed at random times within each 15-s interval. Prey were fed only through the feeder tubes that were submerged at a respective depth treatment (e.g. 20 per each of five tubes at 0.15-m depth, five at each of 20 tubes at 0.60-m depth). 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 ~90° from each other relative to the fish focal point to facilitate 3D analysis.

Data analysis

For each trial, we counted the number of prey captures by viewing the videos. We defined prey capture probability as:

$$\text{The number of prey caught} \times \text{The total number of prey}^{-1} \times 100.$$

For each prey capture, we also identified the video timecode and 3D location of the focal point, capture location, and return point. These data allowed us to estimate swimming distances and speeds for each prey capture, and to assess prey capture probability within the foraging area. See Piccolo (2005) for a detailed description of the 3D analysis. Figure 1 shows an example of the 3D data for coho at 0.15 and 0.60 cm.

We used linear regression (Zar 1999) to assess the effect of water depth on prey capture probabilities and feeding performance measures. The following regressions were fitted separately for coho and steelhead: (i) prey capture probability vs. water depth, (ii) mean prey detection distance vs. water depth, (iii) mean prey interception speed versus water depth, and (iv) mean return speed versus water depth. We tested for significance of the individual regressions ($\alpha = 0.05$), and compared the slopes and elevations between the species using Student's *t*-tests ($\alpha = 0.05$, two-tailed) to test the null hypotheses that (i) the slopes and (ii) and elevations between two regression lines are equal Zar (1999). We also conducted a power analysis to assess our ability to detect differences between the slopes of the regression lines for prey capture probability vs. water depth. We used the *PS* software program, which is designed specifically for assessing power and sample size for comparisons of two linear regressions (Dupont & Plummer 1998).

We held prey encounter rate constant (4 min^{-1}) across all treatments to minimize the likelihood of an interaction between capture probability and handling time. This means that prey density (number of prey per unit volume), however, decreases as depth treatment increases, because water volume increases. To account for this we calculated predicted prey capture rate vs. water depth as follows:

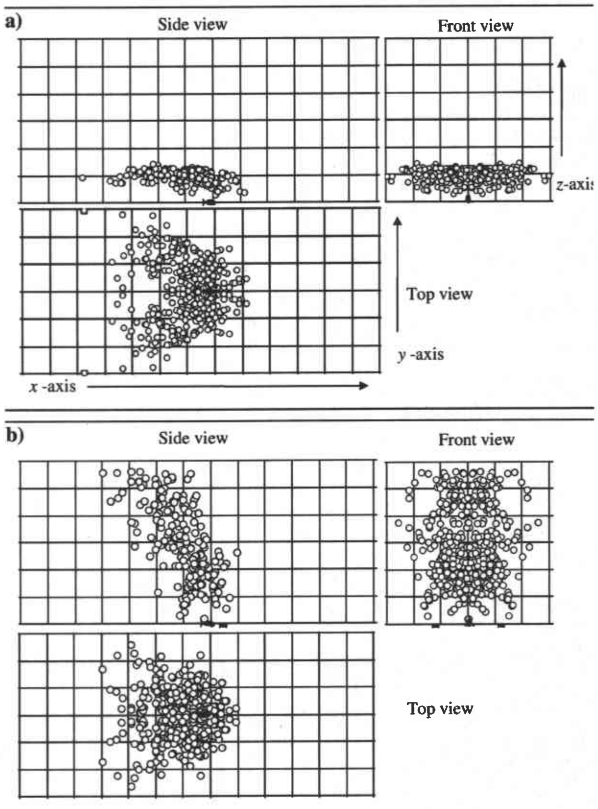

Fig. 1. Capture locations in 3D for coho ($N = 4$) at two depth treatments, (a) 0.15 m and (b) 0.60 m. Each circle represents the *x, y, z* coordinates of a prey capture. Grid squares are 0.1 × 0.1 m.

$$\text{Number of prey caught} \times \text{Treatment depth}/0.60.$$

We plotted the predicted prey capture rate for each fish at each depth, and drew a linear regression line for each species. Because these relationships are derived from the prey capture probability regressions we do not report statistical results for them. These density-corrected relationships provide predictions of how water depth might influence prey capture rate by coho and steelhead in natural streams. We also plotted prey capture probability by 0.15-m horizontal depth layer and by 0.12-m vertical columns within each depth treatment to provide a graphical description of how depth influenced probability within the foraging area.

Results

Prey capture probability

The relationship between prey capture probability and water depth was not significant for either coho

Table 1. Regression equations and significance tests for prey capture characteristics of juvenile coho salmon and steelhead ($N = 4$). Regression x variable in all equations is water depth (m). F values are for significance of individual species' regressions (* = $P < 0.05$, ** = $P < 0.001$). Nonsignificant P-values (>0.05) for t-tests indicate failure to reject the null hypothesis that the slopes or the elevations of species' regression lines are equal (Zar 1999). Test for equal slopes test for equal elevations.

Regression y variable	Regression equation	r^2	F value	Test for equal slopes t-value	Test for equal slopes P-value	Test for equal elevation t-value	Test for equal elevation P-value
No. prey captures							
Coho	$y = 13.8x + 45.5$	0.03	0.49	0.51	0.61	2.36	0.03
Steelhead	$y = -0.05x + 39.9$	<0.01	<0.01				
Prey detection distance (m)							
Coho	$y = 0.53x + 0.12$	0.88	103.53**	1.88	0.07	1.81	0.08
Steelhead	$y = 0.37x + 0.15$	0.69	31.53**				
Interception speed (m s^{-1})							
Coho	$y = 0.14x + 0.26$	0.32	6.64*	0.19	0.85	0.05	0.96
Steelhead	$y = 0.15x + 0.26$	0.37	8.12*				
Return speed (m s^{-1})							
Coho	$y = 0.04x + 0.30$	0.10	1.61	0.91	0.37	3.72	<0.001
Steelhead	$y = -0.002x + 0.34$	<0.01	<0.01				

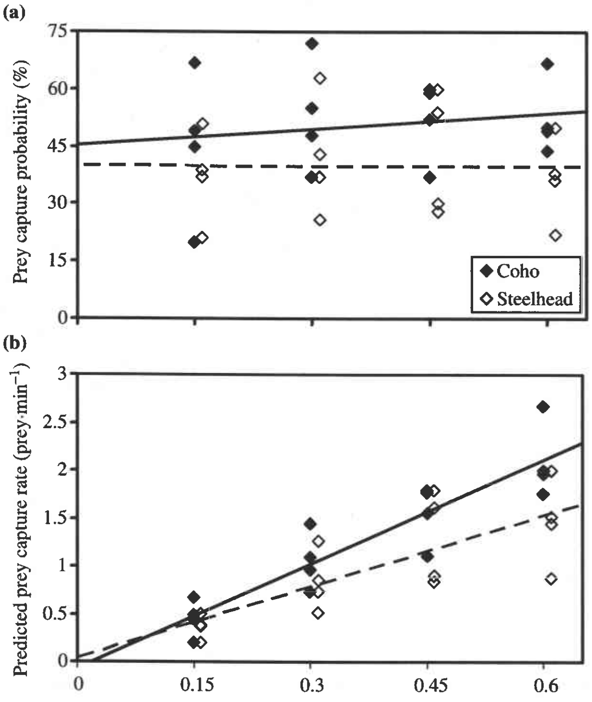

Fig. 2. (a) Prey capture probability, and (b) Predicted prey capture rate, vs. water depth for coho (solid diamonds and lines) and steelhead (open diamonds, dashed lines). Regression equations and significance tests are found in Table 1. Each data point represents the probability or rate for one fish ($n = 4$ of each species). Steelhead data points are offset by +0.01 m for visual clarity.

($P = 0.50$, $r^2 = 0.03$) or steelhead ($P = 0.98$, $r^2 < 0.01$; Table 1; Fig. 2a). The slopes of the regression lines did not differ significantly ($P = 0.61$), but the elevations did ($P = 0.03$), with coho averaging greater capture probabilities across all depths (Table 1; Fig. 2a). Power analysis showed that we had only 5.2% power ($\alpha = 0.05$) of correctly rejecting the null hypotheses that the regression slopes or elevations for coho and steelhead were equal, however, if the observed differences between these slopes and elevations were real. When we corrected for prey density, we found a positive linear relationship between predicted prey capture rate and increasing water depth (Fig. 2b). We did not see the expected asymptote of prey capture rate versus depth for either species.

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

We found a significant linear increase in prey detection distance with increasing water depth for coho ($P < 0.001$, $r^2 = 0.88$) and steelhead ($P < 0.001$, $r^2 = 0.69$; Table 1; Fig. 3a). Neither the slopes nor the elevations of the regression lines differed significantly (Table 1, Fig. 3a). Prey were detected throughout the reaction volume rather than on the surface at maximum detection distance. Mean prey detection locations for both species were further upstream in deeper water (Fig. 4).

We also found a significant linear increase in prey interception speed with increasing water depth for coho ($P < 0.05$, $r^2 = 0.32$) and steelhead ($P < 0.05$, $r^2 = 0.37$; Table 1; Fig. 3b). Neither the slopes nor the elevations of the regression lines differed significantly (Table 1, Fig. 3b). Because fish swam faster to cover the increased detection distance, the mean downstream (x-axis) capture location changed little with increasing water depth (Fig. 4). At 0.15 and 0.30 m depths fish swam slower than their predicted maximum sustainable swimming speeds [$V_{\max}$, 0.33 m s^{-1}, as calculated using equations for juvenile sockeye salmon of the same size (Brett & Glass 1973)]. At 0.60 m depth they swam faster than $V_{\max}$ (Fig. 3b).

Prey capture probabilities by 0.15-m depth layer within depth treatments were always lower in the surface layer (Fig. 5). In deeper treatments probabilities were greater near the substrate, and they dropped

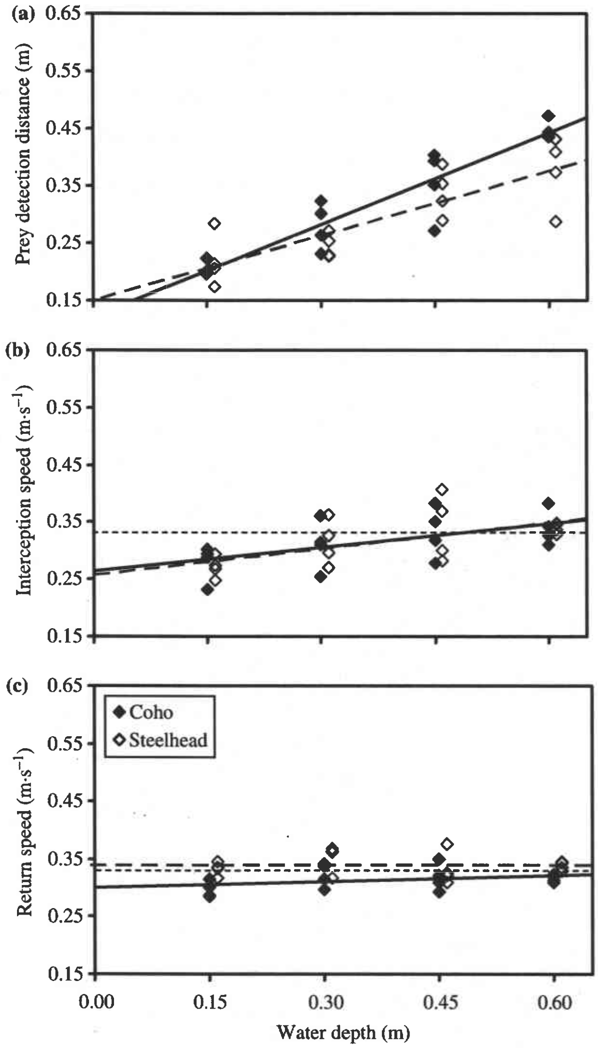

Fig. 3. Mean: (a) prey detection distance, (b) interception speed, and (c) return speed, versus Water Depth for coho (solid diamonds and lines) and steelhead (open diamonds, dashed lines). Regression equations and significance tests are found in Table 1. Each data point represents the mean value of the *y* variable for one fish. 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 +0.01 m for visual clarity.

off in the surface layers, particularly at the lateral edges (Figs 5 and 6).

The speed of return to the focal point was not significantly related to water depth for coho ($P = 0.23$, $r^2 = 0.10$) or steelhead ($P = 0.95$, $r^2 < 0.01$; Table 1; Fig. 3c). The slopes of the regression lines did not differ significantly ($P = 0.37$), but the elevations lines did ($P < 0.001$) with steelhead retuning at slightly faster speeds across all depths (Table 1, Fig. 3c). Fish returned to the focal point at approximately $V_{\max}$ at all depths (Fig. 3c).

Discussion

We found little relationship between water depth and prey capture probability for either coho or steelhead. With increasing depth, capture probability for coho increased only 6.2%, whereas probability for steelhead changed little (<1%). This suggests that any benefit of foraging in deeper water would be due more to an increase in prey encounter rate (i.e. greater volume searched) than to a physical response to foraging in deeper water (e.g. an increase in prey detection probability). For example, the observed increase in prey detection distance in deeper water for both coho and steelhead might be expected to lead to an increase in prey detection and capture probabilities. The fact that we did not see this, however, suggests that the benefits of increased prey detection distance in deeper water may be countered by a reduction in search efficiency within a greater volume of water. This is supported by our finding of increased capture probabilities near the focal point in conjunction with low probabilities in the surface layers in the deeper treatments (Figs 5 and 6). Our finding that an increase in search volume in faster water also decreased capture probabilities (Piccolo 2005) further supports the idea that search efficiency decreases as search volume increases.

Although capture probabilities did not increase in deeper water, predicted capture rates did increase. Because capture probabilities were constant across all depths, prey capture rate increased proportionally to depth. The relationship between prey capture rate and water depth, therefore, is additive; i.e. assuming equal water velocities and prey densities, each increase in depth adds more potential prey without a loss or gain in overall capture probability. We used relatively small fish and small prey, and deep water, but we were unable to demonstrate the asymptote in capture rate that we predicted would occur at depths beyond the fishes' maximum prey detection distance. Our fish (~60 mm) are predicted to have a reaction distance of ≤0.80 m for the size of prey we used (Dunbrack & Dill 1983), and the maximum prey detection distance in our 0.60 m depth treatment (0.79 m) closely agrees with this. Because our fish detected some prey almost directly overhead, an asymptote in prey capture rate might not be seen until depths of >0.80 m for fish and prey of these sizes. To maximize prey capture rate, therefore, fish should select the deepest water available up to their maximum prey detection distance, assuming equal velocity and prey density (other factors, such as predation risk, notwithstanding). Two-mm prey are typical in diets of YOY juvenile salmonids in Southeast Alaska, although they take both smaller and larger prey (Allan *et al.* 2003). Fish would also be expected to select depths based upon the reaction

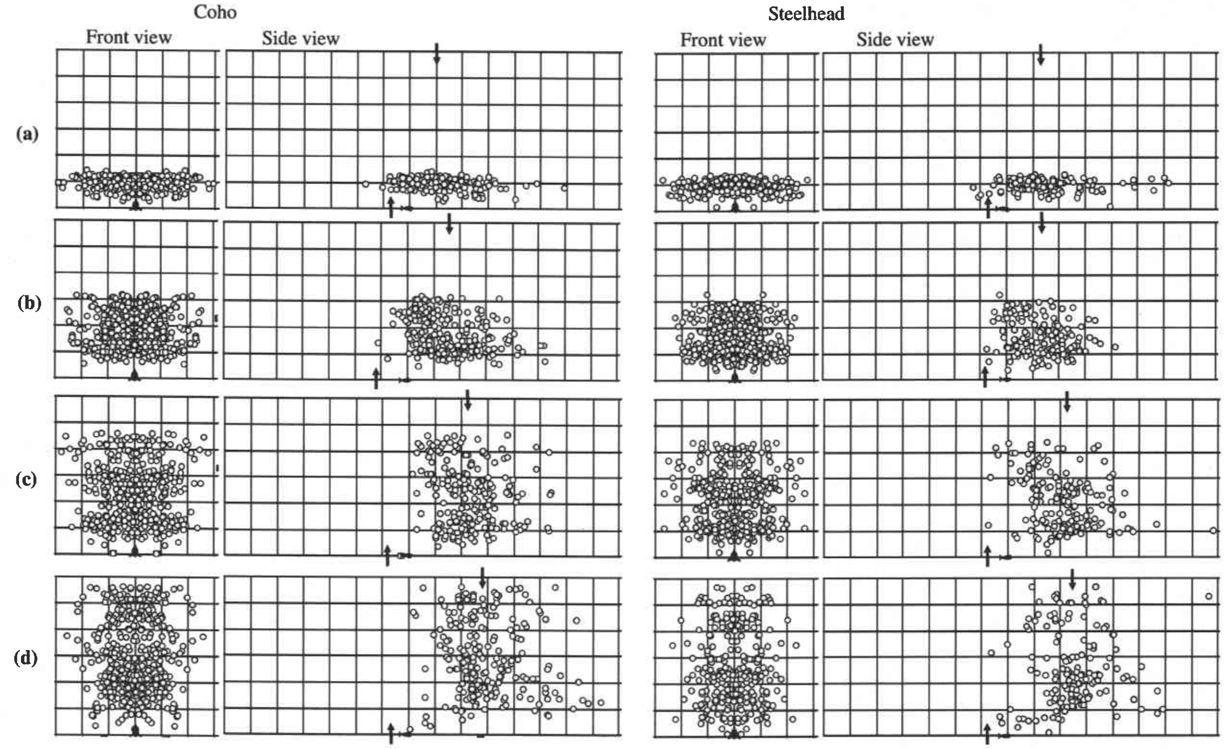

Fig. 4. Front and side view of prey detection locations for coho (left) and steelhead (right) at depths (m) of (a) 0.15, (b) 0.30, (c) 0.45 and (d) 0.60. Data are pooled for all fish at each treatment (n = 4 of each species). Arrows indicate mean x-axis distances for prey detection (pointing downward) and prey capture (pointing upward). Grid squares are 0.10 × 0.10 m.

distance to the size of prey upon which they are foraging.

Water depth is one of the most commonly reported habitat descriptors for coho and steelhead (Bugert *et al.* 1991; Beecher *et al.* 1995, 2002) and for stream salmonids in general (Everest & Chapman 1972; Greenberg *et al.* 2001; Heggenes 2002; Polacek & James 2003). The value of deeper water has been attributed to increased survival by providing cover (Bustard & Narver 1975; Gibson & Power 1975; Kruzic *et al.* 2001) and to foraging benefits because of reduced prey capture costs (Rosenfeld & Boss 2001; Young 2004). Our results show that increased prey capture rate may also be an important factor in depth selection.

We hypothesized that at least one species would display significantly better foraging capabilities in their respective preferred habitat (i.e. coho in deeper or steelhead in shallower water). The similar response to water depth by both species, however, mirrors our findings on the effects of water velocity, and it strengthens the evidence that both species are equally capable of exploiting a wide range of habitats. The fact that the age classes (and mean sizes) of fish differed between the depth and velocity experiments suggests that these equal foraging capabilities continue through time. Despite the widely cited pattern of stream habitat segregation of coho in pools and steelhead in riffles (Hartman 1965; Bugert *et al.* 1991) both species are also successful in rearing in lakes or ponds (Swain & Holtby 1989; Behnke 1992; Irvine & Johnston 1992; Hayes 1995) where they cruise feed for zooplankton, small fish, or aerial invertebrates. It is apparent that a considerable amount of flexibility in foraging behaviour is maintained within the genomes of both coho and steelhead (e.g. Dill 1983).

Comparing manoeuver characteristics between our depth and velocity experiments provides further evidence of the flexibility of coho and steelhead foraging behavior. In the depth experiments prey detection distance and interception speed increased, and return speed remained constant, with increasing water depth. Conversely, in response to increasing water velocity interception speed remained constant and return speed increased (Piccolo 2005). This suggests that juvenile salmonids are capable of adjusting to changes in their foraging environment to a remarkable degree. In each case the fish were presented with the same problem, capturing a prey and returning to their focal point, but under different environmental gradients (either slow-fast or shallow-deep). In the velocity experiments, where detection

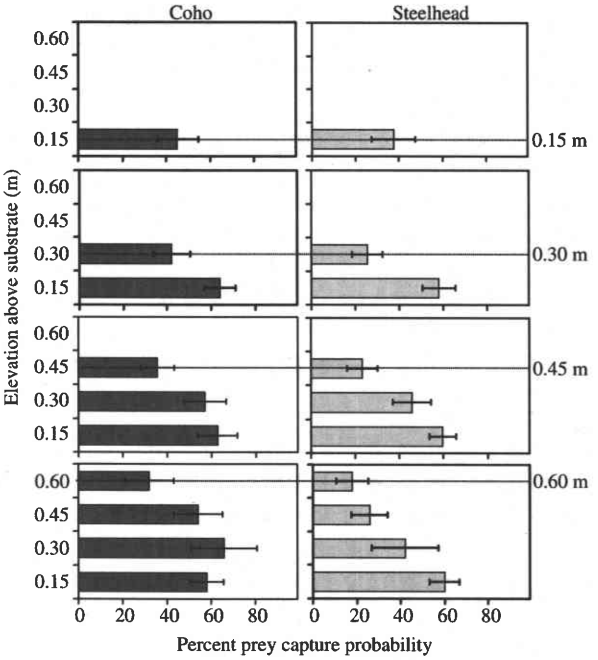

Fig. 5. Prey capture probability versus elevation above the substrate by depth layer within treatments for coho (left, darkly shaded bars) and steelhead (right, lightly shaded bars). Each bar represents the mean of four fish for each species. Error bars are ±1SE. Depth treatment levels are 0.15, 0.30, 0.45, 0.60 m, top to bottom. Horizontal dotted line in each graph shows elevation above the substrate of the water surface.

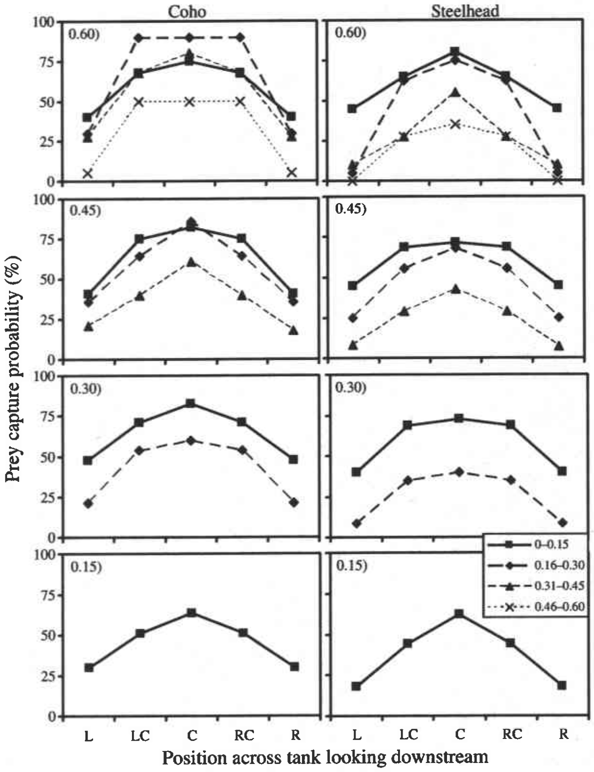

Fig. 6. Prey capture probabilities for coho (left) and steelhead (right) versus lateral position across the stream tank, by 0.15-m depth layers within depth treatment levels. Lateral positions are in 0.12 m increments looking downstream (L = 0–0.12, LC = 0.13–0.24, C = 0.25–0.36, RC = 0.37–0.48, R = 0.49–0.60). Depth treatments (m) are in the upper left of each graph, and depth layers (m) are identified in the legend.

distance declined at faster velocities, they did this by maintaining the same interception speed and increasing their return speed. In the depth experiments, where they had the opportunity to detect prey at increasing greater distances, they increased their interception speed, and held return speed constant.

Fish size also plays a role in stream salmonid habitat selection and segregation, because fish move into faster deeper water as they grow (Lister & Genoe 1970; Everest & Chapman 1972). We found that the smaller fish used in the depth experiments (~60 mm) had lower prey capture probabilities than did larger fish (~80 mm, Piccolo 2005) when tested at the same depth and velocity. At 0.30-m depth and 0.30 m s^{-1} velocity, mean capture probabilities were 48% for the smaller fish and 65% for the larger fish (17% difference), whereas differences between species were 11% and <1% for the small and large classes, respectively. Fish size, therefore, appears to have a greater influence on prey capture ability than does species. Hartman (1965) hypothesized that competition between coho and steelhead was minimized by differences in body size because of earlier emergence of coho. Although he documented that steelhead grow faster than do coho, he noted that coho emigrated as smolts early in their second year, thus avoiding potential competition during the second summer when fish of both species would be of equal size. In the northern end of their distributions, coho and steelhead spend this second summer in sympatry, and they are often of equal size during this period (Groot & Margolis 1991; Lohr & Bryant 1999). There are no published accounts of habitat selection in natural streams by equal-sized coho and steelhead in sympatry so it is currently unknown whether segregation is based on differences in habitat preferences or simply on fish size.

Differences in the elevations, but not in the slopes, of the regression lines show that coho had an equal advantage in prey capture probability among all depth treatments. Although this difference did not appear to be related to water depth (i.e. the slopes of the lines did not differ), it is of some interest. One possible explanation is that the coho were more experienced foragers than were the steelhead, having spent up to 2 months more time foraging in the wild before they were collected in October. In experiments on the effects of water velocity, we used older fish (age I+), which had spent over a year foraging in the wild, and we did not find a systematic species difference (Piccolo 2005). It is possible that the greater relative difference in experience between age 0+ fish gives coho an advantage, but that by their second summer both species have enough experience to render the difference unimportant.

It is also possible that the non-significant differences between coho and steelhead in the slopes of prey capture probability vs. depth represent a true advantage for coho in deeper water. Statistical power for this comparison was low, and the relatively high variation may have masked the treatment effects. There is an indication that coho had greater capture probabilities near the surface in the deeper treatments. This led to the slight increase in the slope of capture probability for coho. Whether this is a true species difference, or one because of age-based differences in experience as discussed in the previous paragraph, remains to be determined.

Clearly, our predicted relationships between water depth and prey capture rate need to be viewed as models that need further experimental confirmation. Our objective was to clearly identify the effects of water depth, a key physical parameter of streams, which is often measured but poorly understood. There are a number of other factors that we did not address, but that are likely to interact with water depth to influence prey capture. These include biotic factors such as fish size, prey density, prey size, prey location (e.g. surface or subsurface), intra- and interspecific competition and predation risk. Abiotic factors such as water temperature, turbidity and available cover are also likely to influence how water depth influences prey capture by drift-feeding fish.

This study demonstrates that foraging in deeper water may increase prey capture rate for drift-feeding juvenile salmonids. Deeper water, however, may also convey other benefits or costs. Deeper water may provide cover from aerial or surface feeding predators such as kingfishers or mergansers (Bugert & Bjornn 1991; Gregory 1993; Grand & Dill 1997); conversely, it may increase predation risk from aquatic predators such as larger fish (Bugert & Bjornn 1991; Gregory 1993). Deeper water may also provide shelter from high flows, one reason pools are often cited as critical overwinter habitat (Bustard & Narver 1975; Maeki-Petaeys *et al.* 2000; Solazzi *et al.* 2000). The results of our foraging experiments need to be considered in light of these larger concerns, but they offer increased insight into the complex association between stream salmonid distribution and physical habitat.

Conclusions

We found little relationship between prey capture probability and water depth for coho and steelhead, but predicted prey capture rates increased with increasing depth. This leads us to conclude that any benefits of foraging in deeper water are more likely due to increased prey encounter rate than to increased capture probability. We did not find a significant difference in prey capture probabilities between coho and steelhead, but statistical power was low. Prey capture manoeuver characteristics were very similar between the species. These included positive relationships between water depth and (i) prey detection distance, and (ii) interception speed. Return speed was constant across all depths. In the deeper treatments, coho had greater capture probabilities nearer the surface than did steelhead, but it is unclear if this was a species difference or one based on the relative amount of foraging experience fish had in the wild prior to capture. We conclude that foraging in deeper water may increase prey capture rates for coho and steelhead, but that further experimental work is needed.

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References

Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A. & Rogers, J. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid foodwebs. Canadian Journal of Fisheries and Aquatic Sciences 60: 309–320.

Allee, B.A. 1981. The role of interspecific competition in the distribution of salmonids in streams. In: Brannon, E.L. & Salo, E.O., eds. Salmon and Trout Migratory Behavior Symposium. Seattle, WA: Publisher of Allee, 1981: University of British Columbia, Vancouver pp. 111–122.

Bagliniere, J.L. & Arribe-Moutounet, D. 1985. Microdistribution of populations of brown trout (*Salmo trutta* L.) and juvenile Atlantic salmon (*Salmo salar* L.) and other species present in the upstream part of the Scorff River (Brittany). Hydrobiologia 120: 229–239.

Beecher, H.A., Carleton, J. P. & Johnson, T.H. 1995. Utility of depth and velocity preferences for predicting steelhead parr distribution at different flows. Transactions of the American Fisheries Society 124: 935–938.

Beecher, H.A., Caldwell B.A. & DeMond S.B. 2002. Evaluation of depth and velocity preferences of juvenile coho salmon in Washington streams. North American Journal of Fisheries Management 22: 785–795.

Behnke, R.J. 1992. Native Trout of Western North America. Bethesda, MD: Publisher of Behnke, 1992: American Fisheries Society, Bethesda MD.

Bisson, P.A., Sullivan, K. & Nielsen, J.L. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117: 262–273.

Bovee, K.D. 1978. Probability-of-use Criteria for the Family Salmonidae. FWS/OBS-78/07, Ft Collins: US Fish and Wildlife Service.

Bravender, B.A. & Shirvell C.S. 1990. Microhabitat requirements and movements of juvenile coho and chinook salmon at three streamflows. In: Kloiya Creek, B.C., ed. Canadian Journal of Fisheries and Aquatic Sciences Data Report, 802, 166 pp.

Brett, J.R. & Glass, N.R. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhychus nerka*) in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30: 379–387.

Bugert, R.M. & Bjornn, T.C. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. Transactions of the American Fisheries Society 120: 486–493.

Bugert, R.M., Bjornn, T.C. & Meehan, W.R. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of American Fisheries Society 120: 474–485.

Bustard, D.R. & Narver, D.W. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32: 667–680.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Sciences 40: 398–408.

Dolloff, C.A. & Reeves, G.H. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch*, and Dolly Varden, *Salvelinus malma*. Canadian Journal of Fisheries and Aquatic Sciences 47: 2297–2306.

Dunbrack, R.L. & Dill, L.M. 1983. A model of size dependent surface feeding in a stream dwelling salmonid. Environmental Biology of Fishes 8: 203–216.

Dunbrack, R.L. & Dill, M.L. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 41: 1176–1182.

Dupont, W.D. & Plummer, W.D.J. 1998. Power and sample size calculations for studies involving linear regression. Controlled Clinical Trials 19: 589–601.

Everest, F.H. & Chapman, D.W. 1972. Habitat selection and spatial interaction by juvenile Chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29: 91–100.

Fraser, F.J. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. In: Northcote, T.G., ed.. Symposium on Salmon and Trout in Streams. Vancouver: Canada Department of Fisheries, pp. 253–266.

Gibson, R.J. & Power, G. 1975. Selection by brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) of shade related by water depth. Journal of Fisheries Research Board of Canada 32: 1652–1656.

Godin, J.J. & Rangeley, R.W. 1989. Living in the fast lane: effects of cost of locomotion on foraging behaviour in juvenile Atlantic salmon. Animal Behaviour 37: 943–954.

Grand, T.C. & Dill, L.M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. Behavioral Ecology 8: 437–444.

Greenberg, L.A. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. Environmental Biology of Fishes 31: 389–401.

Greenberg, L.A., Steinwall, T. & Persson, H. 2001. Effect of depth and substrate on use of stream pools by brown trout. Transactions of the American Fisheries Society 130: 699–705.

Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 50: 241–246.

Groot, C. & Margolis, L. 1991. Pacific Salmon Life Histories. Vancouver, BC: UBC press.

Hartman, G.F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22: 1035–1081.

Harvey, B.C. & Nakamoto, R.J. 1997. Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream. Canadian Journal of Fisheries and Aquatic Sciences 54: 27–31.

Hayes, J.W. 1995. Importance of stream versus early lake rearing for rainbow trout fry in Lake Alexandrina, South Island, New Zealand, determined from otolith daily growth patterns. New Zealand Journal of Marine and Freshwater Research 29: 409–420.

Heggenes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. Transactions of the American Fisheries Society 131: 287–298.

Heggenes, J., Bagliniere, J. L. & Cunjak, R. A. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. Ecology of Freshwater Fish 8: 1–21.

Hesthagen, T., Saksgaard, R., Hegge, O., Dervo, B. K. & Skurdal, J. 2004. Niche overlap between young brown trout (*Salmo trutta*) and Siberian sculpin (*Cottus poecilopus*) in a subalpine Norwegian river. Hydrobiologia 521: 117–125.

Hill, J. & Grossman, G.H. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74: 685–698.

Irvine, J.R. & Johnston, N.T. 1992. Coho salmon (*Oncorhynchus kisutch*) use of lakes and streams in the Keogh River drainage, British Columbia. Northwest Science 66: 15–25.

Johnston, J.M. 1970. Food and Feeding Habits of Juvenile Coho Salmon and Steelhead Trout in Worthy Creek. Seattle, WA: Master's. University of Washington.

Jowett, I.G. 2002. In-stream habitat suitability criteria for feeding inanga (*Galaxias maculatus*). New Zealand Journal of Marine and Freshwater Research 36: 399–407.

Kruzic, L.M., Scarnecchia, D.L. & Roper, B.B. 2001. Comparison of midsummer survival and growth of age-0 hatchery coho salmon held in pools and riffles. Transactions of the American Fisheries Society 130: 147–154.

Lister, D.B. & Genoe, H.S. 1970. Stream habitat utilization by cohabitating underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. Journal of the Fisheries Research Board of Canada 27: 1215–1224.

Lohr, S.C. & Bryant, M.D. 1999. Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. Juneau: USDA General technical report PNW-GTR-407 Pacific Northwest Research Station, Forest Service, USDA.

Maeki-Petaeys, A., Vehanen, T. & Muotka, T. 2000. Microhabitat use by age-0 brown trout and grayling: seasonal responses to streambed restoration under different flows. Transactions of the American Fisheries Society 129: 771–781.

Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121: 617–634.

O'Brien, W.J. & Showalter, J.J. 1993. Effects of current velocity and suspended debris on the drift feeding of Arctic grayling. Transactions of the American Fisheries Society 122: 609–615.

Piccolo, J.J. 2005. The Influence of Water Velocity and Depth on Prey Detection and Capture by Juvenile Coho Salmon and Steelhead: Implications for Habitat Selection and Segregation, PhD Dissertation. Fairbanks Alaska: University of Alaska Fairbanks.

Polacek, M.C. & James, P.W. 2003. Diel microhabitat use of age-0 bull trout in Indian Creek, Washington. Ecology Freshwater Fish 12: 81–86.

Reyjol, Y., Lim, P., Belaud, A. & Lek, S. 2001. Modelling of microhabitat used by fish in natural and regulated flows in the river Garonne (France). Ecological Modelling 146: 1–3.

Rosenfeld, J.S. & Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58: 585–593.

Sheppard, J.D. & Johnson, J.H. 1985. Probability-of-use for depth, velocity, and substrate by subyearling coho salmon and steelhead in Lake Ontario tributary streams. North American Journal of Fisheries Management 5: 277–282.

Solazzi, M., Nickelson, T., Johnson, S. & Rodgers, J. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57: 906–914.

Swain, D.P. & Holtby, L.B. 1989. Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. Canadian Journal of Fisheries and Aquatic Sciences 46: 1406–1414.

Young, K.A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology 85: 134–149.

Zar, J.H. 1999. Biostatistical Analysis, 4th edn. Upper Saddle River, NJ: Prentice-Hall.