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Axes of fear for stream fish: water depth and distance to cover

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Abstract To better understand habitat-specific predation risk for stream fish, we used an approach that assumes animals trade off food for safety and accurately assess risk such that predation risk can be measured as a foraging cost: animals demand greater harvest rates to occupy riskier locations. We measured the foraging cost of predation risk for juvenile salmonids within enclosures in a natural stream at locations that varied in water depth and distance to cover. Measurements relied on a food delivery apparatus and direct observations that allowed estimation of "giving-up" harvest rates – food delivery rates at which animals left the feeding apparatus. Juvenile steelhead about 120 mm fork length exhibited sharp increases in giving-up harvest rate with decreasing water depth and refused to use the feeding device even when offered extreme food delivery rates in water ≤20 cm deep. Giving-up harvest rates were less affected by the distance to cover. Assuming the gradients we observed in giving-up harvest rates reflect predation risk, the results of this study can be applied to spatially explicit models of stream fish populations that incorporate risk into both habitat selection and mortality due to predation.

Keywords Predation risk · Stream fish · Salmonids · Giving-up harvest rate · Water depth · Cover

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Introduction

Habitat selection by animals can incorporate multiple demands, such as food acquisition and predator avoidance, which may present trade-offs under some conditions. Recognizing the influences of multiple demands can be important in understanding and modeling habitat selection. For example, Gilliam and Fraser (1987) successfully predicted habitat selection by a stream-dwelling minnow under experimental conditions, using a rule that incorporated both foraging rate and predation risk. Railsback and Harvey (2002) found that in modeling habitat selection by a stream salmonid, only a selection criterion that incorporated both food acquisition and sensitivity to predation risk completely reproduced a set of widely observed patterns of behavior. Recent field observations that models of habitat selection that include both food acquisition and factors that may influence risk are superior to models including food acquisition alone (e.g., Kawai et al. 2014) correspond with the results of Railsback and Harvey (2002). Successful modeling of habitat selection is critical for predicting population-level phenomena using spatially explicit, individual-based models that incorporate food versus risk trade-offs, which can be critical to population dynamics (Preisser et al. 2005; Railsback and Harvey 2013). Successful modeling of habitat selection that incorporates predation risk, however, requires that the habitat-dependence of that risk is adequately represented.

Researchers have estimated habitat-specific variation in risk using the conceptual framework of J.S. Brown (Brown 1988, 1992; Brown and Kotler 2004) that assumes animals trade off food for safety, such that predation risk can be expressed as a foraging cost. Much of this work has focused on mammals (e.g., Brown et al. 1994; van der Merwe and Brown 2008). Field measurements of the habitat-dependence of predation risk commonly quantify giving-up food density (GUD) for animals willing to use artificial patches of mixtures of food and non-food (e.g., seeds in sand). Higher GUD indicates the perception of greater risk; GUD can be linked to foraging theory by translation to giving-up harvest rates (energy gain/time). Less frequently, spatial variation in the foraging cost of risk has been estimated by manipulation of food delivery to directly measure giving-up harvest rates (Todd and Cowie 1990).

For stream fishes, predation risk is influenced by both water depth and cover – structure that allows fish to hide from predators. Field experiments have revealed influences of both depth and cover on survival (Harvey and Stewart 1991; Lonzarich and Quinn 1995; Reinhardt and Healey 1997). Studies also suggest the existence of steep gradients in risk. For example, when given the opportunity to colonize constructed stream pools either 25 or 50 cm deep, yearling cutthroat trout (*Oncorhynchus clarkii*) occupied only the deeper pools (Lonzarich and Quinn 1995). Such results make sense in light of information on the depth-related capture success of predators such as wading birds (Lotem et al. 1991; Gawlik 2002), which can be important in small streams. However, in some lotic settings prey may also face increasing risk from piscivorous fish with increasing depth (Power 1987; Harvey 1991). The influence of body size on prey vulnerability to different predators adds to the complexity of the risk environment for stream fish.

Existing information has not, however, established useful quantitative relations between predation risk and habitat variables such as depth and distance to cover. One problem is that field experiments that have attempted to directly assess predation risk by measuring survival usually include a limited number of treatment levels, such that extensive extrapolation is needed to develop relationships encompassing a useful range of the independent variables. The dearth of information on relations between predation risk and habitat variables is particularly relevant to process-based, spatially explicit modeling of stream fishes. For example, for one spatially explicit population model of stream trout (*Oncorhynchus* spp.) in which fish incorporate predation risk into habitat selection (Railsback et al. 2009), a sensitivity analysis revealed that a parameter describing the water depth at which fish gain substantial safety from avian and terrestrial predators had the strongest effects on the model's population-level outcomes (Cunningham 2007). A parameter describing the influence of distance to cover on predation risk was also relatively influential. Unfortunately, these parameters are currently derived from few empirical observations. To address this information gap, we sought to estimate the habitat-dependence of predation risk by quantifying variation in fear expressed by stream trout, as indicated by "giving-up" harvest rates along gradients in both depth and distance to cover.

Materials and methods

Study site

We conducted this study in Maple Creek, a coastal stream in northwestern California that drains a catchment dominated by second-growth forest. In the study area (41°05'30" N, 124°05'07" W), Maple Creek has a 0.7% gradient and drains about 42 km^2. Red alder (*Alnus rubra*), coast redwood (*Sequoia sempervirens*) and big-leaf maple (*Acer macrophyllum*) are the most common riparian trees, whereas stink currant (*Ribes bracteosum*), western sword fern (*Polystichum munitum*), and thimbleberry (*Rubus parviflorus*) are common in the riparian understory. Steelhead/rainbow trout (*Oncorhynchus mykiss*), coastal cutthroat trout (*O. clarkii clarkii*), and Pacific lamprey (*Entosphenus tridentatus*) make up the fish assemblage in the study reach. Additional aquatic vertebrates in the reach include coastal giant salamander (*Dicamptodon tenebrosus*), Pacific Coast aquatic garter snake (*Thamnophis atratus*), and coastal tailed frog (*Ascaphus trueii*). Piscivores in the study area include Belted Kingfisher (*Megaceryle alcyon*), Great Blue Heron (*Ardea herodias*), Western Screech Owl (*Megascops kennicottii*), North American river otter (*Lontra canadensis*) and American mink (*Neovison vison*) (R.J. Nakamoto and B.C. Harvey, unpublished data). The stream substrate in the study area is primarily poorly sorted sand, gravel and small cobble. With negligible precipitation in the catchment between July and October, streamflow in Maple Creek remained low (< 0.12 m^3/s) during our observations in summer/early fall of 2014 and 2015; water temperature was stable and favorable for salmonid fish (mean = 14.4 C, SD = 1.3 [measurements every 30 min]).

Experimental protocol

We sought to measure giving-up harvest rates across gradients in both water depth and distance to cover using a field experiment. To do this we placed individual fish in enclosures positioned in pools and offered them food at specific locations via a device that allowed an observer to closely control food delivery rate. We constructed rectangular enclosures of semi-rigid black polyethylene netting (6.5-mm mesh in 2014, 4.5-mm in 2015) held upright with metal fence posts and buried in the substrate along the bottom edge. Enclosure fencing perpendicular to the bank spanned 4 m of wetted stream width and extend about 1 m onto the streambank. Enclosures were 4-m-long in the dimension parallel to the streamflow, such that each enclosed 16 m^2 of wetted area. We placed enclosures where depth increased approximately linearly with distance from the bank, reaching a maximum of 90–100 cm. The units enclosed areas with sand to small cobble substrate and no natural concealment cover for fish. We installed two forms of artificial cover along the length of the upstream wall of each enclosure. A 45-cm wide, floating strip of black cloth provided surface cover. Benthic cover consisted of a continuous line of cover units, each a pair of 30 × 18-cm black plastic plates separated by 2-cm spacers. We covered the tops of each enclosure with clear, 6-mm-mesh, monofilament netting. In 2014, we constructed three enclosures in early July, added the first fish on 21 July and ceased observations on 19 September. In 2015, we constructed two enclosures in early June, added the first fish on 19 June and concluded the experiment on 7 October.

Because we were seeking to measure giving-up harvest rates on a relatively fine spatial scale, we designed a food delivery device that required fish to stay close to the device to capture food. A submersible pump forced food items in a stream of water through 6-mm-inner-diameter tubing such that they drifted across a clear acrylic trough (20-cm long × 3-cm wide × 1.5 cm deep); prey items were extracted through a 2.5-cm outlet with vacuum created by a second submersible pump (Fig. 1). Food items were available to fish for about 1 s as they passed along the trough. The delivery tubing was covered so that fish could not anticipate the arrival of food items. The device rested on the streambed, such that fish captured prey items about 4 cm above the surrounding stream bottom. From a concealed position on the bank adjacent to the enclosure, an operator controlled the rate of delivery of food items and observed fish on a video monitor linked to a pair of underwater cameras. We positioned one camera at the same depth as the feeder ~75 cm downstream and a second camera about ~75 cm upslope of the feeder. We used multiple food items to provide a broad range of potential feeding rates (J/min): brine shrimp (*Artemia* sp.; 10 J), chironomid larvae (*Chironomus* spp.; 23 and 41 J) and calliphorid (blow fly) larvae (*Phaenicia sericata*; 607 J). We purchased frozen adult brine shrimp and chironomid larvae; calliphorid larvae were obtained live and frozen upon receipt. Food items were thawed in water before being individually placed in the feeding system.

We began trials by removing via backpack electrofishing any fish trapped in an enclosure during construction, then introducing individual trout (111–145 mm fork length [FL]) captured by electrofishing within a few hundred meters of the enclosures. In 2014 the mesh size of enclosure fences allowed passage of small age-0 salmonids (< about 50 mm FL); in 2015 the enclosures excluded age-0 fish. We attempted to acclimate fish to the feeding device by placing it in relatively deep water (> 70 cm) immediately adjacent to cover, then offering fish brine shrimp or chironomid larvae every 5–10 s for at least 1 h per day. We considered acclimation complete when fish consistently began capturing introduced prey at the feeder within 30 min of the beginning of food delivery.

After acclimation, we began observations by positioning the feeder at points with specific combinations of water depth and distance to cover. To standardize disturbance, observations at each point were immediately preceded by a diver positioning the feeder and cameras. With the feeder and cameras in place, the observer began delivering a rapid stream of food, one item every 5–10 s, until the fish captured a prey item. At that point, the observer began sending prey items with steadily decreasing frequency. We defined the “giving up” time for a fish at a particular point as the time between the last successful prey capture and the fish leaving the area within 25 cm of the feeder for a period of ≥60 s. The departures of fish were often piecemeal; fish occasionally returned to the feeder with apparent full attention to the device after being out of view for 30–60 s. In those cases, the observer delivered an additional food item. If that item was captured, the observer re-started the process of measuring giving-up time. The procedure allowed fish to develop expectations about the timing

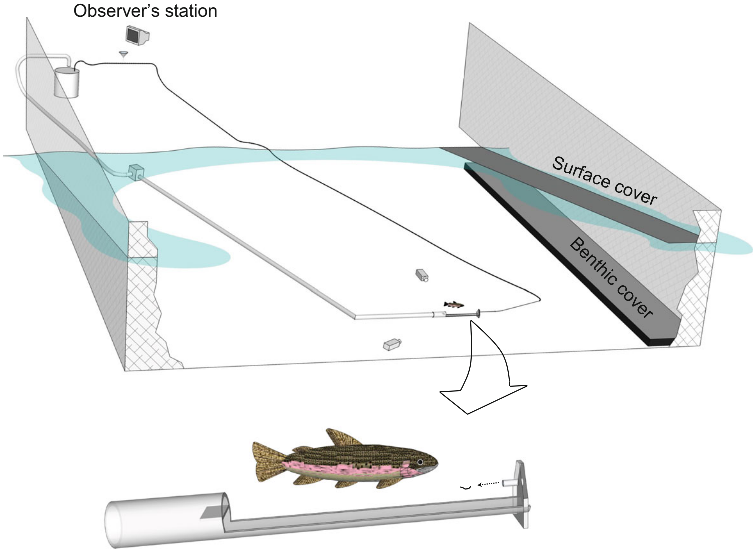


Fig. 1 Schematic diagram of the enclosures and apparatus used to measure giving-up harvest rates by juvenile stream salmonids. Blue shading indicates the water's surface

of food delivery: giving-up times averaged 10% longer than the immediately preceding interval between successful prey captures. We made observations of no more than three points per fish on any 1 d to limit any effect of gut fullness on results. We attempted to identify all the combinations of depth and distance to cover a given fish was willing to occupy when offered a relatively low-value food item (brine shrimp or chironomid larvae) before switching to calliphorid larvae. When possible, we returned to using low-value food items after using calliphorid larvae to make repeat observations at spots fish had previously occupied when offered the lower-value food. We determined the energy content of individual prey by measuring the mean dry mass of individual food items (10 samples of 10–20 individuals each) and using published information on energy density (Cummins and Wuycheck 1971; Caudell and Conover 2006). We determined giving-up harvest rates (J/min) by dividing the energy content of individual prey by the giving-up time. Thus, we assumed fish would have remained at the feeder if a prey item had arrived just before the fish left the feeder.

Fish acclimated to the feeding device refused to use it at some locations within the enclosures; therefore, giving-up harvest rates could not be quantified for those locations. We confirmed these locations with at least three sessions in which we offered fish calliphorid larvae in a steady stream of one prey item every 5 to 10 s, which represents a food delivery rate of about 3000 J/min. For each session at these locations, we confirmed by video monitoring that the subject fish was in a position to perceive the availability of food at the device.

Our approach to estimating the cost of predation uses the patch-use models developed by Brown (Brown 1988, Brown 1992; reviewed in Brown and Kotler 2004) to describe giving-up harvest rate (H) as a function of the metabolic (C), predation (P) and missed opportunity costs (MOC) of foraging:

$$H = C + P + MOC$$

Given the consistent use of the feeding device and consistent environmental conditions, we assumed a constant energetic cost of foraging (C). Given the limited time window of the experiment and the fact fish were almost always observed holding position under or near cover in the deepest parts of the enclosures before we began experimental feeding, we assumed missed-opportunity-costs (MOC) were approximately constant across observations and negative, equal to a fish's metabolic rate under a modest level of activity. (We documented a modest reduction in condition over 11 d for one fish within an enclosure that did not use the feeding device.) Finally, considering the minimal cost of obtaining prey items from the feeder, C and MOC were probably similar in magnitude, such that the giving-up harvest rates we measured approximated the cost of predation (P).

Statistical analysis

Forty-six total observations of three similar-sized steelhead in 2015 provided a dataset suitable for statistical analysis. Because the dataset included censored values for giving-up harvest rate at those sites fish refused to occupy when offered 3000 J/min, we analyzed the data using Tobit regression (SAS QLIM Procedure). We included depth, cover and the depth X cover interaction in the statistical model. The model incorporated variability among individuals by allowing intercepts to vary among them. We log-transformed the response (giving-up harvest rate) to best reflect the scale of ecological interest.

Results

We tested a total of 17 fish in 2014 and 2015 combined. Of the 17 fish, five (one in 2014 and four in 2015) began consistent use of a feeder (size range of fish providing observations: 118–124 mm FL). It took an average of 12 d (range 4–19 d) for the five fish to consistently use the feeder. We gave the other fish the opportunity to acclimate to a feeder for 7–45 d. One fish that persistently explored enclosure fences was released in 4 d.

The fish that yielded observations in 2014 exhibited increased giving-up harvest rates with decreasing depth and increasing distance to cover (Fig. 2). However, the behavior of the fish was also influenced by about 15 age-0 fish that shared its enclosure and readily utilized the feeder in shallow water. Defense of the feeder against age-0 fish by the larger focal individual made giving-up times difficult to discern and clearly influenced use of the feeder by the larger fish. This result motivated the use of finer mesh for the enclosures in 2015, to limit the occurrence of age-0 fish.

We also obtained unique results from the one individual identified as a cutthroat trout (Fig. 3). This fish took 18 d to use the feeder, then did so routinely along the 75-cm depth transect, exhibiting a very modest increase in giving-up harvest rate with distance to cover. While the fish was observed in deeper water near the enclosure fence with the feeder at depths <75 cm, unlike other fish tested it never attempted to capture food at shallower depths.

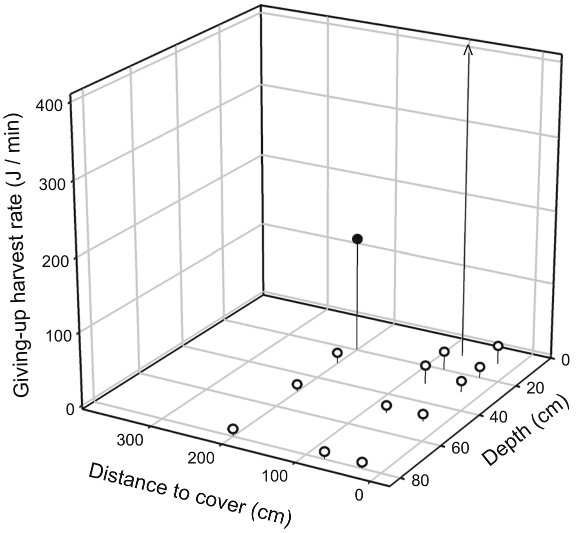


Fig. 2 Giving-up harvest rates for a 121-mm FL steelhead determined using a combination of brine shrimp (○) and calliphorid larvae (●) prey. Data from this fish are likely affected by the presence of approximately 15 young-of-the-year steelhead. The upward-pointing arrow at Depth = 10 cm and Distance to cover =75 cm indicates the fish refused to occupy the feeder to consume calliphorid larvae delivered at >3000 J/min. The x-y planes in Figs. 2–4 correspond with the floors of the enclosures

The three steelhead that provided data in 2015 exhibited substantial individual variation, but depth had a strong overall effect on giving-up harvest rate (Fig. 4; $P < 0.0001$). At a given distance to cover, giving-up harvest rates were consistently inversely and non-linearly related to depth. All three fish refused to use the feeder at either 20 or 30 cm of depth. Overall effects

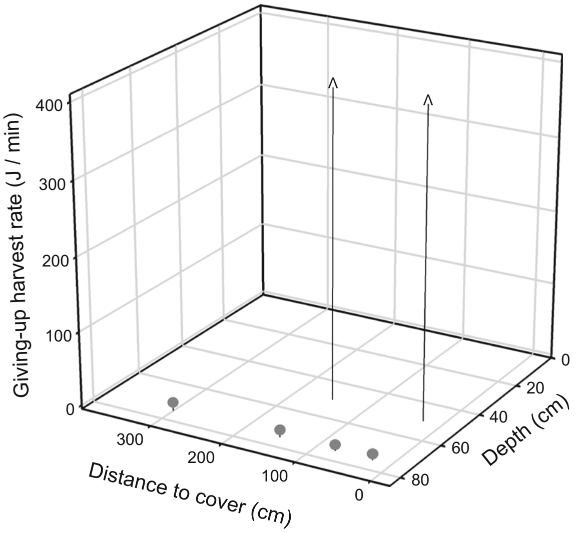
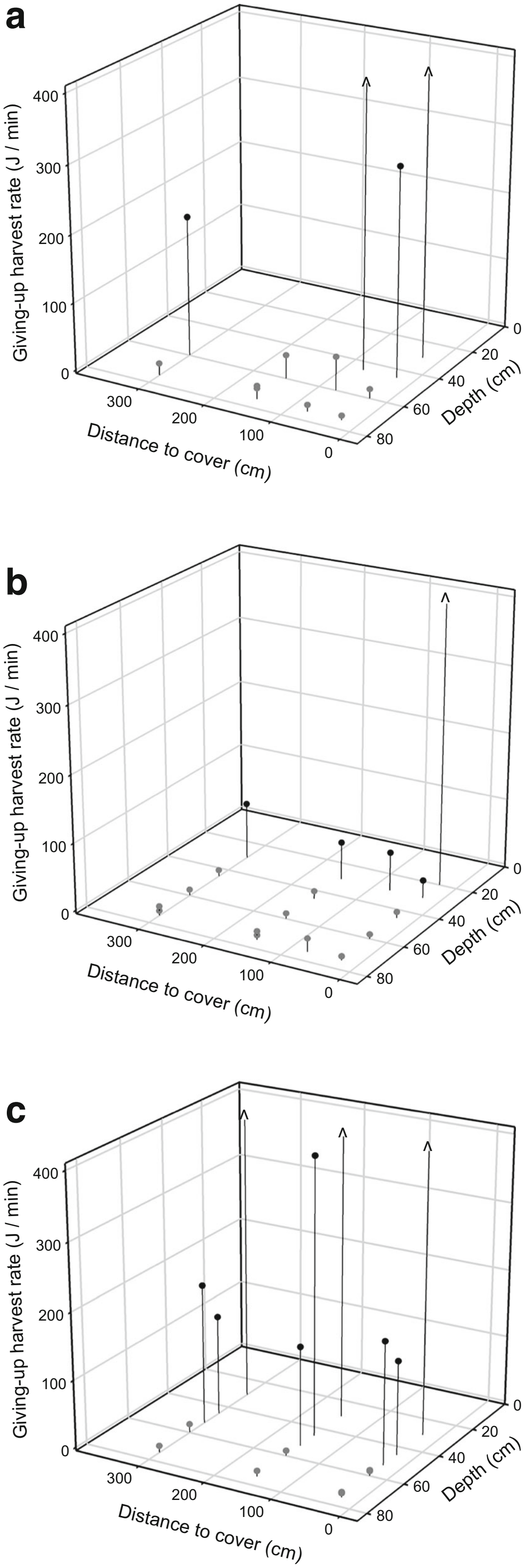


Fig. 3 Giving-up harvest rates for a 124-mm-FL juvenile cutthroat trout, determined using a combination of chironomid larvae (●) and calliphorid larvae prey. Upward-pointing arrows identify locations where fish refused to occupy the feeder when offered calliphorid larvae at > 3000 J/min



◀**Fig. 4** Giving-up harvest rates for three juvenile steelhead (118–123 mm FL), determined using a combination of chironomid larvae (●) and calliphorid larvae (●) prey. Upward-pointing arrows identify locations where fish refused to occupy the feeder at a food delivery rate > 3000 J/min

of cover (*P* = 0.22) and the depth X cover interaction (*P* = 0.10) were not strong in the statistical model. However, inspection of the data indicated that the marginal *P* value for the interaction could be explained by observations in shallow water close to cover: at the shallowest depth they were willing to feed, two of the steelhead from 2015 were willing to feed 25 cm but not 75 cm from cover. The third steelhead from 2015 required >2X the harvest rate at 75 cm compared to 25 cm (52 J/min versus 22 J/min). Results further from cover were inconsistent (Fig. 4).

We recorded length and mass at both introduction and removal for four of the fish in 2015 (all identified as steelhead; three fish that used a feeder and one that did not). As determined from a standard weight equation for juvenile steelhead from McLaughlin (2009) that relates weight to an expected weight for a given length, the relative weights of the three fish that used a feeder increased on average from 97% to 101% over a mean of 33 d, while the relative weight of the fish that did not use the feeder declined from 99% to 97% over 11 d. The increase in condition over the course of observations did not appear to strongly affect results: fish exhibited similar giving-up harvest rates at specific locations at the beginning and end of observations.

As noted in Methods, fish using the feeder rarely exhibited a sudden and complete departure from the apparatus. We occasionally observed sudden departures from feeders when fish responded to stimuli such as the passing shadows of birds by retreating to deep water and cover; strong flight responses by a focal fish in response to short-term stimuli led us to cease data collection for the day.

Discussion

Variation in giving-up harvest rates for stream trout in this study indicated strong gradients in fear with water depth where water velocity is negligible. This observation corresponds with the potential for high risk for stream fish in shallow water suggested by a variety of studies (e.g., Power 1984; Matthews et al. 1986; Harvey and Stewart 1991; Lonzarich and Quinn 1995; Gowan 2007). For solitary juvenile steelhead of about 120 mm FL unaccompanied by abundant age-0 fish, giving-up harvest rate began to increase dramatically in the depth range of 52.5–30 cm. Similar to previous studies of similar-sized stream fish, trout refused to use water ≤20 cm deep even where such locations offered large foraging benefits (Power 1984; Gowan 2007). The specific depths at which fear and presumably predation risk sharply increase are important, because they strongly influence the proportion of the stream likely to be inhabited by fish. This point is reflected in Cunningham's (2007) observation that population-level results from an individual-based model of stream trout in which predation risk affects both mortality and habitat selection were most sensitive to a parameter that describes the relationship between water depth and predation risk. For example, in simulations of a trout population in a stream similar in size to the Maple Creek site used in this study, a change from 100 to 40 cm in the depth at which fish gain 90% protection from terrestrial predators results in a 2.5X increase in long-term average population biomass.

In comparison to depth, distance to cover influenced giving-up harvest rates less strongly and consistently, but observations close to cover in shallow water corresponded with prior observations of cover's potential to lower the perception of predation risk for fish (e.g., Grand and Dill 1997; Johnsson et al. 2004). Few studies of fish have addressed distance to cover per se. In a laboratory experiment, Abrahams and Dill (1989) varied risk for guppies (*Poecilia reticulata*) from a piscivorous fish by manipulating distance to cover; overall the energetic equivalence of risk increased by about 2.4X between distances to cover of 2 versus 32 cm. Three additional studies that directly (McLean and Godin 1989; Dill 1990) or indirectly (Grant and Noakes 1987) included distance to cover as an independent variable all found increasing reactive distances to approaching predators with increasing distance to cover, in the range of 0–100 cm for prey species smaller than the trout we studied. But this range also appeared important in our study, in that all three fish for which we have observations 25 cm and 75 cm from cover exhibited sharp increases in giving-up harvest rates between those distances in the shallowest water in which they were willing to use the feeder. The significance of greater distances to cover to the cost of predation is not clear from our data, in that we did not consistently observe increasing giving-up harvest rates with distance. One possible contributing factor to this result is any negative effect of cover on the ability of fish to detect predators; the relative detection abilities of predator and prey can strongly influence final outcomes. Distance to cover did not strongly influence giving-up harvest rates in deeper water. This apparent interaction between depth and cover parallels results from Gibson and Erkinaro (2009), who found increasing use of cover by juvenile Atlantic salmon (*Salmo salar*) with decreasing depth in an artificial-stream experiment.

Although our observations were limited to juvenile salmonids within a narrow size range at one study site within the late dry season, individual fish exhibited highly variable patterns in giving-up harvest rates. The presence of abundant age-0 fish in enclosures in 2014 and not 2015 almost certainly contributed to that variability: territorial behavior by fish we studied affected their willingness to occupy shallow water when smaller fish were present. More generally, Brown's models that describe optimal quitting harvest rates when animals use patches under predation risk (Brown 1988, 1992; Brown and Kotler 2004) provide a framework for understanding individual variation. These models include several terms that likely varied among individuals and over time in our experiment: the marginal fitness value of energy, the survivor's fitness and missed opportunity costs. The marginal value of energy will change with an animal's energetic state, as indicated by the willingness of hungry fish to take greater risks (Gotceitas and Godin 1991). Both the marginal value of energy and the fitness of survivors are likely to vary among species, between sexes (Abrahams and Dill 1989) and with time of year, perhaps even within the time frame of our observations (Brown et al. 1994). We presented data on two species and did not determine the sex of individuals. To the extent our assumption that missed opportunity costs were minor in the experimental enclosures during our observations was incorrect, we over-estimated giving-up harvest rates: fish would not be expected to use a feeder in a risky position if background food levels allowed them to achieve satiation while feeding in safe areas in the enclosures. Finally, variation in the personalities of individual fish would be expected to add variation to our results (e.g., Mazué et al. 2015).

Across sites, a variety of biotic factors will influence the strong gradient in risk with depth suggested by this and other studies, including: 1) the abundance of predators effective in shallow water, 2) prey body size, 3) the significance of piscivores with contrasting patterns of depth-dependent prey capture success; and 4) the specific characteristics of the predators and prey involved, such as antipredator behaviors or morphological adaptations of prey. A wide variety of avian and terrestrial piscivores are effective in shallow water (Harvey and Nakamoto 2013); substantial spatio-temporal variation in their abundance should be expected. In general, the risk from shallow-water predators increases with the body size of the prey (Harvey and Stewart 1991); that pattern was reflected in this study by the willingness of age-0 fish around 50 mm FL to use feeders without regard to depth. In some settings, prey may face significant risk from predators likely to be more effective in deeper water, such as piscivorous fish (Harvey 1991). Finally, as an example of the importance of specific predator and prey characteristics, McLean and Godin (1989) observed that of the four fish species they tested, only the one lacking body armor and spines demonstrated a positive relationship between distance to cover and the distance between predator and prey at which prey initiated a flight response.

Stream trout have several characteristics that make unsurprising our low success rate in acclimating trout to the food delivery device. Stream trout most commonly sit-and-wait for food in positions that allow them to capture food as it is carried past by water currents; water velocity is normally a critical cue in selecting foraging positions (Gowan 2007). In addition, trout commonly swim rapidly to intercept prey before returning to positions they hold for foraging (Piccolo et al. 2008). That the method we used required fish to maintain position near a device positioned on the stream bottom represents a sharp contrast with common trout foraging behavior. While this fact probably contributed to the inefficiency of the method, as Brown (1988) pointed out, it is not necessary to mimic natural resources when the focus is on estimating differences in predation risk among microhabitats.

This study reveals that the approach of measuring the cost of predation as a foraging cost (Brown and Kotler 2004) can be applied to the challenge of estimating the influence of physical habitat characteristics on predation risk for stream fish. Both water depth and distance to cover are clearly influential in the perception of risk for stream salmonids. While a wide variety of factors create variability in the habitat-dependence of predation risk for stream fish, this study provides unique observations useful in parameterizing spatially explicit, individual-based models of stream salmonids that incorporate spatial variation in risk.

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