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FRESHWATER FISH

Instream cover and shade mediate avian predation on trout in semi-natural streams

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Accepted for publication February 22, 2015

Abstract – Piscivory by birds can be significant, particularly on fish in small streams and during seasonal low flow when available cover from predators can be limited. Yet, how varying amounts of cover may change the extent of predation mortality from avian predators on fish is not clear. We evaluated size-selective survival of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in replicated semi-natural stream sections. These sections provided high (0.01 m^2 of cover per m^2 of stream) or low (0.002 m^2 of cover per m^2 of stream) levels of instream cover available to trout and were closed to emigration. Each fish was individually tagged, allowing us to track retention of individuals during the course of the 36-day experiment, which we attributed to survival from predators, because fish had no other way to leave the streams. Although other avian predators may have been active in our system and not detected, the only predator observed was the belted kingfisher *Megaceryle alcyon*, which is known to prey heavily on fish. In both treatments, trout >20.4 cm were not preyed upon indicating an increased ability to prey upon on smaller individuals. Increased availability of cover improved survival of trout by 12% in high relative to low cover stream sections. Trout also survived better in stream sections with greater shade, a factor we could not control in our system. Collectively, these findings indicate that instream cover and shade from avian predators can play an important role in driving survival of fish in small streams or during periods of low flow.

Key words: trout survival; refuge; piscivory; body size; low flow; experiment

Introduction

Avian predation is widely recognised as a key factor influencing the survival of fishes in stream ecosystems (Draulans 1988; Roby et al. 2003; Steinmetz et al. 2003), but it can be difficult to directly observe (Steinmetz et al. 2003; Harvey & Nakamoto 2013; Orrock et al. 2013). Successful foraging by avian predators is influenced by characteristics of prey species, density of prey and distribution of habitat features (Lantz et al. 2010). Whereas benthic fishes are less susceptible to avian predation (Lonzarich & Quinn, 1995), fish that occupy the water column in streams are potential prey. Accordingly, these fish display a variety of antipredator tactics, including the use of local habitat features as refuge to avoid capture by predators (Power 1984; Lima & Dill 1990; Harvey & Stewart 1991; Allouche & Gaudin 2001).

In small streams where water depths are too shallow (under 20 cm) to provide refuge to fish from avian predators (Power 1984; Harvey & Stewart 1991) and cover is reduced by seasonal low flow (Harvey & Stewart 1991; Allouche & Gaudin 2001), available cover may be a limiting factor for trout survival. Instream cover comes in the form of surface turbulence, boulders, cobbles, wood and undercut banks. If they are important for mediating avian predation, then alterations to instream cover should translate into changes in numbers or size distributions of fish. Avian predation may reduce numbers of fish directly through mortality or by motivating fish to emigrate (Steinmetz et al. 2003). Changes in size distributions of fish may be related to size selectivity by

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doi: 10.1111/eff.12221

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predators (Harvey & Stewart 1991; Steinmetz et al. 2003) as well as size-related differences in ability of fish to avoid predators (Dill & Fraser 1984) or access instream cover. The relationship among avian predation, instream cover and fish size under low flow conditions is still not clear (Berger & Gresswell 2009), but as low flow conditions become more prevalent from climate change, this information may become more important.

In this study, we experimentally manipulated availability of instream cover to coastal cutthroat trout *Oncorhynchus clarkii clarkii* held in replicate semi-natural streams to directly evaluate whether instream cover mediates survival when exposed to avian predation pressure. We additionally considered the role of shade and size of trout in relation to individual survival because they may be important factors influencing predation. Studies examining the effect of avian predation on fish have been generally based on either tethered fishes (Post et al. 1998; Harvey & Nakamoto 2013) or diets of birds without observation of fish responses (Draulans 1988). Studies that have considered fish responses, however, have not been designed to distinguish between the effects of fish mortality from fish emigration (Steinmetz et al. 2003). Harvey & Stewart (1991) considered cover in pool habitats only and found that there was higher survival for larger fish than smaller fish in shallow water. In our study, fish were free to move within the confines of each stream section to eliminate the possibility of emigration. Thus, the only way fish could leave the streams was via predation. We predicted that there would be higher overall survivorship when cover was more available, when there was more shade, and that larger trout would be more likely to survive. We predicted the latter because fish >12 cm are seldom consumed by piscivorous birds such as belted kingfisher *Megaceryle alcyon* (Salyer & Lagler 1946; Hamas 1994), which is a common predator in our study area. An additional factor potentially contributing to greater survival of larger trout is their ability to monopolise access to instream cover when it is in limited supply (Jenkins 1969), thus leaving smaller fish potentially more vulnerable to predators.

Methods

Experimental design and semi-natural stream sections

Our experiment approximated conditions experienced by stream-living fishes during seasonal low flow in small streams in the Oregon Coast Range, USA (Fig. 1). Under such conditions, instream cover is limited, water depths are shallow, shade is patchy, and fish survival is 20–50% less than at other times of the year (Berger & Gresswell 2009). Hence, it seems likely that predation may play a key role in reducing trout survival during seasonal low flow. In natural streams, trout tend to use instream cover in the form of cobble and boulders more than any other cover type, including undercut banks, turbulence, vegetation or wood (Andersen 2008). Trout generally select cobble and boulders that fit their body length (Andersen 2008).

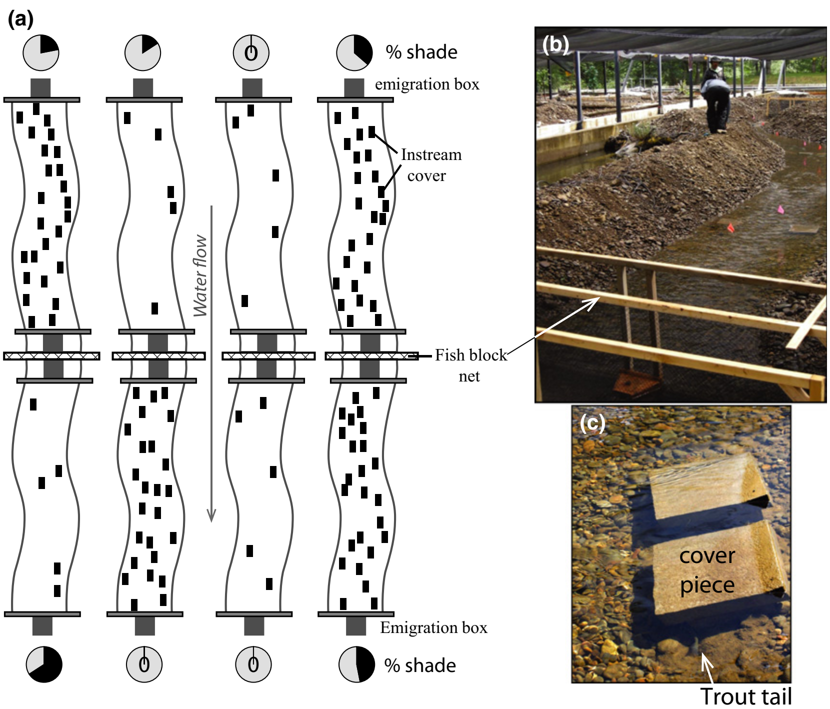

Fig. 1. (a) Design of experimental area with location of stream sections for low-density (n = 4) and high-density (n = 4) instream cover coupled with amount of shade for each stream section. Emigration boxes were at each end of a stream section. Mesh screens prevented fish passage to other stream sections as indicated by fish block nets. (b) Example low-density stream section with fish block net indicated. All stream sections were 20 m long and 2 m wide (wetted width). (c) Adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) using instream cover piece. Each cover piece consisted of a 30.5- by 30.5-cm concrete paver top-piece with a 30.5-by 20.3-cm paver bottom-piece glued underneath in the centre creating two 5.1-by 30.5-cm equal-sized spaces on each end for cover.

We conducted a 36-day (29 June 2009 to 03 August 2009) manipulative experiment at the Oregon Hatchery Research Centre (http://www.dfw.state.or.us/fish/OHRC/). Before the start of our study, we drained the streams for a week and then we reshaped their morphology with heavy machinery. We divided the four existing outdoor stream channels in half creating eight stream sections that were 20 m long and 2 m wide (wetted width; Fig. 1a). Mesh screens prevented fish passage to other stream sections, but within a section fish could move around freely (Fig. 1b). We maintained a minimum flow in stream sections to hold other potentially confounding covariates associated with instream cover, such as water depth, turbidity, food and velocity, as constant as possible. Hence, water depths were maintained between 15 cm and 30 cm by managing incoming flows and by filling deeper pools prior to the start of the study. We also removed larger river rock (>8 cm) that could have been used as instream cover from each stream section. Drift and benthic invertebrates were present in stream sections, but no additional food was added. We electroshocked at the beginning and end of the experiment to eliminate the presence of other aquatic vertebrates, such as amphibians, but none were captured or observed. Water comes from adjacent Fall Creek, which flows into Alsea River. Water temperature ranged from 10.20 to 12.11 °C and stream flows were 33–23 $l{\cdot}s^{-1}$. The greater experimental area was enclosed by a metal frame that had black mesh screens extending 3.5–6.0 m above ground level, except for a 2-m-wide opening in the top running the length of the study area allowing access to birds or other potential avian predators (Fig. 1).

Manipulation of instream cover

We manipulated instream cover availability with two levels: high (0.01 m^2 of cover per m^2 of stream) or low (0.002 m^2 of cover per m^2 of stream). These two cover levels allow us to capture the high and low spectrum of instream cover found in the Oregon Coast Range during seasonal low flow (Andersen 2008). We randomly assigned each level of cover across four statistical blocks which allowed us to account for potentially dissimilar environmental conditions among stream sections. For example, the study area is bordered by a natural stream (Fall Creek) on one side and a gravel road on the other. Because coastal cutthroat trout prefer substrate over all cover other types (Andersen 2008), we built the instream cover to represent their preferred substrate type, large cobble and boulders. A single piece of cover consisted of a 30.5- by 30.5-cm concrete paver top-piece with a 30.5- by 20.3-cm paver bottom-piece glued underneath in the centre creating two 5.1- by 30.5-cm equal-sized spaces on each end for cover (Fig. 1c). We also examined stream shading in a *post hoc* exploratory measurement of canopy, because there was unequal shading from nearby trees that may have influenced survival of trout. To quantify shading of the active channel of the stream section, we took densiometer readings every 3 m along each stream section between 1200 and 1300 h and summed the proportion of covered area in each cardinal direction.

Collection and acclimation of coastal cutthroat trout

We collected wild coastal cutthroat trout ranging from 8.4 to 21.1 cm (fork length) and 9.62–99.2 g (wet weight) from nearby streams by backpack electrofishing in May 2009. While anesthetised, we measured the fork length and weight of each individual, and we uniquely identified individual trout with an implanted 2.3-cm half-duplex passive-integrated transponder (PIT) tag. Using PIT tags, we could identify individual trout to understand which trout survived and which tags could not be recovered. After 3 days of acclimation in darkened indoor tanks, we randomly assigned and moved 20 tagged trout (controlling for overall fish biomass) to each stream section. The density of trout across our stream sections (~0.5 $trout{\cdot}m^{-2}$ at the beginning of our experiment) was comparable to that of nearby streams supporting coastal cutthroat trout (0.2–0.6 $trout{\cdot}m^{-2}$; D. Bateman, Oregon State University, unpublished data). We controlled for length and weight of trout by assigning trout of a similar size to each stream section based on what was captured in the field. Within 2 days of the start of the experiment, predators were observed inside the study area. At the end of the study, we used backpack electroshockers (eight passes in each section) in combination with handheld PIT tag readers over 3 days to ensure that we captured all surviving trout.

Predator observations

We carried out extensive observations during daylight hours by checking for predators every 30–60 min and sporadic visual observations during the time between sunset and sunrise during our study. We had an opening in the canopy running the length of the study area allowing access to birds or other climbing predators. We did not have evidence of intrusion or predation by any mammals in the stream channels during this or any other research projects at the OHRC (10 years operation). Once an individual entered the study area, it had access to all stream sections.

Statistical analyses

We used a general linear mixed model on a randomised complete blocks design to examine whether the number of surviving trout was a function of instream cover availability (categorical) with trout size (continuous) and shade (continuous) as covariates (Bolker et al. 2009). We determined survival of trout by dividing a count of trout present at the end of the study for each stream section by 20 (which is the number of trout at the beginning of the study). The unit of observation was one of the eight stream sections. Due to our experimental design, we set block and block × cover availability (this allows individual fish to be considered for trout size) as random effects. We set cover availability, shade, trout size and all two- and three-way interactions as fixed effects. However, interactions that were not significant or did not improve the strength of the main effects, measured by the magnitude of the *P*-value, were removed from the model (Ramsey & Schafer 2002; Bolker et al. 2009). We calculated the degrees of freedom using the Kenward–Roger approximation to account for imbalance introduced to our model by the covariates, which is the standard approach for such circumstances. We also used a general linear mixed model to examine whether the change in individual weight (g) was a function of instream cover availability. We set block and block × cover availability as random effects and cover availability as a fixed effect. We set alpha to 0.1 for both analyses because predation can be patchy (Kerfoot & Sih 1987), and our small sample sizes permit only very large effects to be significant (Ramsey & Schafer 2002; Nakagawa & Cuthill 2007). All statistical analyses were performed using the PROC MIXED procedure in SAS software 9.3 (SAS Institute Inc., Cary, NC, USA). Diagnostic plots suggest no deviations from standard linear mixed model assumptions, based on standard diagnostic plots.

Results

Belted kingfisher *Megaceryle alcyon* was the only predator we observed in these streams, and they entered the experimental area during daylight hours in groups of one to three, resulting in variable predation pressure on trout over time. Sightings included one male on 11 July 2009, two individuals (male and female) on 15 July 2009, three individuals (male, female and fledgling) on 21 July 2009 and one male on 23 July 2009 often staying for 6 h at a time. Trout were removed by predators (i.e. trout bodies found dead next to stream $n = 4$ or in stream $n = 8$ with evidence of attack) or had inferred mortality when the tag or body of individual fish was not recovered, $n = 54$, from stream sections.

Instream cover significantly influenced survival of trout ($F_{1,4.28} = 4.31$, $P = 0.10$; Fig. 2). Mean survival was 12% higher in high cover stream sections than low (90% CI: 0.07–0.30). The low cover stream section that displayed the highest overall survival coincidentally had the heaviest shade (see Fig. 2). Shade significantly contributed to survival of trout with more shaded stream sections having higher trout survival compared to less shaded stream sections ($F_{1,4.28} = 5.39$, $P = 0.08$). We only considered the interaction between cover availability and shade because it is the only interaction that improved the strength of the main effects (Ramsey & Schafer 2002; Bolker et al. 2009). The interaction between cover availability and shade was not as significantly related to trout survival ($F_{1,4.21} = 2.80$, $P = 0.17$). The size of trout, however, strongly affected survival ($F_{1,153} = 26.46$, $P < 0.0001$; Fig. 3). Regardless of instream cover availability, all trout >20.4 cm survived during the experiment, whereas the abundance of smaller individuals was reduced, especially those <16.0 cm. All trout that survived to the end of study lost weight and cover availability did not contribute to how much weight an individual lost ($F_{1,4.28} = 0.20$, $P = 0.73$). Mean weight loss over the 36-day study was 6.30 grams per individual (ranging from 6 to 65% loss per individual). Cannibalism was not observed during this study, based on stomach contents and direct observations.

Discussion

Our results suggest that instream cover and shade can mediate the impact of predation by belted kingfishers and potentially other avian predators on the survival of trout during seasonal low flows. Both shade and instream cover, more generally referred to as refuge

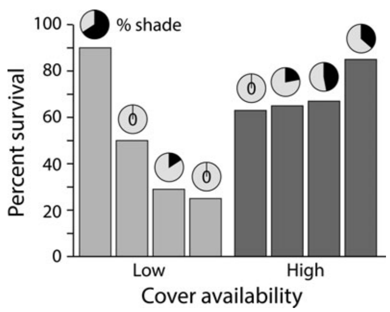

Fig. 2. Percent survival of adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in low-density (light grey, $n = 4$) and high-density (dark grey, $n = 4$) instream cover stream sections due to predation by belted kingfisher (*Megaceryle alcyon*) and potentially other avian predators. Pie charts show the amount of shade over each stream section.

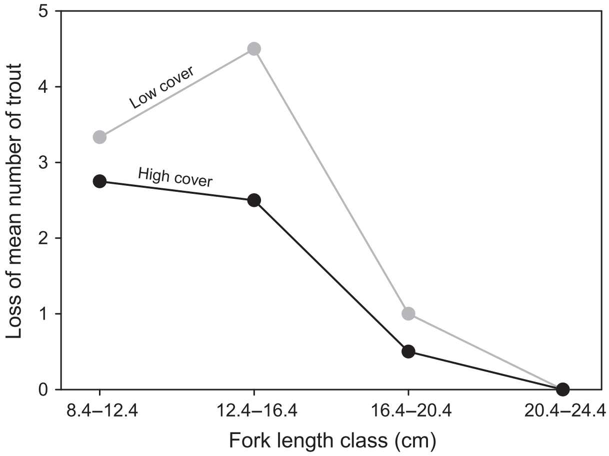

Fig. 3. Loss of mean number of adult coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) by size class from before and after the 36-day study where predation occurred by belted kingfisher (*Megaceryle alcyon*) and potentially other avian predators in high-density (black, $n = 4$) and low-density (light grey, $n = 4$) instream cover stream sections. Size classes were based on quartiles of the overall distribution of fish sizes.

or shelter, offer a place for trout to avoid detection by visual predators. Field studies of coastal cutthroat trout in small streams in the region indicate that survival is lowest during periods of low flow, positively associated with instream boulders and negatively associated with fish size (Berger & Gresswell 2009). Our findings are consistent with the first two observations, although we found that size positively influenced survival. Although we did not have a large amount of replication, our findings illuminate aspects of the role of instream cover, body size and shade in response to predation risk.

Our findings highlight that availability of instream cover can increase trout survival by mediating the effect of predation by belted kingfishers and potentially other avian predators. Reduced amounts of instream cover resulted in fewer trout overall, and even fewer smaller-sized trout because of elevated predation risk. Although use of instream cover by trout has important benefits of increasing a trout's chance of being eaten, it can incur significant costs, such as decreased growth, activity and fecundity (Orrock et al. 2013). During seasonal low flow periods in this region, trout have the lowest consumption of food (Raggon 2010) which could partially result from increased use of instream cover and other types of refuge.

Our results indicate size-biased survival towards larger trout, and this is most likely due to three factors. First, belted kingfishers, the only predator observed during our study, are gape-limited consumers and may key in on smaller trout (Salyer & Lagler 1946; Hamas 1994). Notably, the smaller-sized trout that were taken in our study (<16 cm) are larger than previously noted for belted kingfishers (Salyer & Lagler 1946; Hamas 1994). Second, there was no observed evidence in our study of a predator capable of consuming large trout, and if such predators were present, but not detected, there likely would have been removals of larger trout, especially when instream cover was limiting. There are, however, a host of other predators naturally found in the region that are capable of preying upon larger individuals, because they differ in their mode of predation and gape limitations (Harvey & Nakamoto 2013). Such predators common to the area include stream amphibians (coastal giant salamander *Dicamptodon tenebrosus*), other birds (western screech owl *Megascops kennicottii*) and mammals (North American river otter *Lontra canadensis*). Third, larger trout typically dominate access to food and preferable foraging locations in streams that are often associated with instream cover (Jenkins 1969; Grant 1990), leaving smaller trout exposed or to occupy less desirable habitat that may be more susceptible to increased predation risk.

We showed that all trout lost weight over the duration of the study, which is a reflection of reduced seasonal availability and consumption of food for trout during seasonal low flow (Raggon 2010). Although not observed here, others have seen increased risk-taking behaviour in juvenile coho salmon *Oncorhynchus kisutch* as levels of consumption decrease (Dill & Fraser 1984) suggesting that movement may be critical during low flow to decrease the probability of starvation. Although not always the case (Biro et al. 2004; Sundström & Devlin 2011), larger fish can be more vulnerable to starvation mortality, given their greater overall food requirements (Hughes & Grand 2000).

Survival of trout may have been inconsistent among our replicated stream sections due to shade, in addition to availability of instream cover. Most notable was high survival of trout in a stream section with low availability of instream cover and greater shading. Accordingly, we suggest that shade from overhead riparian vegetation helps reduce avian predation, especially when instream cover is limiting. Lower levels of light can limit the ability of birds to detect prey (Butler & Hawthorne 1968). Visibility is likely an important factor for belted kingfishers because they hunt in clear water and when water is turbid they go elsewhere (Davis 1980). Other factors, such as availability of perches, may be important as well (Cornwell 1963) and could contribute to local variability in predation pressure. Perches were observed to be relatively available throughout our experimental area. Although the role that shade plays as refuge from predators needs to be considered further, it seems possible that shade, in addition to maintaining the natural variability of stream temperatures

(Groom et al. 2011), could provide a zone where fish may have reduced threats from avian predators. In addition, the interaction of shade and cover availability needs to be investigated further with other factors such as flow, food availability and body size.

In conclusion, our study demonstrates that the risk of predation on trout was mediated by instream cover and shade. The relationship among instream cover, shade and body size under predation risk revealed here provide a basis to evaluate survival estimates of trout in natural settings (Berger & Gresswell 2009). All trout lost weight over the duration of the study likely due to food scarcity during seasonal low flow suggesting that this could be an additional source of mortality or increased risk-taking behaviour as time goes on. Our results may be applicable to fish in a variety of shallow streams especially as low flow conditions become more prevalent due to climate change and as riparian plant communities change with land use and forest succession. We offer that shade may be particularly important in streams with extreme low flows conditions and instream cover may be more critical in streams that have recently been harvested. Conservation strategies for trout should consider management tactics that maintain or improve stream habitat using both instream cover and shade as options in areas of high natural predation, especially when coupled with changing environmental conditions.

Acknowledgements

BEP was funded by an Environmental Protection Agency STAR grant, a J Frances Allen scholarship from American Fisheries Society, a grant from the U.S. Geological Survey to Oregon State University, the Watersheds Research Cooperative and various scholarships through the Graduate School and the Department of Fisheries and Wildlife at Oregon State University. We thank Ryan Couture, Joseph O'Neil and Joyce Mahr at the Oregon Hatchery Research Centre. Dave Leer, Doug Bateman, Steve Clark, Ivan Arismendi and others helped during the experiment. Michael Young, Aaron Berger, Dave Wiens, Andrew Hafs and the Editor, Javier Lobon-Cervia, improved this manuscript. Pat Cunningham provided statistical advice. Kathryn Ronnenberg helped with graphical illustrations. Fish collections were authorised by Oregon Department of Fish and Wildlife scientific taking permit #13881 and by Oregon State University Institutional Animal Care and Use Committee proposal #3910. The use of trade or firm names here is for reader information only and does not constitute endorsement of any product or service by the US Government.

References

Allouche, S. & Gaudin, P. 2001. Effects of avian predation threat, water flow and cover on growth and habitat use by chub, Leuciscus cephalus, in an experimental stream. Oikos 94: 481–492.

Andersen, H.V. 2008. Transferability of models to predict selection of cover by coastal cutthroat trout in small streams in western Oregon, USA. Corvallis, OR: MS. Thesis, Oregon State University.

Berger, A.M. & Gresswell, R.E. 2009. Factors influencing coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) seasonal survival rates: a spatially continuous approach within stream networks. Canadian Journal of Fisheries and Aquatic Sciences 66: 613–632.

Biro, P.A., Morton, A.E., Post, J.R. & Parkinson, E.A. 2004. Overwinter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Science 61: 1513–1519.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24: 127–135.

Butler, R.L. & Hawthorne, V.M. 1968. The reactions of dominant trout to changes in overhead artificial cover. Transactions of the American Fisheries Society 97: 37–41.

Cornwell, G.W. 1963. Observations on the breeding biology and behavior of a nesting population of Belted Kingfishers. The Condor 65: 426–431.

Davis, W.J. 1980. The Belted Kingfisher, *Megaceryle alcyon*: Its ecology and territoriality. Cincinnati, OH: MS Thesis, University of Cincinnati.

Dill, L.M. & Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behavioral Ecology and Sociobiology 16: 65–71.

Draulans, D. 1988. Effects of fish-eating birds on freshwater fish stocks: an evaluation. Biological Conservation 44: 251–263.

Grant, J.W.A. 1990. Aggressiveness and the foraging behavior of young-of-the-year brook charr (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences 47: 915–920.

Groom, J.D., Dent, L., Madsen, L.J. & Fleuret, J. 2011. Response of western Oregon (USA) stream temperatures to contemporary forest management. Forest Ecology and Management. 262: 1618–1629.

Hamas, M.J. 1994. Belted Kingfisher (*Ceryle alcyon*). Number 84. In: Poole, A. & Gill, F., eds. The birds of North America. Philadelphia, PA: Academy of Natural Sciences, pp. 1–16.

Harvey, B.C. & Nakamoto, R.J. 2013. Seasonal and among-stream variation in predator encounter rates for fish prey. Transaction of the American Fisheries Society 142: 621–627.

Harvey, B.C. & Stewart, A.J. 1991. Fish size and habitat depth relationships in headwater streams. Oecologia 87: 336–342.

Hughes, N.F. & Grand, T.C. 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. Environmental Biology of Fishes 59: 285–298.

Jenkins, T.M. Jr 1969. Social structure, position choice, and micro-distribution of two trout species (*Salmo trutta* and

Salmo gairdneri) resident in mountain streams. Animal Behaviour Monographs 2: 56–123.

Kerfoot, W.C. & Sih, A. 1987. Predation: direct and indirect impacts on aquatic communities. Hanover, NH: University Press of New England. 386 pp.

Lantz, S.M., Gawlik, D.E. & Cook, M.I. 2010. The effects of water depth and submerged aquatic vegetation on the selection of foraging habitat and foraging success of wading birds. Condor 112: 460–469.

Lima, S.L. & Dill, L.M. 1990. Behavioral decision made under the risk of predation – A review and prospectus. Canadian Journal of Zoology 68: 619–640.

Lonzarich, D.G. & Quinn, T.P. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. Canadian Journal of Zoology 73: 2223–2230.

Nakagawa, S. & Cuthill, I.C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews 82: 591–605.

Orrock, J.L., Preisser, E.L., Grabowski, J.H. & Trussell, G.C. 2013. The cost of safety: refuges increase the impact of predation risk in aquatic systems. Ecology 94: 573–579.

Post, J.R., Parkinson, E.A. & Johnston, N.T. 1998. Spatial and temporal variation in risk to piscivory of age-0 rainbow trout: patterns and population level consequences. Transaction of the American Fisheries Society 127: 932–942.

Power, M.E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance. Ecology 65: 523–528.

Raggon, M.F. 2010. Seasonal variability in diet and consumption by cottid and salmonid fishes in headwater streams in western Oregon, USA. Corvallis, OR: MS. Thesis, Oregon State University.

Ramsey, F.L. & Schafer, D.W. 2002. The statistical sleuth: a course in methods of data analysis. Pacific Grove, CA: Wadsworth Group.

Roby, D.D., Lyons, D.E., Craig, D.P., Collis, K. & Visser, G.H. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach: Caspian terns and juvenile salmonids in the Columbia River estuary. Canadian Journal of Zoology 81: 250–265.

Salyer, J.C. & Lagler, K.F. 1946. The Eastern Belted Kingfisher, *Megaceryle alcyon alcyon* (Linnaeus) in relation to fish management. Transactions of the American Fisheries Society 76: 97–117.

Steinmetz, J., Kohler, S.L. & Soluk, D.A. 2003. Birds are overlooked top predators in aquatic food webs. Ecology 84: 1324–1328.

Sundström, L.F. & Devlin, R.H. 2011. Increased intrinsic growth rate is advantageous even under ecologically stressful conditions in Coho Salmon (*Oncorhynchus kisutch*). Evolutionary Ecology 25: 447–460.