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NOTE

Seasonal and Among-Stream Variation in Predator Encounter Rates for Fish Prey

Bret C. Harvey* and Rodney J. Nakamoto
U.S. Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521, USA

Abstract

Recognition that predators have indirect effects on prey populations that may exceed their direct consumptive effects highlights the need for a better understanding of spatiotemporal variation in predator–prey interactions. We used photographic monitoring of tethered Rainbow Trout *Oncorhynchus mykiss* and Cutthroat Trout *O. clarkii* to quantify predator encounter rates for fish in four streams of northwestern California during winter–spring and summer. To estimate maximum encounter rates, provide the clearest contrast among streams and seasons, and provide an empirical estimate of a key parameter in an individual-based model of stream salmonids, we consistently placed fish in shallow microhabitats that lacked cover. Over 14-d periods, predators captured fish at 66 of the 88 locations where fish were placed. Eight species of birds (including two species of owls) and mammals were documented as capturing fish. Thirty-six percent of the predator encounters occurred at night. Predator encounter rates varied among streams and between seasons; the best-fitting model of survival included a stream × season interaction. Encounter rates tended to be higher in larger streams than in smaller streams and higher in winter–spring than in summer. Conversion of predator encounter rates from this study to estimates of predation risk by using published information on capture success yielded values similar to an independent estimate of predation risk obtained from calibration of an individual-based model of the trout population in one of the study streams. The multiple mechanisms linking predation risk to population dynamics argue for additional effort to identify patterns of spatiotemporal variation in predation risk.

Predators affect prey populations directly by consumption and indirectly through a variety of nonconsumptive effects, such as alteration of habitat selection and diel activity patterns. Nonconsumptive effects of predators can have greater effects on prey demographics than consumptive effects (Preisser et al. 2005), suggesting that overall predator effects may be more important to prey population dynamics than traditional ecological theory suggests. Fully recognizing the potential significance of predation to prey population dynamics highlights the need for understanding the magnitude of predation risk and its spatiotemporal variation. For stream fishes, high rates of fish consumption by various endothermic predators have been observed (e.g., Alexander 1979; Heggenes and Borgstrøm 1988; Dolloff 1993), along with significant annual variation in the presence–absence of important predators. A variety of studies have addressed the influence of local habitat features (e.g., cover, depth, and water velocity) on predation risk, while advances in long-term monitoring of tagged fish have allowed large-scale studies of survival in general (e.g., Berger and Gresswell 2009; Xu et al. 2010). However, both in general and for purposes of fish population modeling (e.g., Railsback et al. 2009), it would be useful to know more about reach-scale and shorter-term temporal variation in predation risk.

In this study, we sought to examine spatiotemporal variation in predator encounter rates for fish occupying four streams in northwestern California. Our specific objectives included detection of seasonal and diel patterns in predator encounters and the identification of predators. We also sought to empirically estimate a parameter in the individual-based stream trout model of Railsback et al. (2009). This model utilizes a stream reach-scale parameter that represents the minimal rate of survival of predation risk from nonaquatic predators. Because this parameter cannot be routinely measured and is highly uncertain, it is commonly adjusted in the model calibration process to match model results to empirical observations.

STUDY SITES

We made observations in Jacoby and Little Jones creeks, which both drain forested catchments in northwestern California. In the study reach (at an elevation of about 250 m), Jacoby Creek is a second-order stream draining 10–15 km^2 of

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*Corresponding author: bharvey@fs.fed.us
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second-growth forest and grassland. Red alder *Alnus rubra* and bigleaf maple *Acer macrophyllum* dominate much of the riparian zone; coast redwood *Sequoia sempervirens* and Douglas-fir *Pseudotsuga menziesii* provide most of the forest cover in the catchment and also commonly occur in the riparian zone. The active stream channel in the reach averages about 4 m wide, with a gradient of 1.5%. Water temperature ranges from 9°C to 16°C in summer and from 4°C to 12°C in winter. Streamflow in the study reach averages less than 0.05 m^3/s in the summer and approximately 0.75 m^3/s in the winter. The Rainbow Trout *Oncorhynchus mykiss* is the only fish species in the Jacoby Creek study reach. The stream also supports semiaquatic vertebrates, including the coastal giant salamander *Dicamptodon tenebrosus*, northern red-legged frog *Rana aurora*, Pacific Coast aquatic garter snake *Thamnophis atratus*, and coastal tailed frog *Ascaphus trueii*. Both the coastal giant salamander and the Pacific Coast aquatic garter snake are known to prey on fish.

Little Jones Creek is a third-order tributary of the Middle Fork Smith River in northwestern California, draining about 27 km^2 of steep, forested terrain. The Little Jones Creek reach used in this study drains 15–20 km^2 of mostly second-growth forest. Red alder dominates the riparian vegetation. The active stream channel is about 8 m wide, and stream gradient in the study reach averages 1.8%. Water temperature ranges from 11.5°C to 16°C in the summer and from 3°C to 11°C in winter. Streamflow averages 0.15 m^3/s in the summer and 2.5 m^3/s in the winter.

We also included two first-order tributaries of Little Jones Creek in this study. The first (informally named "Big Head Creek") enters Little Jones Creek 1.6 km upstream of the confluence of Little Jones Creek and the Middle Fork Smith River and drains 2.7 km^2 (<2.0 km^2 in the study reach). The second (informally named "Weejak Creek") enters Little Jones Creek 3.3 km upstream of the Middle Fork Smith River–Little Jones Creek confluence and drains 1.7 km^2. Both tributaries have average streamflows of less than 0.01 m^3/s in the summer and 0.1 m^3/s or less in the winter. The Cutthroat Trout *O. clarkii* is the only fish species in the Little Jones Creek catchment. Semi-aquatic vertebrates include the coastal giant salamander, foothill yellow-legged frog *Rana boylii*, Pacific Coast aquatic garter snake, and coastal tailed frog.

METHODS

We initially attempted to quantify predator encounter rates by using artificial lures. The behavior of potential predators in the vicinity of the lures was recorded via the photographic methods described below. In each of three different approaches, we used artificial lures designed to resemble 150-mm FL Rainbow Trout. Each lure had articulations just anterior and posterior to the dorsal fin and had a soft plastic caudal fin, which gave the lure an apparently natural swimming motion when tethered in water velocities of 5–10 cm/s. The treble hooks on each lure were removed and replaced with split shot to position the lure just below the water's surface with a horizontal orientation. In the first approach, single lures were positioned in shallow (<10 cm), slow-moving water by attachment to a 0.5-m-long monofilament line secured at the upstream end to a small metal stake driven into the streambed. In the second approach, we tethered three lures at each monitoring location; the lures were separately secured by lines anchored 10 cm apart. Finally, we attempted to attract predators by constructing an apparatus in which three lures "responded" to predators by exhibiting short movements. This device incorporated an infrared motion detector, a battery-powered servo motor, and a suspended counterweight. Lures were connected to other parts of the apparatus by at least 3 m of monofilament line to minimize the influence of the apparatus on predator behavior. When the mechanism was triggered by the infrared sensor, the servo motor pulled and released attachment lines multiple times, moving the lures approximately 15 cm with each cycle. Over 17–42 d of testing, the three approaches described above failed to attract predators, although cameras recorded raccoons *Procyon lotor* and great blue herons *Ardea herodias* in the vicinity of the lures.

The failure of artificial lures to attract predators that we had observed consuming fish at the study sites (e.g., great blue herons and belted kingfishers *Ceryle alcyon*) prompted an investigation of live-fish tethering methods. Extensive daily behavioral observations of tethered live fish revealed that (1) the tethered fish remained quiescent except when disturbed at close range; (2) a simple tether arrangement in unobstructed habitat eliminated the risk of entanglement; and (3) tethered fish remained in good condition after 5–7 d in place.

After establishing the effectiveness of the method, we monitored tethered fish with remote cameras to assess predator encounter rates across streams and seasons. Trout used in the experiment (Rainbow Trout in Jacoby Creek and Cutthroat Trout in Little Jones Creek and its tributaries) were collected from the study reaches by electrofishing; we assumed that the difference in trout species between Jacoby and Little Jones creeks did not influence the results. Fish averaged 114 mm FL (SD = 17); this size reflected our desire to minimally affect fish populations while using fish that were large enough to be relatively vulnerable to avian and mammalian predators. After receiving anesthesia, fish were tethered via a 30-cm monofilament line to a 340-g lead weight that was partially buried in the substratum. The line was attached to the fish through the musculature immediately anterior to the insertion of the dorsal fin. All fish were observed until they had completely recovered from the anesthesia. We placed tethered fish in shallow locations (depth = 8–15 cm) with low water velocity (0–5 cm/s) and gravel or sand substratum to maximize their vulnerability and to allow approximation of the minimum survival parameter in the individual-based model of Railsback et al. (2009). We also anticipated that consistent placement of fish in vulnerable locations would preclude any interaction between tethering artifacts and the independent variables of interest; such interactions have been a concern in some previous studies that have used prey tethering (Barshaw and Able 1990; Aronson et al. 2001). We positioned cameras about 1.5 m from the locations of tethered fish. Each camera was mounted on a metal stake so that the camera was about 60 cm above the water's surface. Cameras were triggered with a passive infrared motion sensor; we set cameras to record five images approximately 0.75 s apart when triggered.

We set a maximum of six tethered fish in each stream at any time, with tether locations separated by at least 20 m of stream length. We visited tether locations at 5–7-d intervals. Fish that survived over an interval were released. Survival of two fish over successive intervals at one location was classified as an observation of "no predation." In some cases, logistical constraints dictated that observations of no predation constituted less than 10–14 d. If predators preferentially visited locations of prior success in capturing fish, this could affect our measurements; therefore, each location provided only one observation, regardless of outcome. We anticipated that the density and distribution of tethered fish would preclude any interactions between predator density and tethering, which have been an issue in some smaller-scale, short-term studies (Kneib and Scheele 2000). Observations for each combination of stream and season spanned 25–34 d. We made winter–spring observations from 20 January to 16 May 2011 and summer observations from 14 July to 17 August 2011. The cameras recorded the date and time of predation events (so that survival time could be quantified), and the photos allowed us to identify predators. We summarized the data by building survival curves for each combination of stream and season. We also distinguished daytime versus nighttime predation events, with daytime defined as extending from 1 h before sunrise to 1 h after sunset.

We used the Kaplan–Meier estimator (Therneau and Grambsch 2010) to construct survival curves for the eight combinations of stream and season. To explore the influence of stream and season on survival, we used Cox regression (Therneau and Grambsch 2010) with stream and season as dummy variables. The raw data for these analyses were observed survival times, including observations of no predation over known time spans. We used Akaike's information criterion (AIC) to compare five models of survival: (1) a null model (no covariates); (2) a model with stream as the independent variable; (3) a model with season as the independent variable; (4) a model that included both stream and season; and (5) the full model, which included stream, season, and a stream × season interaction. Using the Cox regression results for the full model, we also computed hazard ratios to contrast results by season and stream size (Jacoby and Little Jones creeks versus the two tributaries of Little Jones Creek). Laplante-Albert et al. (2010) provide a more detailed description of the general approach to survival analysis used here.

RESULTS

The field methods appeared to be generally effective. Parallel to our preliminary observations, we never observed fish straining at the end of their tethers except immediately after the tethering procedure or during the release procedure. Photographs provided evidence that encounter rates with some predators were not increased by the tethering procedure. Potential predators, including the great blue heron, American marten *Martes americana*, American black bear *Ursus americanus*, American mink *Neovison vison*, raccoon, and North American river otter *Lontra canadensis*, were recorded by the cameras as passing within 0–2 m of tethered fish, apparently without detecting them. All surviving fish were released in good condition. All of the photographed predators were identifiable to species (Figure 1).


FIGURE 1. Two examples of photo-documented predator encounters for tethered fish: (upper panel) a belted kingfisher capturing a fish during the daytime and (lower panel) a western screech-owl capturing a fish at night.

In total, we documented 66 predator encounters (i.e., with prey being removed) and 22 instances of no predation. On six occasions (three in winter–spring and three in summer), fish were not recovered from the tether location, but no photographs of predation events were recorded. These six fish were probably removed by predators that did not trigger the infrared motion sensor of the camera; ectothermic predators, such as coastal giant salamanders or Pacific Coast aquatic garter snakes, may have been responsible.

Although the study was limited to four streams in two small catchments, we documented encounters by eight species of avian and mammalian predators. Birds were responsible for 41 (62%) of the 66 documented predator encounters: belted kingfisher (18 prey captures), western screech-owl *Megascops kennicottii* (11 captures), great blue heron (6 captures), common merganser *Mergus merganser* (3 captures), barred owl *Strix varia* (2 captures), and red-tailed hawk *Buteo jamaicensis* (1 capture). Raccoons were responsible for 18 captures, and North American river otters were responsible for seven captures. Twenty-four (36%) of the 66 total encounters occurred at night. Four predator species captured fish at night: barred owls (100% of captures were at night), western screech-owls (36% at night), North American river otters (57% at night), and raccoons (78% at night).

Survival curves by stream and season revealed noteworthy spatiotemporal variation (Figures 2, 3). Between-season differences varied among streams; for example, the largest stream included in the study (Little Jones Creek) exhibited modest differences between seasons (Figure 2), in contrast to the differences observed for the smallest stream (Weejak Creek; Figure 3). As this result suggests, the Cox regression model that included season, stream, and the season × stream interaction had the strongest support, as indicated by AIC (Table 1). Although the significant season × stream interaction demands caution in interpreting main effects, computation of hazard ratios suggested that the risk of encountering predators was about 2.8 times greater in winter–spring than in summer. Comparison of the two larger streams with the two smaller streams suggested that the risk of predator encounter was about 2.9 times greater in the larger streams.

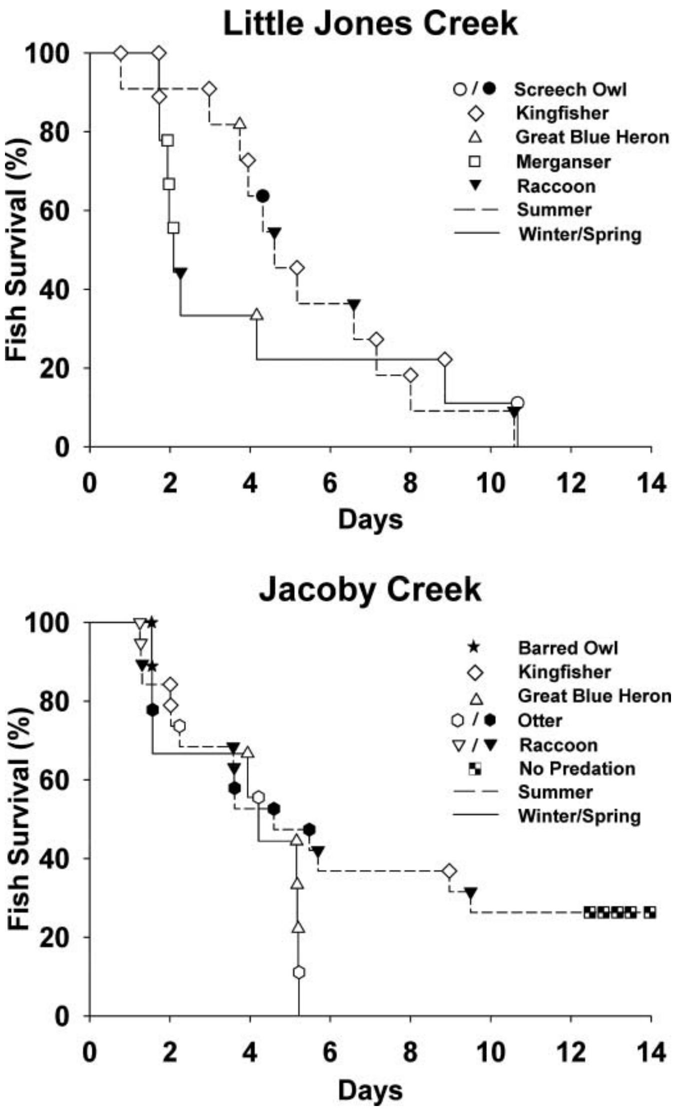

FIGURE 2. Kaplan–Meier survival curves by season for fish in Jacoby Creek (tethered Rainbow Trout) and Little Jones Creek (tethered Cutthroat Trout), northwestern California, 2011. Symbols indicate photo-documented prey captures or observations of surviving fish. Shaded symbols indicate nighttime predation events (screech-owl = western screech-owl; kingfisher = belted kingfisher; merganser = common merganser).

DISCUSSION

Tethering experiments require careful interpretation (e.g., Barbeau and Scheibling 1994; Post et al. 1998). The method used here probably measures prey detection reasonably well for several predators (e.g., kingfishers, great blue herons, and owls) that almost certainly detected and attacked quiescent fish. In some cases, tethering may have affected prey detection and capture; although raccoons were photographed on several occasions in which they did not detect fish, they were probably over-represented in our data set because tethering appeared to enhance their probability of capturing fish. To estimate predation risk for free-swimming fish based on the observations presented here, information on predators' capture success in the pursuit of free-swimming fish is needed. A variety of previous observations of capture success indicate that the survival curves presented here, which reflect predator encounter rates, would require significant modification to reflect predation risk. For

TABLE 1. Comparison of five models of fish survival (based on tethered Rainbow Trout and Cutthroat Trout) in four small streams of northwestern California. The difference in Akaike's information criterion (ΔAIC) indicates the difference in model fit between the given candidate model and the best-fitting model (i.e., the model with the lowest AIC value). Akaike weights (*w*) reflect the relative likelihoods of the models (Burnham and Anderson 2002).

Model	ΔAIC	*w*
Null (no covariates)	26.1	<0.0001
Season	17.4	0.0002
Stream	15.7	0.0004
Season + stream	4.5	0.0947
Season + stream + (season × stream)	0	0.9047

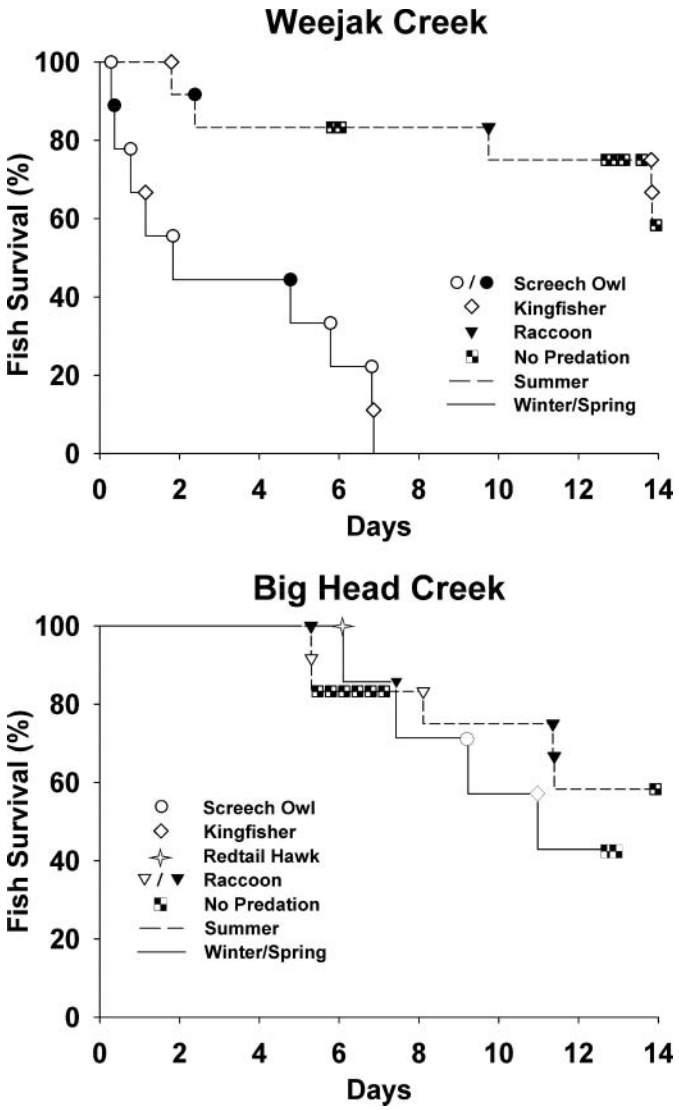

FIGURE 3. Kaplan–Meier survival curves by season for fish (tethered Cutthroat Trout) in two first-order tributaries of Little Jones Creek (Weejak and Big Head creeks), northwestern California, 2011. Symbols indicate photo-documented prey captures or observations of surviving fish. Shaded symbols indicate nighttime predation events (screech-owl = western screech-owl; kingfisher = belted kingfisher).

example, pied kingfishers *Ceryle rudis* had 19% capture success when feeding on fish along the shoreline of Lake Malawi (Johnston 1989). Abbruzze and Ritchison (1997) reported that six radio-tagged eastern screech-owls *Megascops asio* were 23% successful in 35 attacks on prey that included birds, insects, crayfish, small mammals, leeches, and fish. For several species of wading birds feeding on fish in shallow-water areas that lacked habitat complexity, the capture success averaged 31% (Lantz et al. 2010). In addition, common mergansers feeding on the smolts and fry of Coho Salmon *O. kisutch* had a capture success rate of 36%, but they succeeded in subduing and eating only 18% of the prey they pursued (Wood and Hand 1985).

Prior application of an individual-based model to the Cutthroat Trout population in Little Jones Creek (Harvey and Railsback 2009, 2012) provides context for the empirical observations of predator encounter rates presented here, as the model includes a parameter that represents the daily survival rate for fish in the habitat offering the lowest survival (Railsback et al. 2009). In application of the model to the Cutthroat Trout population in Little Jones Creek, calibration using multiple years of empirical data on age-specific abundance and size yielded an estimate of 98.7% for the minimum daily survival parameter. From the current study, the loss of 66 out of 88 fish yields a predator encounter rate of 75% over 14 d. Applying a capture success rate of 35%—a conservative estimate according to the literature reviewed above—to this encounter rate would yield a mortality rate of 22.5% and therefore a survival rate of 77.5% over 14 d (this assumes that all of the live fish we recovered would have survived for a complete observation period). This rate converts to a daily survival of 97.8%. If we exclude fish that were captured by raccoons from the number of fish encountered by predators (i.e., because the probability that raccoons will detect and pursue fish is almost certainly overestimated in this data set), the same exercise produces a daily survival rate of 98.5%. Although this exercise necessarily relies on a highly speculative estimate of overall capture success rate from the literature to convert encounter rates to capture rates, we find encouraging the correspondence between the two distinct approaches to estimation of predation risk.

Our findings suggest that for fish in the streams we studied, there is a significant chronic risk from a variety of predators. Because fish are unlikely to be able to perceive and avoid several of the predators we observed prior to a prey capture attempt, the results indicate that predation risk could have persistent effects on habitat selection by fishes. Such effects are exemplified by Power's (1984) observation that predation risk from birds prevented herbivorous fishes from occupying and feeding in shallow-water areas within a Panamanian stream, thus leading to "bathtub rings" of algae in pools. The cost of risk-sensitive habitat selection may be less severe for drift-feeding fishes, such as salmonids, in that some stream habitats may offer both relative safety and superior foraging opportunities. For example, large elements in stream channels (e.g., boulders and woody debris) can provide cover and cause local streambed scour that increases water depth. Both cover and depth can reduce predation risk (e.g., Harvey and Stewart 1991), while pool habitat can provide the most favorable feeding conditions for relatively large fish in small streams (Rosenfeld and Boss 2001). Fish seeking to minimize energy expenditure rather than to maximize foraging efficiency, as may be the case at cold temperatures (Cunjak 1996), may commonly encounter habitats that offer both low predation risk and favorable energetic conditions in the form of microhabitats with low water velocity and cover that provides concealment. However, these observations do not preclude an important role for the indirect effects of predation risk on salmonid population dynamics because low-risk habitat and foraging opportunities do not consistently overlap.

Our observations suggested a greater risk of predator encounters in winter–spring than in summer for fish in the small streams we studied. Where this pattern applies, its effect on predation risk would be compounded by any additional negative effects of water temperature on fish swimming performance (Webb 1978) and the associated consequences for the susceptibility of fish to endothermic predators, as suggested by several authors (e.g., Fraser et al. 1993; Cunjak 1996; Reeves et al. 2010). Predators may shift toward smaller stream channels in winter–spring, when high streamflows make prey detection and capture in larger channels more challenging. Another possibility is that endothermic predators may increase their focus on fish when the availability of alternative prey declines. For example, piscivory by owls may increase in winter, when some of their terrestrial prey are hibernating.

The preponderance of daytime predator–prey encounters we observed (64% of encounters) corresponds with previous conclusions that fish in other lotic systems face lower predation risk at night. Using information on predator diet, density, and energetics, Metcalfe et al. (1999) estimated that primarily nocturnal predators were responsible for 10.5% of the predation on juvenile salmon in Scottish rivers. For the present study, the exclusion of raccoons, which seem unlikely to have a high capture success with free-swimming fish in continuous stream systems, would lower the percentage of encounters occurring at night from 36% to 21%. The potential seems great for spatiotemporal variation in predator assemblages to result in variation in diel risk patterns for stream fish. For example, our observations suggest that owls can be important nocturnal predators of fish in some streams, but the density and distribution of piscivorous owls probably vary dramatically. The ongoing range expansion of the barred owl in western North America may be causing changes in the risk environment of stream fishes, amphibians, and crustaceans. The flexibility in diel behavior exhibited by salmonid fishes (e.g., Metcalfe et al. 1999; Reeves et al. 2010) and the potential consequences of predation risk for population dynamics (e.g., Railsback and Harvey 2011) suggest that diel variation in predation risk deserves attention in population modeling.

These initial observations of predator encounter rates in streams indicate a lower risk for fish in smaller streams, but this result may have been strongly influenced by specific features of the streams included in our study. For example, the two tributaries of Little Jones Creek had sharply different patterns of fish survival in winter. This difference may relate to the extent of riparian vegetation closely overhanging the stream, which could be a useful covariate in future studies. In some settings, an overall pattern of decreasing risk upstream could to some extent offset detrimental features of upstream habitat, such as the risk of habitat loss from stream drying and lower food availability, as indicated by lower growth rates upstream (Harvey 1998).

This study revealed, within a geographically limited area, a broad array of predators and substantial spatiotemporal variation in predator encounter rates for stream fish. Broader observations may identify key predator–prey combinations and geographic and seasonal variation in predator encounter rates that could help to explain differences in fish behavior and population dynamics. While our goal of informing fish population models led us to focus on these predator–prey interactions from the perspective of vulnerable prey, more information on the behavior and capabilities of specific piscivores would clearly be useful in improving our understanding of terrestrial–aquatic linkages.

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REFERENCES

Abbruzzese, C. M., and G. Ritchison. 1997. The hunting behavior of eastern screech-owls (*Otus asio*). Pages 21–32 *in* J. R. Duncan, D. H. Johnson, and T. H. Nicholls, editors. Biology and conservation of owls of the northern hemisphere: second international symposium. U.S. Forest Service General Technical Report NC-190.

Alexander, G. R. 1979. Predators of fish in coldwater streams. Pages 153–170 *in* H. R. Stroud and H. Clepper, editors. Predator–prey systems in fisheries management: proceedings of the international symposium on predator-prey systems in fish communities and their role in fisheries management. Sport Fishing Institute, Washington, D.C.

Aronson, R. B., K. L. Heck Jr., and J. F. Valentine. 2001. Measuring predation with tethering experiments. Marine Ecology Progress Series 214:311–312.

Barbeau, M. A., and R. E. Scheibling. 1994. Procedural effects of prey tethering experiments: predation of juvenile scallops by crabs and sea stars. Marine Ecology Progress Series 111:305–310.

Barshaw, D. E., and K. W. Able. 1990. Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters *Homarus americanus*. U.S. National Marine Fisheries Service Fishery Bulletin 88:415–417.

Berger, A. M., and R. E. Gresswell. 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.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):267–282.

Dolloff, C. A. 1993. Predation by river otters (*Lutra canadensis*) on juvenile Coho Salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) in southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 50:312–315.

Fraser, N. H. C., N. B. Metcalfe, and J. E. Thorpe. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proceedings of the Royal Society of London B 252:135–139.

Harvey, B. C. 1998. Influence of large woody debris on retention, immigration, and growth of Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) in stream pools. Canadian Journal of Fisheries and Aquatic Sciences 55:1902–1908.

Harvey, B. C., and S. F. Railsback. 2009. Exploring the persistence of stream-dwelling trout populations under alternative real-world turbidity regimes with an individual-based model. Transactions of the American Fisheries Society 138:348–360.

Harvey, B. C., and S. F. Railsback. 2012. Effects of passage barriers on demographics and stability properties of a virtual trout population. River Research and Applications 28:479–489.

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

Heggenes, J., and R. Borgstrøm. 1988. Effect of mink, *Mustela vison* Schreber, predation on cohorts of juvenile Atlantic Salmon, *Salmo salar* L., and Brown Trout, *S. trutta* L., in three small streams. Journal of Fish Biology 33:885–894.

Johnston, D. W. 1989. Feeding ecology of pied kingfishers on Lake Malawi, Africa. Biotropica 21:275–277.

Kneib, R. T., and C. E. H. Scheele. 2000. Does tethering of mobile prey measure relative predation potential? an empirical test using Mummichogs and grass shrimp. Marine Ecology Progress Series 198:181–190.

Lantz, S. M., D. E. Gawlik, and M. I. Cook. 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.

Laplante-Albert, K. A., M. A. Rodríguez, and P. Magnan. 2010. Quantifying habitat-dependent mortality risk in lacustrine fishes by means of tethering trials and survival analyses. Environmental Biology of Fishes 87:263–273.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology 68:371–381.

Post, J. R., E. A. Parkinson, and N. T. Johnston. 1998. Spatial and temporal variation in risk to piscivory of age-0 Rainbow Trout: patterns and population level consequences. Transactions 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.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? the effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509.

Railsback, S. F., and B. C. Harvey. 2011. Importance of fish behaviour in modelling conservation problems: food limitation as an example. Journal of Fish Biology 79:1648–1662.

Railsback, S. F., B. C. Harvey, S. K. Jackson, and R. H. Lamberson. 2009. InSTREAM: the individual-based stream trout research and environmental assessment model. U.S. Forest Service General Technical Report PSW-GTR-218.

Reeves, G. H., J. B. Grunbaum, and D. W. Lang. 2010. Seasonal variation in diel behaviour and habitat use by age 1+ steelhead (*Oncorhynchus mykiss*) in Coast and Cascade Range streams in Oregon, U.S.A. Environmental Biology of Fishes 87:101–111.

Rosenfeld, J. S., and S. Boss. 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.

Therneau, T. M., and P. M. Grambsch. 2010. Modeling survival data: extending the Cox model. Springer-Verlag, New York.

Webb, P. W. 1978. Temperature effects on acceleration of Rainbow Trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 35:1417–1422.

Wood, C. C., and C. M. Hand. 1985. Food-searching behaviour of the common merganser (*Mergus merganser*) I: functional responses to prey and predator density. Canadian Journal of Zoology 63:1260–1270.

Xu, C. L., B. H. Letcher, and K. H. Nislow. 2010. Size-dependent survival of Brook Trout *Salvelinus fontinalis* in summer: effects of water temperature and stream flow. Journal of Fish Biology 76:2342–2369.