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**Seasonal and spatial fluctuations in *Oncorhynchus* trout diet
in a temperate mixed-forest watershed**

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1 Abstract

2 To examine seasonal and spatial factors affecting prey consumption by
3 *Oncorhynchus* trout, we examined trout diet from mainstem and tributary sites at Hinkle
4 Creek, Oregon. Benthic invertebrate densities were similar across seasons and did not
5 differ between tributaries and the mainstem. Fluctuations in diet followed seasonal
6 changes in invertebrate sizes and abundances. Average prey biomass consumed was
7 positively correlated with fish size. Consumption rates were high in spring and summer
8 but fell significantly in fall when fewer and smaller prey were eaten. A switch in
9 consumption from 36% terrestrial prey biomass in spring to 85% in summer, coincided
10 with an increase in terrestrial prey size and decrease in benthic prey size. Location within
11 the watershed also affected prey consumption. Despite similarities in diet composition,
12 tributary trout consumed somewhat more biomass than trout in the mainstem but grew
13 relatively slower. Because stream fishes like *Oncorhynchus* trout feed opportunistically
14 on varied prey, studies incorporating multiple seasons and stream types are important to
15 understanding energy exchanges between terrestrial and aquatic ecosystems.

Seasonal and spatial fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed

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Fisheries biologists and fishermen have long known that salmonids feed on a combination of benthic invertebrates, emergent aquatic adults and terrestrial invertebrates (Dimick and Mote 1934; Allen 1951; Edwards and Huryn 1995). As mobile trout grow from juvenile to adult stages their behavior and preferences for habitat and food resources will change, just as the kinds and sources of prey are changing (Northcote 1997, Bramblett et al. 2002). The phenologies of lotic insects tend to flux synchronously, leading to seasonal peaks of abundance and emergence of adults (Ward and Stanford 1982; Sweeney 1984). The timing of these biological fluxes, reflecting physiological and genetic responses to physical conditions, varies with annual and regional patterns of hydrology, temperature and other climate-related phenomena (Hogg and Williams 1996, Harper and Peckarsky 2006, Li et al. 2010). Similarly, terrestrial insects become more active and possibly more abundant in warm seasons of the year in association with plant phenologies and terrestrial life history patterns. The ways in which these fluxes occur likely provide critical resource options for opportunistic fishes (Nakano and Murakami 1999, Kawaguchi and Nakano 2001), however many salmonid diet studies have been restricted to late summer or autumn (Syrjänen et al. 2011), and the number of empirical studies examining seasonal fluctuations are few (Wipfli and Baxter 2010).

43 Terrestrial invertebrates potentially represent cross-ecosystem contributions from
44 multiple sources. Ground-dwelling invertebrates such as millipedes, some beetles or
45 spiders, might be washed in from the stream edge, while plant-dwelling terrestrials may
46 fall directly from adjacent riparian vegetation. Others derive from upstream and arrive in
47 surface drift. As many terrestrial insects are winged and mobile, they may be dispersed
48 by wind or fly in from an even wider range. The variety of terrestrial prey consumed by
49 fish reflect this diversity of cross-system origins.

50 While salmonids feed opportunistically on the surface, in the water column and
51 benthos (Syrjänen et al. 2011; Allan et al. 2003) they can also show selectivity for prey.
52 They are visual predators, and their size-selectivity makes larger, more visible prey most
53 vulnerable (Allan 1981). Social status can confer advantages to larger, dominant fish that
54 outcompete smaller fish for prime feeding locations (Nakano et al. 1999). These
55 advantages can result in larger fish catching the larger prey (Syrjänen et al. 2011). In
56 concert with seasonal changes in aquatic and terrestrial prey, changes in trout
57 consumption may also reflect availability of the largest prey.

58 For the delivery of terrestrial invertebrates, close proximity of riparian canopy and
59 vegetation has been shown to be important in a great diversity of streams around the
60 world; the highest in-fall rates are often in deciduous canopies (Mason and MacDonald
61 1982, Chloe and Garman 1996, Syrjänen et al. 2011). Some of the highest rates of
62 terrestrial prey consumption by salmonids have been reported in temperate deciduous
63 forests (Kawaguchi & Nakano 2001, Romero et al. 2005), particularly by *Oncorhynchus*
64 trout species (see review by Syrjänen et al. 2011). In the Pacific Northwest many Douglas
65 -fir forests that were cut in the mid-twentieth century have grown back to 40 to 60 year-

old stands. Riparian trees in those forests are often a mix of conifers with deciduous alders and maples. At the time of our study, Hinkle Creek watershed in the southern Cascade Mountains of Oregon, had such a forest with relatively homogenous riparian canopies.

Our objective was to examine seasonal and spatial factors affecting prey consumption by coastal cutthroat trout, *Oncorhynchus clarkii clarkii*, and steelhead, *O. mykiss irideus*, in Hinkle Creek. We hypothesized that the types of prey consumed would fluctuate with seasonal changes in abundance and size of prey from aquatic and terrestrial sources. Secondly, we hypothesized that the amount of prey consumed would be positively associated with increasing fish size. In our spatial comparison between tributaries and the mainstems we hypothesized that warmer temperatures in the mainstems would result in higher consumption and greater fish growth in those mainstem sites.

Methods

Study Sites

Hinkle Creek is a tributary stream in the Umpqua River drainage, located in the foothills of the Cascade Mountains of southwestern Oregon, U.S.A. The land within the Hinkle watershed is entirely privately owned and managed for timber production; a 50-60 year old second growth Douglas-fir forest was dominant throughout the watershed at the start of this study. The watershed is composed of two sub-basins - the North Fork and the South Fork (Figure 1) and drains 19.4 square kilometers. For this fish diet study, there were six mainstem sampling sites (four on South Fork, two on North Fork), and five sites on fish-bearing tributaries (three in the South Fork, two in the North Fork). Colleagues

also working in the Hinkle watershed (Kibler et al. 2013) provided water temperature data from four sites (2 mainstem and 2 tributary) where data were collected year-round during the course of our study.

Field collection and sample processing

We collected trout for stomach contents by electrofishing, except in spring 2004 when fish were collected by hook and line. Salmonids ≥ 80 mm fork length were categorized as either coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) or steelhead (*O. mykiss irideus*). Most *O. mykiss* in this study were anadromous as determined by observation and tagging, so we refer to them as “steelhead” though we recognize that resident forms, i.e. rainbow trout, can co-occur (McMillan et al. 2012, Tattam et al. 2013). Differentiating these trout species based on external characteristics was not reliable for smaller individuals; therefore, trout < 80 mm were considered as a single group of “unknown species.” In 2004, 71% were cutthroat trout, 16.3% steelhead, and 13% were unknown. In 2005 all trout ≥ 80 mm fork length in the tributaries, and 90% in the mainstem were coastal cutthroat; the remaining 10% of mainstem trout were steelhead. Fish were collected only at sites where there was a strong likelihood of obtaining twenty fish for diet analyses; because previous fish sampling indicated low trout densities at certain locations, we did not collect fish diet samples in all the tributaries (Figure 1).

We compared diet between seasons in 2004 at five mainstem sites (Figure 1); diet samples were collected on April 28 – May 4 (spring), August 30 (summer) and October 14 and 22 (fall). Spatial differences were examined explicitly the next year, in spring 2005 (May 2-5) between tributary and mainstem sites. Range of distances between

tributaries and closest mainstem sites in the North Fork were from 387 to 826 m, and from 606 to 1706 m on the South Fork (Figure 1).

After fish at least 60mm in fork length were captured, they were anesthetized, and fork length and wet weight were recorded. Fish stomach contents were gently flushed out using a squirt bottle filled with water, into a large metal tray. Contents of the tray were poured through a funnel containing a small coffee filter that retained the entire sample. After stomach samples were collected, fish were held in buckets with stream water until they recuperated, then were returned to the stream. Optimally twenty fish per site or as many fish as could be collected when densities were low, were sampled for diet at each site per date. Monte Carlo simulations were run to explore the number of fish needed to attain varying levels of precision in predicting prey consumption. These consisted of 1000 simulations for composites of 54 spring, 83 summer and 68 fall mainstem samples.

Invertebrate prey from stomach contents preserved in 70% ethanol were identified and enumerated in the laboratory. Each prey item was measured so that length/weight regressions could be used to determine biomass/prey item (Hodar 1996, Benke et al. 1999, Sabo et al. 2002). If invertebrate bodies were not whole, head widths were used in regressions based on whole organisms in gut samples to calculate body lengths. Identifications were made to the finest level possible, typically family or order. Prey organisms were also classified according to their sources: benthic (meaning bottom or stream water column), flying adults of aquatic, or terrestrial. We omitted a few fish from calculations of diet because we did not have suitable length/weight regression coefficients for a few types of prey organisms in the diet of those fish (4% of fish in

134 2004, 6% of fish in 2005) or because their stomachs were empty (5% of fish in 2004,
135 <1% of fish in 2005).

136 Benthic invertebrates were collected prior to fish sampling at each sampling site
137 in 2004 and 2005 (Figure 1). Sampling for seasonal comparisons occurred in mainstem
138 sites on April 29, August 10-12, and October 11, 2004. For comparisons between
139 tributaries and mainstem sites, benthic samples were taken from April 5-12, 2005. Sites
140 were 100 m long in mainstems and 30 m long in tributaries. Six randomly located
141 samples per site were collected with Surber nets. Benthic invertebrate samples were
142 processed in the lab by combining the six stream-bottom samples (total area sampled 0.54
143 square meters) from each site and subsampling randomly with a gridded sieve (Caton
144 1991) to get a minimum count of 500 organisms. Invertebrates were identified to the
145 lowest practical taxonomic level and enumerated. In general, insects were identified to
146 genus except for chironomids and ceratopogonids, which were only identified to
147 subfamily/tribe. Snails were identified to genus. Other non-insects were identified to
148 coarser taxonomic levels.

149 Additional fish sampling was also performed to assess trout growth in mainstems
150 and tributaries. Single-pass electrofishing (Bateman et al. 2005) was conducted annually
151 during late-summer, low-discharge periods (15 August–15 September) to capture trout in
152 all fish-bearing portions of the stream network. Upon capture, fish were anesthetized, and
153 fork length and wet weight were recorded. All trout ≥ 100 mm were surgically implanted
154 with a 23-mm half-duplex (HDX) passive integrated transponder (PIT) tag (Texas
155 Instruments, Inc., Dallas, Texas, USA) following procedures described by Bateman and
156 Gresswell 2006. Subsequently, all trout ≥ 100 mm captured were scanned with an

Allflex® (Allflex USA, Inc., Dallas, Texas, USA) handheld PIT-tag scanner and any untagged trout ≥ 100 mm found were implanted with PIT tags. After handling, all fish were allowed to recover (defined by upright swimming) in an aerated bucket of stream water and then were returned to their location of capture. Growth was calculated for PIT-tagged fish that were recaptured in subsequent annual sampling events. We used data from 2003-2005 to compare tributary and mainstem growth; data from all mainstem fish were used, but we only included tributary fish data from tributaries where we collected fish diet samples. In addition, through the use of gate readers at tributary junctions, we were able to monitor fish movement year-round. Relatively few tagged fish moved between tributaries and mainstems. Only growth data from fish that lived exclusively in mainstems or tributaries were compared. Growth data from more mobile fish that moved between tributaries and mainstems were excluded, since it would be difficult to interpret how habitat affected growth for these individuals.

Analyses

Differences in gut content weight among seasons and between tributary and mainstem sites were analyzed using analysis of covariance (ANCOVA). We ran two separate one-way ANCOVAs using mixed models, one for season as the fixed effect (using only mainstem 2004 data) and one for tributary versus mainstem as the fixed effect (using only spring 2005 data). In each model, fish weight was used as the covariate; site location was treated as a random effect. Fish weight and gut content weight were both skewed and were log-10 transformed for this and all subsequent statistical analyses.

Overall differences in diet composition patterns were examined with non-metric multidimensional scaling (NMS) ordination. Two separate ordinations were run to

examine seasonal (2004) and spatial (spring 2005) patterns. Prey biomass (log transformed) was used for these analyses, in which prey were categorized by order and source (benthic, adult aquatic, terrestrial). To identify invertebrate prey orders and sources distinctive for fish consumption in the seasonal analysis we calculated indicator values (IV) (Dufrene and Legendre 1997). These values quantified fidelity of a prey category to a season (B_{ij}) and specificity of that prey category to a season (A_{ij}), with the equation: $IV_{ij} = A_{ij} * B_{ij} * 100$.

In contrast to other analyses where we used data on a per fish basis, to compare changes in prey size across seasons and by prey type, we used biomass data from all individuals of each prey type in each season, without considering which fish they came from. Seasonal differences in average biomass per prey type were tested with a two-way ANOVA using log-transformed biomass data. Log transformation corrected highly skewed data distributions.

Relative growth rates of tributary versus mainstem trout (change in length / initial length / time between sampling events: $\text{mm} * \text{mm}^{-1} * \text{year}^{-1}$) were analyzed using a mixed model one-way ANOVA. Site location within tributary or mainstem was treated as a random effect.

Differences in benthic invertebrate densities between seasons (in 2004) were tested using a one-way analysis of variance (ANOVA). To compare spring 2005 benthic densities in tributaries v. mainstems, a t-test was used. For all these analyses, data were log-transformed to normalize data.

Results

Seasonal Variation

Initially, our goal for sampling was to capture 20 fish at each site. We were able to obtain diet from an average of only 14.7 fish per site. According to Monte Carlo simulations, a composite total of only 20 fish for the entire mainstem would have been needed in spring or summer to estimate the proportion of terrestrial prey consumed (standard deviation $\pm 5\%$); a composite size of more than 25 fish would have been required in fall. These outcomes suggest our seasonal sampling provided robust estimates of prey composition.

In general, the amount of prey biomass consumed increased with individual fish biomass (ANCOVA $F_{1,189} = 38.47$, $p < 0.001$; Figure 2a). Fish collected in spring weighed more (median weight = 21.3 g) than those collected in summer and fall (median weights of 13.6 g and 11.0 g respectively). The wider ranges of fish sizes and smaller median sizes of fish sampled for diet in summer and fall resulted from young of the year trout too small to be sampled in spring that became sufficiently large to be sampled later in the year. After accounting for this trend in fish size, prey consumption declined significantly in the fall (back-transformed Least Square Mean = 4.95 mg) compared to spring and summer (back-transformed LSM = 33.43 mg and 33.64 mg respectively) (ANCOVA: $F_{2,189} = 59.99$, $p < 0.001$). There was no significant difference between prey biomass consumed in spring and summer.

Average weights of benthic invertebrates, adult aquatics and terrestrial invertebrates found in trout diet differed significantly between seasons (ANOVA: $F_{2,4619} = 22.99$, $p < 0.001$) (Figure 3) and between prey types (ANOVA: $F_{2,4619} = 210.93$, $p < 0.001$); a significant interaction between these factors revealed that differences between prey types varied with season (ANOVA: $F_{4,4619} = 62.89$, $p < 0.001$). Notably, benthic

invertebrates were smaller than other prey types in spring and summer, while adult aquatics and terrestrial invertebrate average weights overlapped in those seasons. Benthic prey were larger in spring than in summer or fall. Terrestrial prey were largest in summer, and smallest in fall when adult aquatics were significantly larger than terrestrial or benthic invertebrates.

Trout diet switched in relative proportions of prey types from a mixture of benthics (mean = 45% of biomass, 67% of abundance), terrestrials (mean = 36% of biomass, 19% of abundance) and adult aquatics (mean = 15% of biomass, 10% of abundance) in spring to primarily terrestrials in summer (mean = 85% of biomass, 62% of abundance) (Figure 4a). Aquatic adult biomass comprised a small proportion of prey biomass overall. The switch in diet composition, driven by high proportions of terrestrial prey in summer, was also apparent in NMS analysis (Figure 5a). In the fall, when overall consumption rates were low, almost half the diet was made up of terrestrial prey (mean = 48% of biomass).

Significant seasonal differences in prey composition were generally described by Indicator Species Analysis (Table 1). Aquatics were important in the spring when benthic and adult Ephemeroptera, Plecoptera and Diptera, and benthic Trichoptera were indicative of diet. Terrestrial Coleoptera and Diptera were also characteristic of spring samples. Terrestrial Hymenoptera were good indicators in summer (Indicator variable, IV = 61); 892 ants comprised 45% of terrestrial prey biomass consumed that season. Indicator values for Homoptera, Hemiptera and Isoptera in summer were lower than for Hymenoptera in part because they were consumed by only a portion of the fish in summer.

Examining biomass per taxa in each season revealed other contributors to diet among non-indicator taxa, particularly less abundant but heavier prey. While the high numbers of ants were important in summer diet, less numerous, larger ants in the spring (average = 12.1 mg, $n = 36$) made up 38% of total terrestrial prey. In summer larval Plecoptera contributed 27.5% of benthic biomass eaten, and adult Trichoptera ($n = 30$) comprised 86% of total adult aquatics. Forty-three caddisflies made up 97% of adult aquatics in fall. Small Collembola ($n = 59$) were only fairly good indicators of fall samples ($IV = 25.7$) when overall consumption was much lower than in other seasons. Benthic Ephemeroptera, Trichoptera and Diptera comprised 85% of benthic prey biomass consumed in fall when benthic invertebrates constituted 39% of prey biomass eaten. Occasionally big, uncommon prey, such as gerrid water striders in the summer, and Diplopoda (millipedes) and Orthoptera (namely cave crickets) in the fall, contributed disproportionately large portions of total biomass consumed. Conversely, small invertebrates like aquatic Diptera in spring ($n = 407$) and terrestrial Collembola in fall, constituted very small portions of total biomass consumed.

Spatial variation

Average prey consumed increased with fish size in spring 2005 (Figure 2b). We noted that fish in tributaries tended to consume more than fish of the same size in the mainstem (Figure 2b), and as a group tributary trout weighed less than trout in the mainstem (median weights = 9.6 g and 12.9 g respectively). After accounting for the trend in fish size, fish in the tributaries tended to consume more than in the mainstem sites (back-transformed LSM = 23.07 mg and 10.08 mg respectively) (ANCOVA: $F_{1,134} = 4.22$, $p = 0.06$). However, relative growth rates of trout at tributary sites (LSM = 0.178

mm * mm⁻¹ * year⁻¹) were somewhat lower than at mainstems (LSM = 0.249 mm * mm⁻¹ * year⁻¹) (ANOVA: $F_{1,124} = 4.75$, $p = 0.06$; Figure 6). Benthic invertebrates comprised > 60% of prey biomass consumed in both tributary and mainstem sites (Figure 4b), and there was considerable diet overlap among fishes in the two stream types (NMS, Figure 5b).

Mean daily water temperatures were, on average, 1.5 °C warmer in mainstems than in tributaries during summer (Figure 7a). However, temperature differences between mainstems and tributaries were less pronounced at other times of the year. As a result, average cumulative degree days accumulated over a year at tributary sites (3315.6) differed by about 6% from those accumulated at mainstem sites downstream (3515.0). In both mainstems and tributaries, mean daily temperatures (Figure 7a) and seven-day moving averages of the daily maximum water temperatures (Figure 7b) remained below 18 °C.

Benthic Invertebrates

In samples collected contemporaneously with trout diet, benthic densities were slightly higher in summer (mean = 2678 m⁻²) compared to spring (mean = 2155 m⁻²) and fall (mean = 1980 m⁻²), but there were no significant differences between seasons (ANOVA: $F_{2,15} = 2.3$, $p = 0.14$). In spring 2005 benthic invertebrate densities were slightly, but not significantly higher in the mainstems (mean = 2559 m⁻²) than in tributaries (mean = 2040 m⁻²) ($t = 1.25$, $p = 0.23$).

Discussion

Cutthroat trout and steelhead at Hinkle Creek were opportunistic predators, eating prey from aquatic and terrestrial sources throughout the year. By collecting an average of

15 diet samples per site we were able to overcome the high variability in fish diets and develop robust measures of prey consumption as confirmed by Monte Carlo simulations. In our study, diet biomass was positively related to increasing fish size. The seasonal dynamics of prey availability and size were key to fluctuations in fish diet, particularly for fish switching from a mixed diet in spring to terrestrial prey in the summer, and for fish consuming dramatically less prey in the fall.

Invertebrate patterns of phenology were apparent in our seasonal comparisons of fish diet. Typical life history patterns of benthic invertebrates were detected among benthic prey consumed. In spring, as many taxa prepared to emerge, benthic larvae were larger than at other times of the year. Terrestrial invertebrates were largest in the summer, and greater activity levels likely contributed to their increased availability to fish. By autumn, diversity and numbers of terrestrial prey consumed declined dramatically, when benthic invertebrates remained small. Seasonal changes among invertebrates translated into what was available and most vulnerable to fish predation.

Terrestrial prey were important components of trout diet in all seasons at Hinkle Creek, increasing from spring to summer (ie. from 36% to 85% of biomass consumed). In Japan consumption by salmonids switched from very low to high levels of terrestrial prey (Nakano and Murakami 2001, Kawaguichi and Nakano 2001), coinciding asynchronously with a dramatic decrease in benthic availability. At Hinkle Creek, trout also switched to higher consumption of terrestrial invertebrates in summer even though benthic invertebrate densities did not change from spring to summer. A decrease in benthic prey abundance was not likely the primary mechanism for the switch; rather, preference for larger, easily detectable terrestrial prey probably played a role. Benthics

were significantly smaller in the summer, and trout selected larger terrestrial prey, particularly ants and termites. Though this study was not designed to assess the rate of terrestrial infall, the fish response suggests that a seasonal pulse of terrestrial prey was likely. Greater visibility of terrestrial insects in the drift, especially patchily distributed larger individuals, and greater ease of capture with less energetic cost, likely favored terrestrial prey consumption. Adult aquatics were among the largest prey in any season but were never the dominant prey consumed. Thus we believe availability, in addition to size and visibility, also played a role in trout selection.

One of the strongest seasonal signals detected in our study was a dramatic decrease in prey eaten by trout in the fall. Water temperatures for the October 2004 sampling were comparable to those in early summer, and were not extremely warm or cold. Other abiotic factors might have been in play, such as reductions in suitable habitat prior to fall rains. However the very small size of prey consumed (e.g. Collembola and small Ephemeroptera), in combination with the lack of large taxa that had been available in other seasons, suggest that resource scarcity was likely. Fish mortality at Hinkle Creek was also high in the fall (Berger and Gresswell 2009). In coastal streams of the Pacific Northwest food can be limiting to cutthroat trout in the summer (Boss and Richardson 2002), but in the southern Cascades trout weighed less, ate significantly less, and prey appeared to be most limited in the critically dry autumn. Fish did eat benthic mayflies and true flies in the fall, but terrestrial prey (including spiders, occasional millipedes and cave crickets) comprised almost 50% of the diet during that season. Terrestrial invertebrates were mortalities resulting from infall to the stream; therefore predation by fish had little

or no effect on terrestrial communities. Conversely, the energetic resources provided by terrestrial prey appeared to be critical for fish survival in the autumn.

Experiments in Japan suggested terrestrial subsidies in the summer could buffer effects of fish predation, allowing benthic populations to recover or grow while fish switch to terrestrial prey (Nakano et al. 1999b, Kawaguichi et al. 2003, Baxter et al. 2004). Because benthic abundances in summer at Hinkle did not differ from spring, trout switching to terrestrial prey may result in a similar buffering effect. Reduced trout predation on aquatic prey may increase availability to other aquatic insectivores (Baxter et al. 2005) such as salamanders, riparian spiders (Marczak and Richardson 2007) and birds (Wright et al. 1997).

To understand apparent contradictions between relatively higher consumption rates and slower growth rates in Hinkle tributaries, we considered differences in habitat availability and the energetics of foraging. The proportion of age-0 fish lavaged at tributary and mainstem sites were relatively the same (18% and 16% respectively); thus it was unlikely that differences in age classes explained differences in size. Spring through fall water temperatures at Hinkle Creek occurred within a 10 – 18 °C range, providing a large scope for growth (Dwyer and Kramer 1975) and minimizing stress from excessively warm water temperatures (Boyd and Sturdevant 1997). Though cumulative degree days in tributaries were only 200 degree days lower than those at mainstem sites, when temperature differences were greatest in mid-summer digestion rates might have been lower in tributaries and led to lower growth rates. Models developed by Railsback and Rose (1999) for *O. mykiss* predicted that growth is more affected by food consumption than temperature, but at Hinkle Creek tributaries, trout sizes and growth rates were lower

than in the mainstem despite moderately higher rates of food consumption. We believe that bioenergetics models (*sensu* Arismendi et al. 2013, Penaluna et al. 2015) could help us determine if small temperature differences, particularly in the summer, were important to growth.

Other habitat characteristics can also affect trout growth (Rosenfeld et al. 2000). During an enclosure study in British Columbia, Canada, both age-0 and older cutthroat trout had higher growth rates in pools relative to riffles; age-0 fish experienced positive growth in riffles while older fish tended to lose weight (Rosenfeld and Boss 2001). Trout surveyed in Hinkle Creek tributaries also lived in higher gradient, swifter reaches where there were fewer pools for refuge or feeding stations, compared to the mainstem. These habitat associations suggest that tributary trout were smaller potentially because they spent more energy feeding in high gradient riffles compared to fish downstream. Diet composition was similar in tributaries and mainstems, but trout in the tributaries ate more than those in bigger reaches at apparently at higher energetic cost. In our springtime comparison, hydrologic and thermal differences in habitats probably created greater demands for prey consumption and may have resulted in relatively slower growth.

Located in the temperate, mesic climate of southern Oregon, the riparian vegetation in the managed forest of the Hinkle Creek watershed was a mix of Douglas-fir, alder and maple overstory. Like homogeneously deciduous canopies noted elsewhere (Mason and MacDonald 1982, Allan et al. 2003, Syrjänen et al. 2011) the forest's capacity for invertebrate production was high. Differences in riparian diversity and composition, even within a region, can influence the availability and timing of invertebrate litterfall. In a study of three widely separated coastal Oregon streams

(Romero et al. 2005) sites varied in riparian species, including Sitka spruce and Douglas-fir conifers, red alder and big-leaf maple deciduous species. At those sites, the peak in terrestrial prey consumption occurred in the fall, whereas at Hinkle Creek terrestrial prey clearly contributed more to summer trout diet. Both the warmer, more southern location and more contiguous, homogenous deciduous riparian vegetation at Hinkle are likely contributed to the higher availability of terrestrial prey in the summer and prey scarcity in the fall. These contrasts suggest that the dynamics of seasonal patterns is likely watershed-specific, and the timing of prey resource limitations and fish vulnerability probably varies with a wide range of conditions including climate, landscape morphology and forest type.

Because *Oncorhynchus* trout are opportunistic, they consume both aquatically- and terrestrially-derived prey throughout the year. In our study, summer reductions in benthic prey size coincided with timely fluxes of terrestrial invertebrates that probably provided a temporal buffer for benthic organisms to grow. Seasonal fluctuations in fish consumption were driven by prey abundance and prey size, especially as trout switched from benthic to terrestrial prey in summer. Identifying seasonal patterns within a watershed is important not only for describing seasonal highs, but also for site-specific timing of resource lows and critical stress periods. Behavioral adaptations, such as increased food consumption in higher gradient, cooler tributaries, may not fully compensate for more demanding environmental conditions. Multi-seasonal, watershed-wide studies provide the most complete approach to understanding the fluctuations and dynamics between these fish predators and their prey resources.

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References

- Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquat. Sci. 38(2): 184–192. doi:10.1139/f81-024.
- Allan, J.D., Wipfli M.S., Caouette J.P., Prussian, A., and Rodgers, J. 2003. Influences of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Can. J. Fish. Aquat. Sci. 60: 309-320.
- Allen, K.R. 1951. The Horokiwi Stream: a study of a trout population. New Zealand Dept. of Fisheries Bull. 10.
- Arismendi I., Johnson, S.L., Dunham, J.B., and Haggerty, R. 2013. Descriptors of natural thermal regimes in streams and their responsiveness to change in the Pacific Northwest of North America. Freshwater Biology 58: 880-894.
- Bateman, D.S., Gresswell, R.E., and Torgersen, C.E. 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. J. Freshwat. Ecol. 20(2): 335-345.

- 431 Bateman, D.S., and Gresswell, R.E. 2006. Survival and growth of age-0 steelhead after
432 surgical implantation of 23-mm passive integrated transponders. N. Am. J. Fish.
433 Manage. 26: 545-550.
- 434 Baxter, C.V., Fausch, K.D., and Saunders, W.C. 2005. Tangled webs: reciprocal flows of
435 invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.
- 436 Benke, A.C., Huryn, A.D., Smock, L.A., and Wallace, J.B. 1999. Length-mass
437 relationships for freshwater macroinvertebrates in North America with particular
438 reference to the southeastern United States. Journal of the North American
439 Benthological Society 18: 308–343.
- 440 Berger, A.M., and Gresswell, R.E. 2009. Factors influencing coastal cutthroat trout
441 (*Oncorhynchus clarkii clarkii*) seasonal survival rates: a spatially continuous
442 approach within stream networks. Can. J. Fish. Aquat. Sci. 66: 613-632.
- 443 Boss, S.M., and Richardson, J.S. 2002. Effects of food and cover on the growth and
444 movement of cutthroat trout (*Oncorhynchus clarki*) in coastal stream. Can. J. Fish.
445 Aquat. Sci. 59: 1044–1053.
- 446 Boyd, M. and Sturdevant, D. 1997. The scientific basis for Oregon's stream temperature
447 standard: common questions and straight answers. Oregon Department of
448 Environmental Quality. Salem. OR.
- 449 Bramblett, R.G., Bryant, M.D., Wright, B.E., and White, R.G. 2002. Seasonal use of
450 small tributary and mainstem habitats by juvenile steelhead, coho salmon, and Dolly
451 Varden in a southeastern Alaska drainage basin. Transactions of the American
452 Fisheries Society 131: 498–506.

- 453 Caton, L.W. 1991. Improved subsampling methods for the EPA 'Rapid Bioassessment'
454 benthic protocols. North American Benthological Society Bulletin 8: 317–319.
- 455 Chloe, W.W., and Garman, G.C. 1996. The energetic importance of terrestrial arthropod
456 input to three warm-water streams. Freshwater Biology 36: 105-114.
- 457 Dimick, R.E., and Mote, D.C. 1934. A preliminary survey of the food of Oregon trout.
458 Agricultural Experiment Station, Oregon State Agricultural College and Oregon
459 State Game Commission, Station Bulletin 323. 22p.
- 460 Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need
461 for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.
- 462 Dwyer, W.P., and R.H. Kramer. 1975. The influence of temperature on scope for activity
463 in cutthroat trout, *Salmo clarki*. Transactions of the American Fisheries Society 3:
464 552-554.
- 465 Edwards, E.D., and Huryn, A.D. 1996. Annual contribution of terrestrial invertebrates to
466 a New Zealand stream. N.Z. J. Mar Freshwater Res. 29: 467-439.
- 467 Haapala, A., Muotka, T., and Markkola, A.M. 2001. Breakdown and macroinvertebrate
468 and fungal colonization of alder, birch and willow leaves in a boreal forest stream.
469 Journal of the North American Benthological Society 20(3): 395-407.
- 470 Harper, M.P., and Peckarsky, B.L. 2006. Emergence cues of a mayfly in a high-altitude
471 stream: potential response to climate change. Ecological Applications 16: 612–621.
- 472 Hodar, J.A. 1996. The use of regression equations for estimation of arthropod biomass in
473 ecological studies. Acta Oecologica 17: 421–433.
- 474 Hogg, I.D., and Williams, D.D. 1996. Response of stream invertebrates to a global-
475 warming thermal regime: an ecosystem-level manipulation. Ecology 77: 395–407.

- 476 Kawaguchi, Y., and Nakano, S. 2001. Contribution of terrestrial invertebrates to the
477 annual resource budget for salmonids in forest and grassland reaches of a headwater
478 stream. *Freshwater Biology* 46: 303-316.
- 479 Kawaguchi, Y., Taniguchi, Y., and Nakano, S. 2003. Terrestrial invertebrate inputs
480 determine the local abundance of stream fishes in a forested stream. *Ecology* 84(3):
481 701-708.
- 482 Kibler, K.M., Skaugset, A., Ganio, L.M., and Huso, M.M. 2013. Effect of contemporary
483 forest harvesting practices on headwater stream temperatures: initial response of the
484 Hinkle Creek catchment, Pacific Northwest, USA. *Forest Ecology and Management*
485 310: 680-691.
- 486 Li, J.L., Johnson, S.L., and Sobota, J.B. 2010. Three responses to small changes in stream
487 temperature by autumn-emerging aquatic insects. *Journal of the North American*
488 *Benthological Society* 30: 474-484.
- 489 Marczak, L.B. and Richardson, J. S. 2007. Spiders and subsidies: results from the
490 riparian zone of a coastal temperate rainforest. *Journal of Animal Ecology* 76:687-
491 694.
- 492 Mason, C.F., and MacDonald, S.M. 1982. The input of terrestrial invertebrates from tree
493 canopies to a stream. *Freshwater Biology* 12: 305-311.
- 494 McMillan, J.R., Dunham, J.B., Reeves, G.H., Mills, J.S., and Jordan, C.E. 2012.
495 Individual condition and stream temperature influence early maturation of rainbow
496 and steelhead trout, *Oncorhynchus mykiss*. *Environmental Biology of Fishes* 93:
497 343-355.

- 498 Meissner, K., and Muotka, T. 2006. The role of trout in stream food webs: integrating
499 evidence from field surveys and experiments. *J. Anim. Ecol.* 75(2): 421–433.
500 doi:10.1111/j.1365-2656.2006. 01063.x. PMID:16637995.
- 501 Nakano, S., and Murakami, M. 2001. Reciprocal subsidies: dynamic interdependence
502 between terrestrial and aquatic food webs. *Proceedings of the National Academy of*
503 *Science, U.S.A.* 98: 166-170.
- 504 Nakano, S., Kawaguchi, Y., Taniguchi, Y., Miyasaka, H., Shibata, Y., Urabe, H., and
505 Kuhara, N. 1999a. Selective foraging on terrestrial invertebrates by rainbow trout in
506 a forested headwater stream in northern Japan. *Ecol. Res.* 14: 351-360.
- 507 Nakano, S., Miyasaka, H., and Kuhara, N. 1999b. Terrestrial-aquatic linkages: riparian
508 arthropod inputs alter trophic cascades in a stream food web. *Ecology.* 80: 2435-
509 2441.
- 510 Northcote, T.G. 1997. Potamodromy in Salmonidae—living and moving in the fast lane.
511 *North American Journal of Fisheries Management* 17: 1029-1045.
- 512 Penaluna, B.E., Railsback, S.F., Dunham, J.B., Johnson, S., Bilby, R.E., and Skaugset,
513 A.E. 2015. The role of environmental regimes and the geophysical template to
514 stream-living trout. *Can. J. Fish. Aquat. Sci.* 72: 893-901.
- 515 Romero, N., Gresswell, R.E. and Li, J.L. 2005. Changing patterns in coastal cutthroat
516 trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies.
517 *Can. J. Fish. Aquat. Sci.* 62: 1797-1807.
- 518 Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile
519 cutthroat trout: energetic costs and benefits in pools and riffles. *Can. J. Fish. Aquat.*
520 *Sci.* 58: 585–593.

- 521 Rosenfeld, J.S., Porter, M., and Parkinson, E. 2000. Habitat factors affecting the
522 abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and
523 coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 57: 766–774.
- 524 Sabo, J.L., Bastow, J.L., and Power, M.E. 2002. Length–mass relationships for adult
525 aquatic and terrestrial invertebrates in a California watershed. Journal of the North
526 American Benthological Society 21: 336–343.
- 527 Sweeney, B.W. 1984. Factors influencing life-history patterns of aquatic insects. Pages
528 56–100 in V.H. Resh and D.M. Rosenberg (editors). The ecology of aquatic insects.
529 Praeger Scientific, New York.
- 530 Syrjänen, J., Korsu, K., Louhi, P., Paavola, R., and Muotka, T. 2011 Stream salmonids as
531 opportunistic foragers: the importance of terrestrial invertebrates along a stream-size
532 gradient. Can. J. Fish. Aquat. Sci. 68: 2146–2156.
- 533 Tattam, I.A., Ruzycki, J.R., Li, H.W., and Giannico, G.R. 2013. Body size and growth
534 rate influence emigration timing of *Oncorhynchus mykiss*. Trans. Am Fish. Soc.
535 142(5): 1406–1414.
- 536 Ward, J.V., and Stanford, J.A. 1982. Thermal responses in the evolutionary ecology of
537 aquatic insects. Annual Review of Entomology 27: 97–117.
- 538 Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in
539 streams: contrasting old-growth and young-growth riparian forests in southeastern
540 Alaska, U.S.A. Can. J. Fish. Aquat. Sci 54: 1259–1269.
- 541 Wipfli, M.S., and Baxter, C.V. 2010. Linking ecosystems, food webs, and fish
542 production: subsidies in salmonid watersheds. Fisheries 35: 373–387.

543 Wright, K.K., Bruner, H., Li, J., Jarvis, R., and Dowlan, S. 2000. The distribution,
544 phenology and prey of harlequin ducks, *Histrionicus histrionicus*, in a Cascade
545 mountain stream, Oregon. Canadian Field Naturalist 114:187-195.
546

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Table 1. Indicator values for invertebrates consumed by trout in three seasons ($p < 0.01$).

IV = Indicator values can range from 0-100, where a value of 100 expresses perfect indication (taxon is found in all samples from that season, and does not occur in any samples from other seasons).

	Spring	IV	Summer	IV	Fall	IV
Benthic	Ephemeroptera	58.7				
	Trichoptera	52.4				
	Diptera	44.1				
	Plecoptera	34.7				
Adult	Ephemeroptera	58.6				
Aquatic	Plecoptera	31.5				
	Diptera	20.6				
Terrestrial	Coleoptera	41.0	Hymenoptera	61.0	Collembola	25.7
	Diptera	40.5	Homoptera	30.9		
			Hemiptera	25.4		
			Isoptera	22.9		

568

569 Figures

570 Figure 1. Map of Hinkle Creek watershed, Oregon, USA, showing invertebrate and fish
571 sampling sites. Fish and invertebrates were collected at mainstem in 2004 and 2005 (gray
572 circles) and at tributary sites in 2005 (black diamonds); black crosses indicate where
573 year-round water temperature data were recorded.

574 Figure 2. Relationships between diet biomass of individual trout v. trout biomass
575 compared a) across seasons, 2004 and b) between tributary and mainstem sites, spring
576 2005.

577 Figure 3. Comparison of prey type sizes in trout gut samples from spring, summer, and
578 fall 2004. Graph is the interaction plot related to two-way analysis of variance showing
579 mean values and 95% Tukey confidence intervals. Note: y-axis is log-scale.

580 Figure 4. Comparisons of average percent benthic, adult aquatic, terrestrial and unknown
581 prey biomass consumed per fish at a) mainstem sites in spring, summer, fall 2004 and b)
582 tributaries and mainstem sites in spring 2005.

583 Figure 5. Non-metric multidimensional scaling (NMS) ordination of prey biomass
584 consumed by individual trout. Prey per fish were represented by invertebrate orders and
585 prey types (benthic, adult aquatic, terrestrial, unknown). Two axes of 3-dimensional
586 ordinations are shown. Vectors indicate strong correlations ($r < 0.6$) with fish gut metrics.
587 a) spring, summer and fall, 2004. Axis 1: $R^2 = 0.219$; Axis 2: $R^2 = 0.195$; Axis 3: $R^2 =$
588 0.298 ; Total $R^2 = 0.712$. b) mainstem + tributaries, spring 2005. Axis 1: $R^2 = 0.309$; Axis
589 2: $R^2 = 0.338$; Axis 3: $R^2 = 0.146$; Total: $R^2 = 0.792$.

590 Figure 6. Annual relative growth rates (2003-2005) for recaptured, pit-tagged, age 1+
591 trout in Hinkle Creek comparing fish that reared in tributaries v. mainstems. The

592 relatively few fish moving between stream types were excluded. Numbers within each
593 box = sample size.

594 Figure 7. Hinkle Creek water temperatures from two mainstem and two tributary sites. a)
595 mean daily water temperatures from 4/1/2004 through 3/31/2005 and b) seven-day
596 moving averages of the daily maximum water temperatures during summer 2004.

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Figure 1. Map of Hinkle Creek watershed, Oregon, USA, showing invertebrate and fish sampling sites. Fish and invertebrates were collected at mainstem in 2004 and 2005 (gray circles) and at tributary sites in 2005 (black diamonds); black crosses indicate where year-round water temperature data were recorded.

177x133mm (300 x 300 DPI)

Figure 2. Relationships between diet biomass of individual trout v. trout biomass compared a) across seasons, 2004 and b) between tributary and mainstem sites, spring 2005.

156x222mm (300 x 300 DPI)

Figure 3. Comparison of prey type sizes in trout gut samples from spring, summer, and fall 2004. Graph is the interaction plot related to two-way analysis of variance showing mean values and 95% Tukey confidence intervals. Note: y-axis is log-scale.

177x105mm (300 x 300 DPI)

Figure 4. Comparisons of average percent benthic, adult aquatic, terrestrial and unknown prey biomass consumed per fish at a) mainstem sites in spring, summer, fall 2004 and b) tributaries and mainstem sites in spring 2005.

153x188mm (300 x 300 DPI)

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177x254mm (300 x 300 DPI)

Figure 6. Annual relative growth rates (2003-2005) for recaptured, pit-tagged, age 1+ trout in Hinkle Creek comparing fish that reared in tributaries v. mainstems. The relatively few fish moving between stream types were excluded. Numbers within each box = sample size.

119x97mm (300 x 300 DPI)

Figure 7. Hinkle Creek water temperatures from two mainstem and two tributary sites. a) mean daily water temperatures from 4/1/2004 through 3/31/2005 and b) seven-day moving averages of the daily maximum water temperatures during summer 2004.

177x220mm (300 x 300 DPI)