

Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies

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Abstract: We examined the influence of riparian vegetation patterns on coastal cutthroat trout *Oncorhynchus clarki clarki* diet and prey from the summer of 2001 through the spring of 2002. Benthic and drifting invertebrates, allochthonous prey, and fish diet were collected from deciduous, conifer, and mixed sections of three Oregon coastal watersheds. The nine sites were best characterized as a continuum of deciduous cover, and shrub cover and proportion of deciduous canopy were positively correlated ($r = 0.74$). Most sources of prey (benthic invertebrate biomass, allochthonous invertebrate inputs, aquatic and total invertebrate drift) and aquatic prey ingested by coastal cutthroat trout were greater where shrub cover was more abundant. Only aquatic drift, total invertebrate drift, and allochthonous invertebrates were positively correlated with deciduous vegetation. Compared with coniferous sites, allochthonous invertebrates under deciduous and mixed canopies were almost 30% more abundant. Stream discharge likely influenced seasonal fluxes of aquatic invertebrate biomass in the benthos and drift. Aquatic insects dominated gut contents during this study; however, terrestrial prey were most common in the diet during the summer and fall. In the Pacific northwest, systematic removal of deciduous riparian vegetation to promote conifers may have unintended consequences on food resources of coastal cutthroat trout and aquatic food web interactions.

Résumé : Nous avons étudié l'influence des patrons de végétation des rives sur le régime alimentaire et les proies des truites fardées côtières (*Oncorhynchus clarki clarki*) de l'été 2001 au printemps 2002. Nous avons mesuré les invertébrés dans le benthos et la dérive, les proies allochtones et le régime alimentaire des poissons dans des sections décidues, conifériennes et mixtes de trois bassins versants côtiers de l'Oregon. Les neuf sites se caractérisent le mieux comme formant un continuum de couverture végétale; il y a une corrélation positive entre la couverture des buissons et la proportion de la canopée formée par les arbres décidus ($r = 0,74$). La plupart des sources de proies (biomasse des invertébrés benthiques, apports d'invertébrés allochtones, dérive aquatique et dérive totale d'invertébrés) ainsi que l'ingestion des proies par les truites fardées côtières sont plus élevées là où le couvert de buissons est plus important. Seuls la dérive aquatique, la dérive totale d'invertébrés et les invertébrés allochtones montrent une corrélation positive avec la végétation décidue. Par comparaison aux sites de conifères, les invertébrés allochtones sont presque 30 % plus abondants sous les couverts décidus et mixtes. Le débit du cours d'eau influence vraisemblablement les apports saisonniers de biomasse des invertébrés aquatiques dans le benthos et la dérive. Les insectes aquatiques prédominent dans les tubes digestifs durant notre étude, alors que les proies terrestres sont plus fréquentes dans le régime d'été et d'automne. Dans la région du nord-ouest pacifique, le retrait systématique de la végétation décidue des rives pour favoriser les conifères peut avoir des conséquences imprévues sur les ressources alimentaires des truites fardées côtières et sur les interactions dans les réseaux alimentaires aquatiques.

[Traduit par la Rédaction]

Introduction

Although understanding of the relationships between riparian vegetation type and salmonid prey availability is growing, temporal variation in these relationships is poorly understood. In forested streams, the phenology of alloch-

thonous deciduous material is important to the structure and function of aquatic food webs (Petersen and Cummins 1974; Cummins et al. 1989). The autumnal input of deciduous plant litter is especially important as a nutritional resource for aquatic organisms (Bocock 1964; Iversen 1974). Nitrogen, an essential nutrient for microbial and invertebrate pro-

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tein, is present in greater quantities in rapidly decomposing red alder (*Alnus rubra*) leaves than in more slowly decomposing needles of coniferous species (Triska et al. 1975). Furthermore, microbial colonization of leaf litter, along with its subsequent invertebrate utilization, occurs more rapidly in red alder leaves than in conifer needles (Sedell et al. 1975). Because deciduous plant litter is preferred by aquatic detritivores (Iversen 1974; Hieber and Gessner 2002), an abundance of these plants may increase aquatic prey for fish for much of the year. We expect that riparian vegetation can contribute not only to detritivorous pathways, but also to herbivorous, and ultimately predacious, interactions of stream food webs.

In some forested headwater systems, invertebrates associated with terrestrial vegetation are important seasonal sources of food for salmonids (Wipfli 1997; Kawaguchi and Nakano 2001; Allan et al. 2003). The contribution of terrestrial invertebrates to the diet of stream salmonids can be substantial, particularly in the summer and fall, when terrestrial invertebrate input to streams peak (Mason and MacDonald 1982; Cloe and Garman 1996; Wipfli 1997). Terrestrial arthropods that accidentally fall into stream channels represent a high-quality food resource directly available to fishes, and these organisms comprise more than 50% of fish diet during some seasons (Hunt 1975; Cloe and Garman 1996; Kawaguchi and Nakano 2001). Because deciduous plants often support greater terrestrial arthropod biomass per stem than conifers (Allan et al. 2003), they potentially contribute more food for fish during periods of high terrestrial prey availability (Wipfli 1997).

In addition to these biological effects on food availability for fish, large conifers in the Pacific Northwest are valued in riparian ecotones for maintaining habitat and water quality for salmonid persistence. Because decomposition rates of coniferous wood in streams are significantly lower than wood from deciduous species (Harmon et al. 1986), persistence of large conifer logs increases organic matter and sediment retention (Speaker et al. 1984; Gregory et al. 1991), provides habitat stability for fish (Gregory et al. 1991), and maintains light and thermal regimes (Johnson and Jones 2000). As these riparian functions are commonly associated with salmonid persistence, current riparian management objectives tend to promote both the retention of existing conifers and the conversion of hardwood-dominated areas to conifers (USDA 1996; ODF 1998). However, deciduous vegetation in headwater streams of the Oregon Coast Range dominates the near stream (15 m) riparian community (Nierenberg and Hibbs 2000). Because these regulations are relatively new, the effect of this conversion on food resources for fish is unclear. We examined the seasonal contributions of aquatic and terrestrially derived invertebrates and the influence of vegetation on food sources to understand how riparian conversion could influence the food resources of coastal cutthroat trout (*Oncorhynchus clarki clarki*) and potentially, the overall productivity of aquatic food webs.

The purpose of our work was to explore how prey sources were affected by seasonal changes in riparian and stream conditions. Located in forested headwater streams of the Oregon Coast Range, our study did the following: (i) compared invertebrate biomass and composition from benthic, drift, and allochthonous sources among stream sections with

deciduous-dominated, conifer-dominated, and mixed (deciduous–conifer) vegetation; and (ii) evaluated seasonal variation in prey availability and the diet of coastal cutthroat trout in these riparian communities.

Methods

Study area

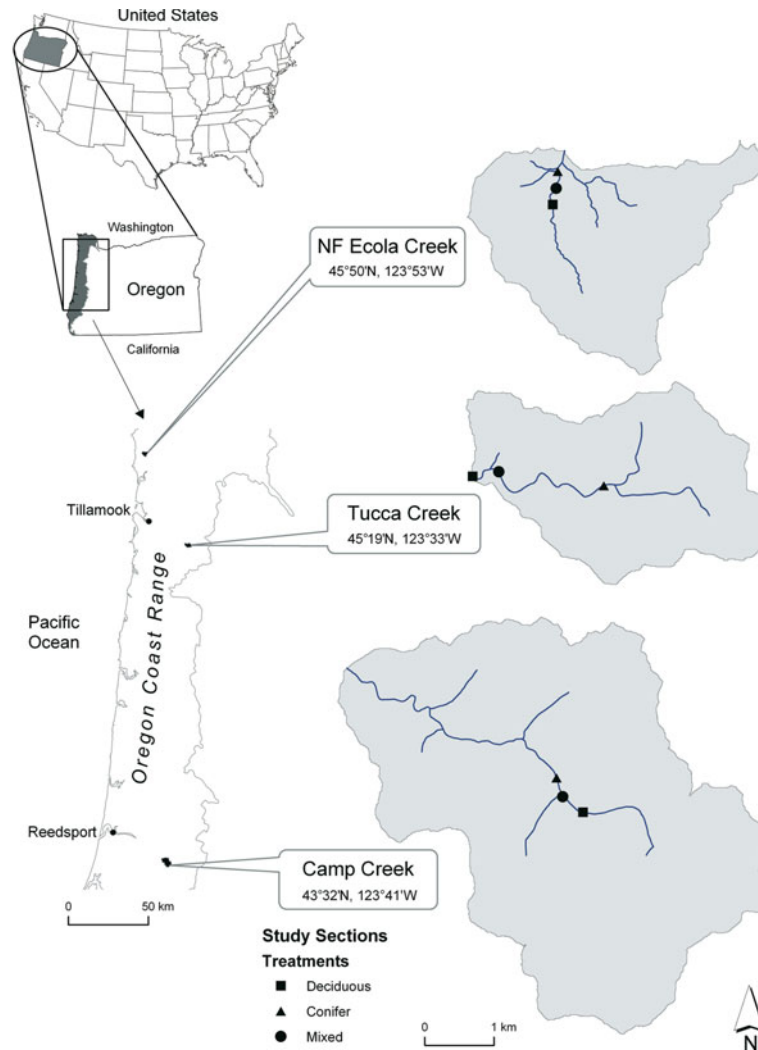
The study was conducted between June 2001 and April 2002 in sections of three headwater streams in the Oregon Coast Range, USA. To avoid the potentially confounding effect of marine-derived nutrients from decomposing salmon carcasses, sites were located above barriers to anadromous fishes. Coastal cutthroat trout and sculpin (*Cottus* sp.) were the only fish species present in these streams.

Study sites were located on Camp Creek (a tributary to the Umpqua River), Tucca Creek (a tributary to the Nestucca River), and North Fork Ecola Creek, which flows directly into the Pacific Ocean (Fig. 1). In each stream there were three study sections; each study section was selected to represent one of three riparian vegetation types (deciduous, conifer, and mixed) (Fig. 1). Sites were chosen to be reasonably similar in drainage area (<1500 ha). The length of individual study sections varied from 10 to 15 active channel widths and ranged from 102 to 190 m long (Table 1). All sites were characterized by pool–riffle channel morphology (Montgomery and Buffington 1997); gradients ranged from 2% to 5% and contained sand to boulder substrata. Channels in study sections of the three streams were generally unconstrained, with mean active channel widths ranging from 5.0 to 9.5 m at deciduous sites, 6.2 to 9.7 m at conifer sites, and 8.6 to 9.6 m at mixed sites (Table 1). During the study, discharge varied from a low of $<0.01 \text{ m}^3 \cdot \text{s}^{-1}$ in October to a high of $0.75 \text{ m}^3 \cdot \text{s}^{-1}$ in January, mean air temperatures ranged from 3 °C in March to 15 °C in July, and mean water temperatures ranged from 4 °C in March to 14 °C in August.

Riparian canopies were predominantly Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), and big-leaf maple (*Acer macrophyllum*). Study sections in Camp Creek were situated in old-growth riparian areas. Timber from some sections along Tucca Creek has been harvested during the last 15 years; however, the conifer study section contained riparian trees that were >100 years old. Approximately 95% of the North Fork Ecola Creek watershed is managed as commercial forestland, and at the time of study, vegetation was dominated by 50-year-old even-aged western hemlock and Sitka spruce.

Riparian habitat survey

To quantify riparian canopy cover and composition in the nine study sections, we measured vegetation along three 50-m transects perpendicular to stream flow at the one-quarter, one-half, and three-quarter length of each study section. Overstory cover was measured using a moosehorn at 15 sample points (stream center, wetted edge, bankfull, and at 5-m intervals upslope for a distance of 25 m from each bank; Bonnor 1967). To characterize riparian understory, we visually estimated shrub cover and composition in 5-m ra-

Fig. 1. Location of streams sampled and sites within streams in the Oregon Coast Range, USA.

dus plots set along transects perpendicular to stream flow at stream center, as well as 5-, 10-, and 20-m locations on each bank.

Water temperature, air temperature, and stream discharge were measured in each study section during the study. A temperature data logger (Optic StowAway, Onset Computer Corporation, Bourne, Massachusetts) was used to record hourly water temperature, and an additional data logger (Hobo, Onset Computer Corporation) recorded hourly air temperature. Stream discharge ($\text{m}^3 \cdot \text{s}^{-1}$) was measured during each sample period with a flow meter (Marsh McBirney Model 2000) by methods described in McMahon et al. (1996).

Invertebrate prey availability

To examine seasonal fluctuations in prey availability, estimates of invertebrate biomass and composition from benthic, drift, and allochthonous sources were obtained four times during the study: summer (6 July – 8 August 2001), fall (1 October – 23 October 2001), winter (10 January – 20 February 2002), and spring (2 April – 19 April 2002). Benthic invertebrates were collected once each season with a 500- μm mesh Surber sampler (0.09 m^2 area) at six random locations in riffle habitat in each study section. Invertebrate drift was

estimated by placing one drift net (500- μm mesh; 0.4 m \times 0.4 m opening at the mouth) in the thalweg of riffle habitat at each end of a study section for 20 min at dawn. Drift nets were positioned to intercept total water column and capture invertebrates floating on the water surface. Because prey availability is difficult to ascertain by physical sampling (Rachlin et al. 1987), we chose to sample when diversity of drifting invertebrates was at a maximum.

During each study period, allochthonous invertebrate inputs were estimated from samples collected in pan traps (0.056 m^2) for 7 days. Twelve pan traps in each study section were suspended 1 m above the water surface on metal stands. Pan traps were filled with 3 cm of water and 2–3 drops of a soap surfactant to retain captured invertebrates. The wetted channel area was divided longitudinally into three subsections (left, center, and right); four pan traps were placed randomly in each subsection (Doolittle and Starkey 2002). Pan-trap contents were sieved (225- μm mesh) at the completion of each 7-day sample period and preserved in a 95% ethanol solution prior to processing.

Invertebrates collected from the benthos, drift, and pan traps were sorted under a dissecting microscope, taxonomically identified (primarily to the family level), enumerated,

Table 1. Physical habitat and vegetation characteristics in study sections of Camp Creek, Tucua Creek, and North Fork Ecola Creek in the Oregon Coast Range.

Variables	Camp Creek			Tucua Creek			North Fork Ecola Creek		
	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed	Deciduous	Conifer	Mixed
Drainage area (ha)	872	1158	903	800	417	686	229	257	250
Elevation (m)	253	244	248	427	524	439	320	311	317
Length (m)	160	190	115	120	150	180	105	102	155
Gradient (%)	2	1.5	2.2	2.8	3.4	2.5	5	3.6	3.7
Mean ACW ^a (m)	9.5 (0.44)	9.7 (0.57)	8.6 (0.43)	7.5 (0.50)	6.5 (0.48)	9.6 (0.54)	5.0 (0.39)	6.2 (0.52)	8.8 (1.1)
Mean discharge (m ³ ·s ⁻¹)	0.18 (0.12)	0.24 (0.17)	0.18 (0.12)	0.24 (0.13)	0.12 (0.17)	0.22(0.12)	0.19 (0.12)	0.20 (0.11)	0.19 (0.12)
Mean water (°C)	9.2 (0.4)	9.2 (0.04)	9.2 (0.4)	7.7 (0.02)	7.2 (0.02)	7.5 (0.02)	7.7 (0.02)	7.5 (0.02)	7.7 (0.02)
Canopy cover (%)	74.0 (4.0)	71.1 (4.9)	82.6 (3.5)	75.5 (4.0)	60.8 (4.9)	50.7 (5.7)	56.1 (5.3)	82.1 (2.4)	65.5 (4.8)
Deciduous proportion of total cover (%)	0.90 (0.04)	0.34 (0.06)	0.84 (0.05)	0.91 (0.04)	0.18 (0.04)	0.51 (0.7)	0.25 (0.06)	0.18 (0.04)	0.26 (0.06)
Shrub cover (%)	51.5 (6.2)	38.1 (5.1)	47.6 (7.4)	64.5 (7.7)	46.5 (5.1)	58.9 (6.7)	23.3 (5.3)	17.1 (3.2)	25.0 (4.2)
Canopy composition ^b	A > M > C	H > M > C	A > M > H	A > M > F	F > A > C	A > H > F	H > S > A	H > S > A	H > A > S
Shrub composition ^c	SF > SB > VM	SF > SB > VM	SB > SF > VM	VM > SF > SB	SF > SB > SC	SB > VM≡SF	HB > SF > FA	HB > SF > FA	SF ≡ HB > FA

Note: Numbers in parentheses indicate ± standard error of the mean.

^aActive channel width.

^bDominant species in order of abundance based on quantified vegetation composition of trees of stems within 25 m of active channel margins: A, alder; C, cedar; F, fir; H, hemlock; M, maple; S, spruce.

^cDominant species in order of abundance based on quantified vegetation composition of understory shrubs within 20 m of active channel margins: FA, false azalea; HB, huckleberry; SB, salmonberry; SC, stink currant; SF, swordfern; VM, vine maple.

and measured to the nearest 0.5 mm using an eyepiece micrometer. Based on residence during larval stage, invertebrates were categorized as terrestrially derived or aquatically derived (Wipfli 1997). Macroinvertebrate biomass was estimated with published taxon-specific length–mass regression equations (Sample et al. 1993; Hodar 1996; Benke et al. 1999).

Benthic invertebrate biomass estimates from Surber samples (dry mass $\text{mg}\cdot\text{m}^{-2}$) were combined to obtain the mean for all samples in a study section by sample period. Allochthonous invertebrate biomass estimates from pan-trap samples (dry mass $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) were also combined to obtain the mean for all samples in a study section by sample period. Drift biomass (dry mass $\text{mg}\cdot\text{m}^{-3}$) was calculated by dividing the weighed dry mass of invertebrates captured per net by the estimated water volume moving through each net during the sample period. Drift rate (dry mass $\text{mg}\cdot\text{h}^{-1}$) for each study section in a sample period was estimated by multiplying the total upstream and downstream net biomass estimates (dry mass $\text{mg}\cdot\text{m}^{-3}$) by water volume filtered ($\text{m}^{-3}\cdot\text{h}^{-1}$) and combining rates for each to obtain the mean (Kawaguchi and Nakano 2001). Although concentration of invertebrate biomass per volume of water (or density) is commonly used to estimate invertebrate availability in the drift, we view drift rate (or abundance) as a more appropriate assessment of prey availability.

Coastal cutthroat trout diet

Coastal cutthroat trout were collected during each study period to sample stomach contents. Fish were collected 24 h following habitat assessment to reduce effects of disturbance associated with instream invertebrate sampling and to allow coastal cutthroat trout to return to natural foraging behavior. A variable waveform backpack electrofishing unit (Model 12, Smith-Root Inc., Vancouver, Washington) was used to capture coastal cutthroat trout. Electrofishing occurred between 10:00 and 16:00 to include stomach contents of prey from aquatic and terrestrial sources. Collection proceeded upstream until 20 coastal cutthroat trout (≥ 80 mm total length) were captured in each study section. Fish were placed in 20-L buckets of water and anesthetized with a solution of water and clove oil (Keene et al. 1998).

Stomach contents were removed by a flushing procedure using a narrow pipetted water bottle, strained into paper coffee filters, and placed into small plastic bags filled with 95% ethanol alcohol (Meehan and Miller 1978). Time and location of capture, as well as total length (to the nearest 1 mm) and weight (to the nearest 0.1 g) were recorded for each fish. All fish were returned to their original capture location when fully recovered.

In the lab, organisms were identified, origins were categorized (aquatic or terrestrial), and individuals were measured for estimating biomass, as described above. Lengths of partially digested prey were estimated from intact individuals of the same taxon that appeared to be similar in size (Wipfli 1997). Biomass of invertebrates ingested by individual fish was combined to obtain the mean for each study section and season.

Statistical analysis

Although the experimental design of this study included three discrete categories of riparian vegetation types that

were replicated on each of three streams and assessed four times throughout the year, natural variation in site-level vegetation distribution confounded classical analysis of variance (ANOVA) of vegetation effects with this design. Great care was taken to identify comparable streams with distinctly coniferous and deciduous reaches, but vegetation surveys revealed that sites were represented by a continuum, rather than by discrete, classes of plant cover. These gradients in riparian vegetation were used to examine patterns of prey availability and fish diet using Pearson's correlation coefficients. Pearson's correlation coefficients were also calculated to identify significant associations between invertebrate biomass (benthos, drift, and allochthonous) and abiotic variables (stream discharge and air temperature) in each stream. A randomized-block design ANOVA was used to access statistical differences in prey availability and fish diet by season, where seasons were treatments and streams were blocked. An α value of 0.05 was used for statistical significance for all tests.

Results

Riparian habitat survey

Overstory trees along stream margins consisted primarily of red alder, big-leaf maple, Douglas fir, western red cedar, western hemlock, and Sitka spruce. Douglas fir and red alder were common at most sites; however, sites at North Fork Ecola Creek were dominated by western hemlock, and Sitka spruce and red alder were sparse. Deciduous trees were $\geq 80\%$ of the proportion of overstory vegetation in deciduous and mixed sections at Camp Creek and the deciduous section at Tucca Creek; however, deciduous vegetation at North Fork Ecola sites was less abundant (Table 1). Although conifer sites in all streams contained some deciduous vegetation, the proportion of deciduous vegetation at conifer sites was lower (0.18–0.34) than at deciduous or mixed sites (Table 1).

Sword fern (*Plystichum munitum*) was abundant at all sites. Salmonberry (*Rubus spectabilis*) and vine maple (*Acer circinatum*) were common among sites at Camp Creek and Tucca Creek, but huckleberry (*Vaccinium* sp.) and false azalea (*Menziesia ferruginea*) were more abundant in North Fork Ecola Creek. Overall, shrub cover over the stream varied from 17% to 65%. Conifer sites contained lower percentages of shrub cover than deciduous and mixed sites in all streams (Table 1). Percentage of shrub cover was positively correlated with proportion deciduous vegetation ($r = 0.74$, $p < 0.02$; Table 2), but there was no strong relationship with percentage of canopy cover ($r = -0.07$, $p < 0.85$).

Invertebrate prey availability

Shrub cover, and to a lesser extent, deciduous cover, were associated with prey availability. When all sites and sample periods were combined, there was a statistically significant relationship between benthic invertebrate biomass and the percentage of shrub cover ($r = 0.69$, $p = 0.04$; Table 2). Similarly, total drifting invertebrate biomass was positively correlated to proportion deciduous cover ($r = 0.69$, $p = 0.04$; Table 2) and shrub cover ($r = 0.79$, $p = 0.01$; Table 2). Although drifting aquatic invertebrate biomass was positively related with proportion deciduous cover ($r = 0.70$, $p = 0.04$; Table 2) and shrub cover ($r = 0.81$, $p = 0.01$; Table 2), rela-

Table 2. Pearson's correlation coefficients for the effect of vegetation on invertebrate prey categories (benthic, drift, and allochthonous) and diet of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream study sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek in the Oregon Coast Range.

Response variables	Proportion deciduous cover	Canopy cover (%)	Shrub cover (%)
Proportion deciduous cover	—	0.40 (0.29)	0.74 (0.02)
Benthic (dry mass $\text{mg}\cdot\text{m}^{-2}$)	0.08 (0.84)	-0.44 (0.23)	0.69 (0.04)
Aquatic invertebrate drift (dry mass $\text{mg}\cdot\text{h}^{-1}$)	0.70 (0.04)	0.26 (0.51)	0.81 (0.01)
Terrestrial invertebrate drift (dry mass $\text{mg}\cdot\text{h}^{-1}$)	0.07 (0.85)	-0.15 (0.69)	0.22 (0.58)
Total invertebrate drift (dry mass $\text{mg}\cdot\text{h}^{-1}$)	0.69 (0.04)	0.26 (0.50)	0.79 (0.01)
Aquatic invertebrate pan (dry mass $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	0.53 (0.15)	-0.19 (0.62)	0.47 (0.20)
Terrestrial invertebrate pan (dry mass $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	0.59 (0.09)	0.31 (0.42)	0.53 (0.14)
Total invertebrate pan (dry mass $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	0.88 (<0.01)	0.03 (0.94)	0.81 (0.01)
Aquatic invertebrates ingested (dry mass $\text{mg}\cdot\text{fish}^{-1}$)	0.48 (0.20)	-0.12 (0.77)	0.70 (0.04)
Terrestrial invertebrates ingested (dry mass $\text{mg}\cdot\text{fish}^{-1}$)	0.53 (0.14)	0.64 (0.06)	0.05 (0.90)
Total invertebrates ingested (dry mass $\text{mg}\cdot\text{fish}^{-1}$)	0.49 (0.19)	0.33 (0.39)	0.37 (0.33)

Note: Numbers in parentheses indicate p values.

tionships between drifting terrestrial invertebrate biomass and vegetation were not statistically significant (Table 2).

Stream discharge appeared to be influential in regulating seasonal fluxes of benthic invertebrate biomass. Seasonal patterns of benthic invertebrate biomass were negatively related to stream discharge in Camp Creek ($r = -0.83$, $p = 0.01$), Tucca Creek ($r = -0.69$, $p = 0.02$), and NF Ecola Creek ($r = -0.64$, $p = 0.03$). Benthic invertebrate biomass was lowest during the winter when stream discharge was highest (Fig. 2). Conversely, benthic invertebrate biomass estimates were greatest during low summer and fall base flows. Differences in benthic invertebrate biomass among seasons were statistically significant ($p < 0.01$; Fig. 2; Table 3).

Both aquatic and terrestrial invertebrates were abundant in the drift, but aquatic invertebrate biomass was greater than terrestrial invertebrate drift biomass in all seasons (Fig. 3). Aquatic invertebrate biomass in the drift ranged from $9 \text{ mg}\cdot\text{h}^{-1}$ in the fall to $215 \text{ mg}\cdot\text{h}^{-1}$ in the winter (Fig. 3), and drifting terrestrial invertebrates declined from high summer levels ($17 \text{ mg}\cdot\text{h}^{-1}$) to a low in winter ($3 \text{ mg}\cdot\text{h}^{-1}$), and then increasing in spring to levels that were similar to the previous summer (Fig. 3). Differences among seasons in drifting invertebrate biomass (both aquatic and terrestrial sources) were statistically significant ($p < 0.05$; Table 3). Seasonal patterns of drifting invertebrate biomass were positively related to stream discharge at Camp Creek ($r = 0.71$, $p < 0.01$) and Tucca Creek ($r = 0.72$, $p < 0.01$), but correlation was not statistically significant in North Fork Ecola Creek ($r = 0.44$, $p > 0.15$). Annual maximum drift biomass rates during winter samples were associated with elevated winter base discharge, and minimum drift biomass rates in fall were related to annual discharge minima.

Differences in allochthonous invertebrate biomass input to pan traps at the conifer-dominated sites ($45 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) varied substantially compared with deciduous and mixed riparian sites (64 and $61 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, respectively). Only total allochthonous invertebrate biomass (i.e., not aquatic or terrestrial components separately) was correlated with percentage of shrub cover ($r = 0.81$, $p = 0.01$; Table 2) and the proportion of deciduous canopy cover ($r = 0.88$, $p < 0.01$;

Fig. 2. Seasonal changes in mean biomass of benthic invertebrates in stream sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek in the Oregon Coast Range. Error bars represent ± 1 standard error of the mean.

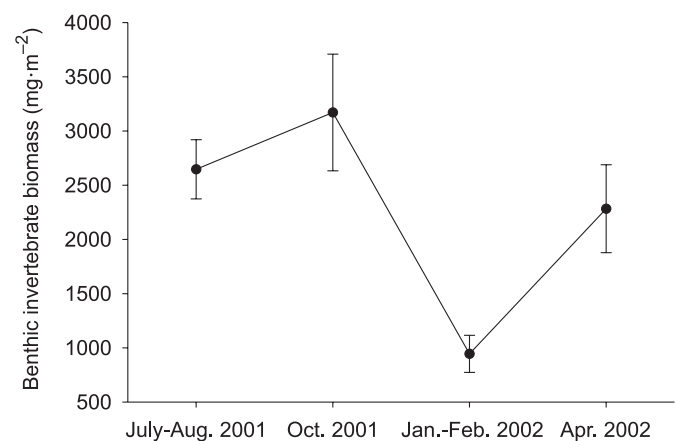


Table 2). Allochthonous invertebrates also varied widely among seasons, declining from a peak in summer to lows in winter and spring (Fig. 4); differences among seasons were statistically significant for aquatic and total invertebrate biomass ($p < 0.05$; Table 3), but terrestrial invertebrate biomass was not statistically significant ($p = 0.08$; Table 3). Invertebrate biomass collected in pan traps was positively correlated with air temperature in Camp Creek ($r = 0.85$, $p = 0.01$) and Tucca Creek ($r = 0.80$, $p = 0.01$), but the relationship was not statistically significant in North Fork Ecola Creek ($r = 0.55$, $p = 0.06$).

Coastal cutthroat trout diet

Coastal cutthroat trout 80–220 mm total length ($n = 667$) ingested a diverse variety of prey that included 70 families in 27 orders (Romero 2004). Aquatic invertebrates were the most common prey ingested, collectively accounting for 56% of total identifiable invertebrate mass ingested. Terrestrially derived invertebrates composed only 35% of the diet by mass.

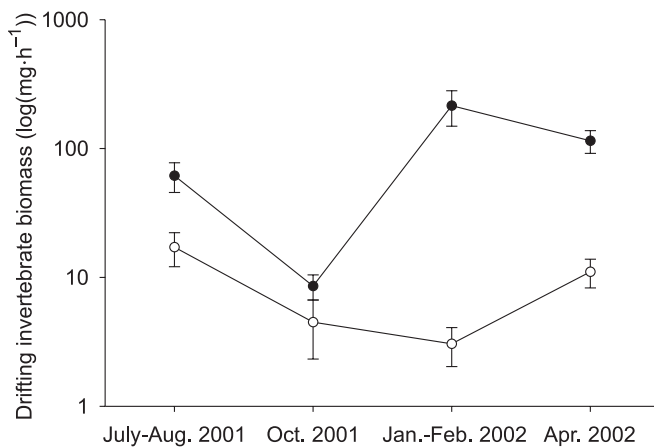
Table 3. Randomized-block analysis of variance and Tukey–Kramer multiple means comparisons for the effect of season on invertebrate prey categories (benthic, drift, and allochthonous) and diet of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream study sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek in the Oregon Coast Range.

Response variables	Summer	Fall	Winter	Spring	F statistic ^a	p value	Group comparison ^b
Benthic	2651	3170	945	2283	9.32	<0.01	Su, F > W
Aquatic drift	62	9	215	115	31.94	<0.01	Su, W, Sp > F; W > Su
Terrestrial drift	17	5	3	11	7.28	0.02	Su > F, W
Total drift	80	13	227	133	26	<0.01	Su, W, Sp > F
Aquatic pan	65	29	7	9	9.98	<0.01	Su > W, Sp
Terrestrial pan	49	32	7	11	3.76	0.08	No difference
Total pan	124	64	15	20	7.93	0.02	Su > W, Sp
Aquatic fish diet	8	5	8	22	13.53	<0.01	Sp > Su, F, W
Terrestrial fish diet	9	10	1	8	7.6	0.02	Su, F, Sp > W
Total fish diet	17	15	10	32	8.78	<0.01	Sp > F, W

^aAnalysis of variance (ANOVA) test based on log-transformed data.

^bTukey–Kramer multiple means comparison among seasons: Su, summer; F, fall; W, winter; Sp, spring.

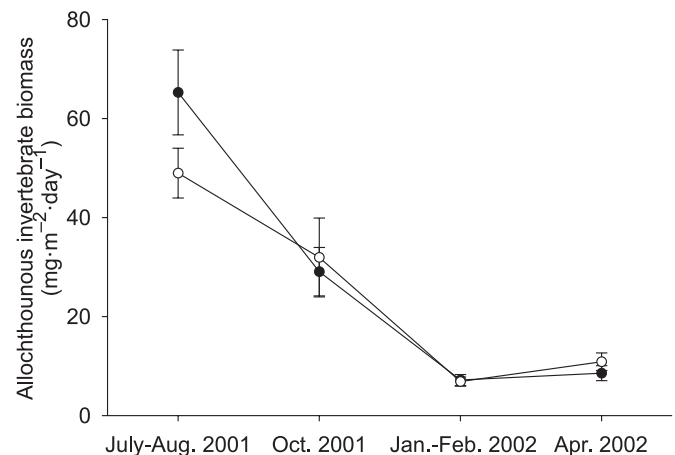
Fig. 3. Seasonal changes in mean drifting invertebrate biomass of (a) aquatic invertebrates (solid circles) and (b) terrestrial invertebrates (open circles) captured in stream sections in stream sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek in the Oregon Coast Range. Error bars represent ± 1 standard error of the mean. Note logarithmic scale.



Aquatic invertebrate mass ingested was positively related to shrub cover ($r = 0.70$, $p = 0.04$; Table 2). Mass of terrestrial invertebrate ingested exhibited a strong relationship with percentage of canopy cover, but the relationship was not statistically significant ($r = 0.64$, $p = 0.06$). Interestingly, the total mass ingested (i.e., aquatic, terrestrial, and unknown sources) was positively related to terrestrial allochthonous invertebrate inputs to pan traps ($r = 0.67$, $p = 0.05$).

Seasonal differences in prey mass ingested by coastal cutthroat trout were statistically significant ($p < 0.05$; Table 3). Invertebrate prey mass of aquatic and terrestrial origin were similar during the summer, but in the fall, terrestrial prey increased and aquatic prey decreased slightly (Fig. 5). In the winter, total ingested prey mass declined to almost half of summer and fall levels, primarily as a result decline of terrestrial prey consumed ($< 1 \text{ mg·fish}^{-1}$). In the spring, terrestrial prey returned to levels similar to the previous summer and fall, but aquatic invertebrate prey mass reached a maxi-

Fig. 4. Seasonal changes in mean biomass of (a) aquatic invertebrates (solid circles) and (b) terrestrial invertebrates (open circles) captured in allochthonous pan traps in stream sections in stream sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek in the Oregon Coast Range. Error bars represent ± 1 standard error of the mean.

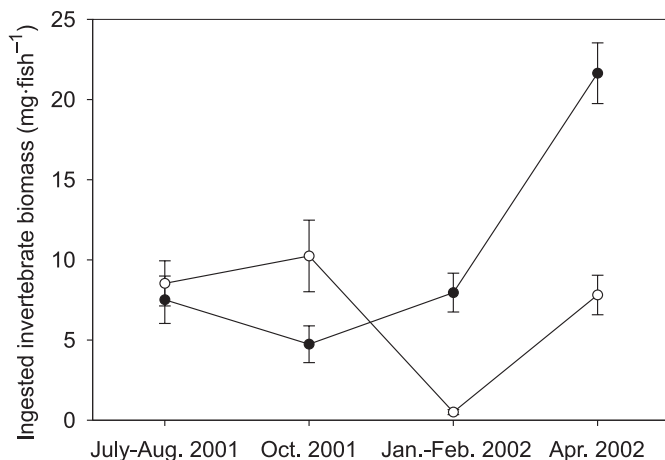


mum (32 mg·fish^{-1}) that was more than twice previously observed levels (Fig. 5).

Discussion

This study examines the influences of riparian plant communities on aquatic food webs in forested headwater streams and explores how these relationships change with season. Although we tried to examine isolated riparian treatment effects, it was difficult to locate similar riparian conditions for all replicate sites. Riparian vegetation in the Oregon Coast Range typically exhibit a mix of deciduous and coniferous trees directly influenced by local disturbance history, and therefore, analyses that reflect the gradient of riparian vegetation along headwater streams are probably more realistic. Detecting vegetation effects in prey availability and diet could have been confounded by high variation in deciduous vegetation among sites, but correlation analyses of riparian vegetation and mean invertebrate availability and fish diet

Fig. 5. Seasonal changes in mean biomass of (a) aquatic (solid circles) and (b) terrestrial invertebrate (open circles) prey ingested by 80- to 220-mm total length coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream sections of Camp Creek, Tucca Creek, and North Fork Ecola Creek in the Oregon Coast Range. Error bars represent ± 1 standard error of the mean.



summarized by site revealed statistically significant relationships with site-specific vegetation.

At the nine riparian sites in this study, shrub cover and deciduous cover were positively related. Benthic invertebrate biomass, allochthonous invertebrate inputs, aquatic and total invertebrate drift, and aquatic prey ingested by cutthroat trout were greater where shrub cover was more abundant. However only aquatic and total invertebrate drift, as well as allochthonous invertebrate inputs, were greater where deciduous vegetation was more abundant. In North Fork Ecola Creek, where both deciduous vegetation and shrub cover were least abundant, all responses were lower. Whereas shrub cover affect localized prey availability, including instream benthos and diet, deciduous canopy may have a more spatially diffuse influence on allochthonous sources and drifting prey. Because these prey sources are mobile, localized responses by fish are more difficult to detect.

Our results are concordant with previous studies (e.g., Wipfli 1997; Allan et al. 2003) that suggest riparian vegetation influences the input of terrestrial invertebrates to streams. Allochthonous invertebrate biomass was approximately 30% higher at deciduous and mixed riparian sites than at sites dominated by conifers. Although input of terrestrial invertebrates sometimes differs considerably among deciduous tree species (Mason and MacDonald 1982), deciduous trees support higher invertebrate mass per stem than conifers (Southwood 1961; Allan et al. 2003). Less dense and less complex understories associated with conifer stands >50 years old, similar to those in this study, would therefore be expected to contribute lower invertebrate biomass.

Our results suggest that the diet of coastal cutthroat trout is influenced by distinct temporal patterns of aquatic and terrestrial invertebrate availability. We found contributions of terrestrial and aquatic prey in the diet were equivalent in the summer, but in the winter and spring, fish ate twice the mass of aquatic prey. Few aquatic invertebrates were available in

autumnal drift, when fish consumed slightly more terrestrial prey. We used two methods for assessing terrestrial prey availability: pan traps for allochthonous infall and nets for drift. Pan-trap data for terrestrial inputs were similar and higher in summer and fall compared with that in the winter and spring. Drifting terrestrial organisms were noticeably higher in summer compared with other seasons, and elevated in the spring compared with the winter. Differences in these measures suggest that fish may efficiently crop allochthonous prey even before the invertebrates could be caught in drift nets.

Seasonal patterns in fish diet were exemplified with the greater consumption of aquatic prey in winter and spring when availability of drifting aquatic prey was over 10 times greater than terrestrial drift. Although cutthroat trout appeared to be feeding opportunistically in the winter and spring, contrasts between availability and diet in the summer and fall suggest fish may have been maximizing consumption of terrestrial prey. In the summer, aquatic drifting biomass was greater than terrestrial, and in pan traps, biomass from the two sources was equivalent; however, prey were consumed by fish in equal proportions from both sources. By the fall, availability was equivalent according to both allochthonous and drifting samples, and fish ate slightly more terrestrial prey. Because allochthonous input and total drift were greater where deciduous vegetation and shrub cover was more abundant, these seasonal patterns may have been more pronounced under deciduous canopy.

Wet winters, moderately wet springs, and dry summer and fall seasons characterize seasonal precipitation patterns of the Oregon Coast Range. Corresponding to episodic high flow events, benthic invertebrate biomass at all sites were lowest during the winter, varying inversely with seasonal changes in stream discharge. In contrast, drifting invertebrate biomass was positively associated with stream discharge. It is probable that as shear stress and bedload movement increases during high flow, many invertebrates become dislodged from the streambed (Scrimgeour and Winterbourn 1989; Angradi 1997), and either enter the drift (Brittain and Eikeland 1988) or are crushed (Scrimgeour and Winterbourn 1989). As discharge increases, easily dislodged detritus and accompanying organisms are quickly entrained, so that peaks of invertebrate drift and fine and coarse particulate matter coincide (O'Hop and Wallace 1983). In addition to affecting life-history adaptations, these turbulent conditions likely contribute to seasonal lows in winter benthic densities.

The influence of stream discharge on seasonal fluxes of drifting invertebrate availability draws attention to appropriate metrics for assessing food availability. Concentration of invertebrate biomass per volume of water is commonly used to estimate invertebrate availability in the drift; samples are standardized in relation to temporal and spatial differences in stream discharge. Our data suggest that invertebrate drift is temporally sensitive and fluxes are mediated by stream discharge. Because access to prey by fish is heavily influenced by the volume of food available during any specific period of time, we argue that abundance, and not density, is a more biologically meaningful measure of food availability among seasons. Controlling for the effects of stream discharge by standardizing drift samples with density estimates

may likely obscure biologically meaningful fluxes in prey availability to fish.

Temporal patterns of allochthonous invertebrate availability in Oregon coastal streams were similar to seasonal trends observed in other temperate regions (Mason and MacDonald 1982; Cloe and Garman 1996; Kawaguchi and Nakano 2001). We assume allochthonous inputs were tracking riparian vegetative production, temperature, and leaf phenology, as has been shown in northern Japan (Nakano and Murakami 2001) and New Zealand (Edwards and Huryn 1995). Although seasonal patterns in the Oregon Coast Range were similar to those of other regions of the world, biomass of terrestrial invertebrate input was much lower, ranging from $7 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ during the winter to $49 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ during the summer. Cloe and Garman (1996) reported $3 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in winter to $223 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in summer for streams in Virginia, USA. Likewise, terrestrial invertebrate input to Horonai Stream in northern Japan ranged from $0.5 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in the winter to $87 \text{ mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ in the summer (Kawaguchi and Nakano 2001). Although summer peak input was lowest in Oregon Coast streams, winter input was greater than comparable studies in other regions.

These comparisons, all based on pan traps, suggest that the terrestrial invertebrate subsidy can differ by at least a factor of two, depending on season and region. This terrestrial subsidy may be particularly important during late summer and early fall when aquatic invertebrate prey in the drift is low, despite high benthic biomass (Hunt 1975; Martin 1984). Low stream discharge, insufficient to induce catastrophic drift, likely influences both aquatic invertebrate availability and diet of cutthroat trout feeding in the water column.

The dependence of coastal cutthroat trout on terrestrial organisms for a substantial portion of their diet during the summer and fall may relate not only to high availability, but also to timing of the terrestrial prey supply. In our study, winged adult aquatic insects comprised approximately half of the biomass captured in pan traps, but their contribution to the diet was minimal. Nocturnal activity in adult aquatic invertebrates reduces their vulnerability to predation by foraging salmonids (Waters 1972; Allan 1978; Miyasaka and Nakano 2001). In contrast, terrestrial insects are generally larger than drifting benthic invertebrates, more active in daylight than adult aquatic insects, and more conspicuous in the drift during the day (Wilzbach et al. 1986; Edwards and Huryn 1996; Nakano et al. 1999). Thus greater visibility and accessibility during the daylight hours render terrestrial invertebrates more vulnerable prey to foraging fish.

During winter, the availability of drifting aquatic invertebrates was much greater than in the summer or fall, but fish did not respond by consuming more aquatic invertebrates. Four factors, operating alone and in combination, may have influenced this observation. First, high turbidity associated with chronic spates may have decreased foraging efficiency of coastal cutthroat trout because of reduced ability to detect prey when suspended sediments are elevated (Sigler et al. 1984; Redding et al. 1987; Barrett et al. 1992). Second, low winter water temperature sets a physiological limit to the rate of consumption, regardless of prey availability. The rate of digestion for salmonids declines at low water temperatures ($1\text{--}5^\circ\text{C}$) and increases at intermediate temperatures

($13\text{--}17^\circ\text{C}$) (Reimers 1963; Brett and Higgs 1970; Dwyer and Kramer 1975). Average water temperature at our sites ranged from 5 to 6°C in winter, and low metabolic levels at low water temperatures likely suppressed coastal cutthroat trout feeding.

Third, increased current velocity influences foraging success (Godin and Ranglely 1989; O'Brien and Showalter 1993) and reaction distance in stream-dwelling salmonids (Grant and Noakes 1986; Godin and Ranglely 1989; Hughes and Dill 1990). Fish sampled in the present study were much smaller ($8\text{--}23 \text{ cm}$) and likely held foraging positions where water velocity was lower. In winter, mean current velocities increased in riffle habitat to $0.52 \text{ m}\cdot\text{s}^{-1}$, and foraging success of small trout may have been depressed. Indeed, Heggenes et al. (1991) demonstrated that coastal cutthroat trout generally avoided habitat with water velocities $\geq 0.20 \text{ m}\cdot\text{s}^{-1}$, and avoidance was highest at water velocities $\geq 40 \text{ m}\cdot\text{s}^{-1}$. Conversely, during the summer and fall, coastal cutthroat trout may have been more efficient at detecting and capturing prey by holding optimal foraging positions when velocity was low and visibility was high. Finally, winter feeding rates of coastal cutthroat trout may have decreased with the shortened photoperiod and lower daytime light levels. In the Oregon Coast Range, daylight hours range from a peak of 15 h during the summer to a low of 8 h during the winter. Although we did not examine diel feeding patterns in this study, previous studies have shown that salmonids do not generally feed at night (Bisson 1978; Angradi and Griffith 1990; Young et al. 1997).

During the spring, mass of aquatic invertebrate prey in the diet reached a maximum that was nearly a threefold increase from winter levels. Declines in stream discharge and increases in water temperature and photoperiod were noted during the spring. These factors may have acted synergistically to increase metabolic activity and stimulate intensive feeding as trout emerged from annual lows of prey consumption during the winter. In southeastern Alaska streams, aquatic prey were particularly important for fish in the spring, and declined through the seasons (Wipfli 1997). Increasing algal growth, larger aquatic invertebrate instars, and increased trout activity from winter to spring occur as increasing water temperature stimulates intensive foraging effort by trout (Reimers 1963).

The response of coastal cutthroat trout to seasonal influences in food availability may have important implications for fitness. When aquatic invertebrates in the drift are low in summer and fall, terrestrial invertebrates are important to the diet during this period when trout are increasing fat reserves and body size to improve overwinter survival (Reimers 1963). Thus, the terrestrial prey subsidy may be necessary for coastal cutthroat trout survival during late summer and fall, as fish are stressed from lower aquatic prey availability, increased water temperature, and low flow conditions.

Because coastal cutthroat trout diet and prey availability were strongly related to shrub cover and somewhat less strongly linked with deciduous canopy, it appears that changes in these riparian components could have a domino effect on stream food webs. Although effects of systematic shrub removal may be more pronounced, harvesting deciduous trees could directly influence shrubs and indirectly affect allochthonous contributions to streams. Such changes

would likely be unintended consequences on food resources of coastal cutthroat trout and the productivity of aquatic food webs in forested headwater streams of the Pacific Northwest. However, we recognize that the trade-off between managing for deciduous versus managing for coniferous forest is complex. Good stewardship of coniferous riparian vegetation includes maintaining mature conifer riparian vegetation and retaining conifer-derived large woody debris to establish long-term channel structure, diversify fish habitat, and retain sediments. These values may outweigh the benefits of increased aquatic invertebrate production and allochthonous invertebrate input from deciduous canopies and streamside shrubs at some sites. Ultimately, total exclusion of either deciduous or coniferous vegetation would probably be undesirable. We suggest spatially and temporally varying mixtures of vegetation may provide the most appropriate conditions for persistence of coastal cutthroat trout in headwater streams.

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