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Patterns of Diversity, Density, and Biomass of Ectothermic Vertebrates in Ten Small Streams Along a North American River Continuum

Abstract

We sampled density, diversity, and biomass of fish and amphibians to test the hypothesis that vertebrate diversity in low- (second- and third-) order, low-elevation streams flowing into large, higher-order streams or rivers is greater than that in low-order headwater streams flowing into streams of the same order or one order higher . Also tested was the hypothesis that vertebrate biomass and density among streams were related to elevation, stream gradient, and drainage basin area. In ten second-order and third-order streams (2.2 to 5.0 m wetted width in summer) in the Pacific Northwest, USA, vertebrate diversity increased with decreasing elevation. Elevation and stream gradient accounted for 86% of the variation among streams in vertebrate diversity. In contrast, elevation, stream gradient or drainage basin area were not significantly related to either vertebrate density or biomass. The observed pattern of progressively greater vertebrate diversity downstream from the headwaters was consistent with the river continuum concept, but the concept must be modified slightly to account for the diversity in low-elevation, low-order streams being higher than in low-order headwater streams. From a management perspective, since similarly-sized low-order streams do not have the same species assemblages, it is necessary to protect small streams through a range of elevations if the full complement of species is to be protected.

Introduction

River systems have been conceptualized as a continuum of abiotic and biotic conditions in an understandable pattern from high-elevation, low-order tributaries to low-elevation, high-order rivers (Vannote et al. 1980). The usefulness and predictive value of the river continuum concept have been considered or tested in various studies (e.g., Minshall et al. 1985; Statzner and Higler 1985; Sedell et al. 1989). Studies have shown, however, that specific conditions in individual rivers and drainage basins can influence the results expected under the river continuum concept (Johnson et al. 1995). For example, in general accordance with the concept, as small, low-order streams converge and give rise to larger, higher-order streams and rivers, additional vertebrate species are typically added to the biota (Horwitz 1978; Platts 1979; Barila et al. 1981). The presence of tributary junctions, however, or the confluence of two segments of different characteristics (i.e., low-order stream meets higher-order stream or river) can influence expected results. Biotic and abiotic conditions at tributary junctions are diverse, and aquatic vertebrate species that are primarily found in larger, high-order rivers may also be found in smaller, low-order tributaries (Olmsted and Cloutman 1974; Platts and Partridge 1978; Frissell et al. 1993). We may thus expect greater vertebrate diversity in first to third order streams that drain into large rivers several orders higher, than in ones that drain into streams of at most only the next higher order. The former streams are also at lower elevation than the latter streams, and may be warmer, so that elevation, water temperature, gradient, and other factors may also influence the observed pattern. This pattern of greater diversity in the lower elevation streams of a given order was reported for the Vermillion River, Illinois (USA) by Osborne and Wiley (1992). They concluded that the larger rivers provided a source of species richness to the small streams through immigration. The inherent, observed higher vertebrate diversity in warmer waters (Li et al. 1987), to which more species are adapted, undoubtedly also plays a role in greater diversity in low-elevation, low-order streams.

Vertebrate density and biomass (standing crop) may often vary in the same pattern as species diversity (i.e., increase downstream). Density and biomass are determined by allochthonous inputs (Vannote et al. 1980) and a wide variety of biotic and abiotic factors (Binns and Eiserman 1979).

Among more readily measured habitat features, elevation, stream gradient and drainage basin area have been successfully related to diversity, density and biomass. Platts (1976) reported that higher fish densities and standing crops were associated with lower elevation streams in the Salmon River drainage, Idaho (USA). Scarnecchia and Bergersen (1987) found that elevation explained significant variation ($P<0.01$) in biomass and production of salmonids in small streams in Colorado (USA). Lower elevation streams, even small ones, had longer growing seasons and higher fish production. Beecher et al. (1988) reported that the number of fish species collected at sites in Washington state was significantly ($P<0.01$) higher with low elevation, low gradient, and large drainage basin area.

Because low-order streams often are shallow during periods of low flow in summer, many vertebrates in small streams are forced into deeper pool habitats (Roper et al. 1994; Schlosser 1991). As a result, summer evaluation of populations of ectothermic vertebrate in pools may reveal patterns of vertebrate diversity, density, and biomass among small streams.

In this paper we describe patterns of ectothermic vertebrate diversity, density, and biomass in pools of ten second- and third-order streams (2.2 to 5.0 m wetted width in summer) at differing elevations within a large forested basin in southwestern Oregon, USA. One objective is to test the hypothesis that the diversity of ectothermic vertebrates in low (second and third) order, low-elevation streams flowing into large, higher order streams is greater than in low-order headwater streams flowing into steams of the same or one higher order. We also evaluate if the biomass and density of ectothermic vertebrates in the ten streams are significantly related to elevation, gradient, and drainage basin area.

Study Area

The upper South Umpqua River is a sixth-order river located in southwestern Oregon, USA (Figure 1). Elevations within the upper river basin range from 240 m to over 2200 m. Average annual rainfall is 94 cm as monitored at the United States Forest Service (USFS) Ranger Station near Tiller (elevation 330 m). More than two-thirds (68%) of the annual precipitation occurs from October to March (Unpublished data, U. S. Forest Service, Tiller, Oregon). Because differences in the chemical makeup of streams can significantly influence stream biomass (Scarnecchia and Bergersen 1987) it was important to determine the range of several chemical components within small streams of the basin. Streams within the basin showed little variability in their chemical constitution. Within six diverse streams (third- and fourth-order) located throughout the South Umpqua basin, the alkalinity (as $CaCO_3$) varied from 19 to 58 mg/l, ammonia and orthophosphate were consistently less than 0.02 mg/l, and pH ranged from 7.3 to 7.8 (B. Roper, unpublished data).

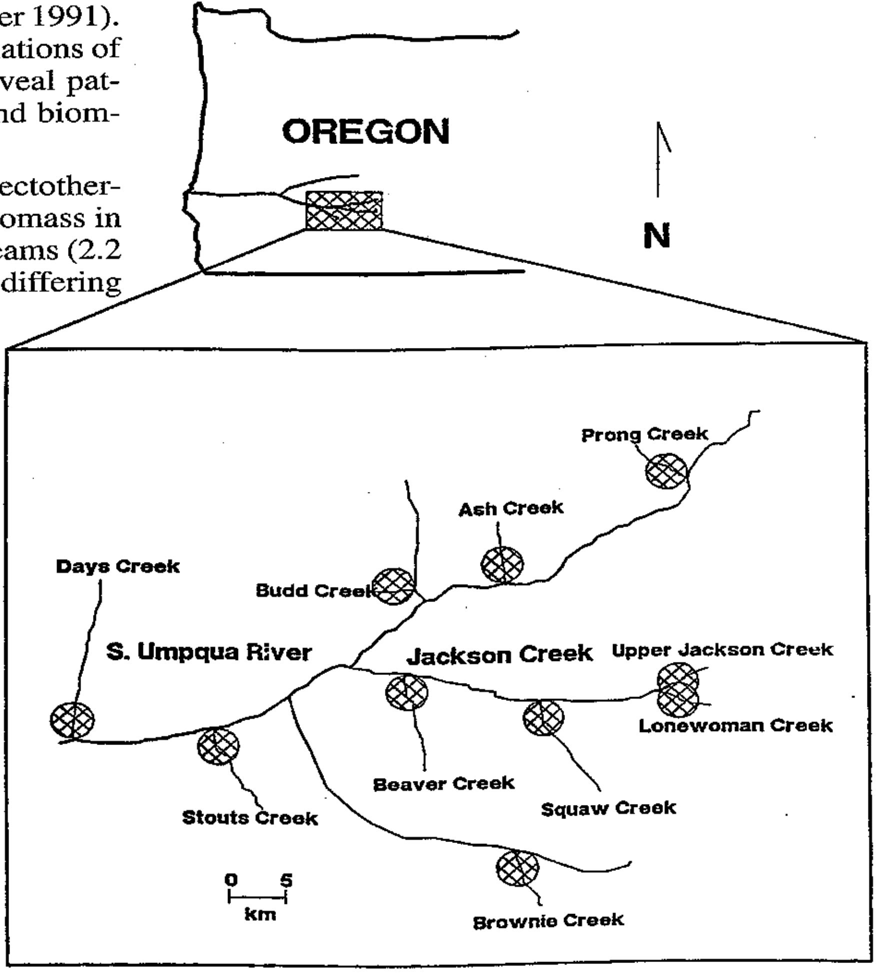

Figure 1. The ten low-order streams sampled within the upper South Umpqua Basin, USA.

Vegetation surrounding the 10 study streams was historically dominated by late succession conifers, with maples (*Acer* spp.) and red alder (*Alnus rubra*) dominating the understory riparian vegetation. Only one of the streams surveyed is currently in a pristine state (federally designated wilderness area). Timber has been harvested from 10% to 60% of the remaining nine basins. In addition, one basin is predominantly agricultural land in the flood plain and timbered slopes at higher elevations. All sampled stream segments were buffered from direct solar radiation by riparian vegetation.

The number of vertebrate species in the South Umpqua River is high for a west coast (USA) watershed, but low compared to many other regions of the USA (Snyder 1908). Fishes include chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead (*O. mykiss*), cutthroat trout (*O. clarki*), speckled dace (*Rhinichthys osculus*), Umpqua dace (*R. evermanni*), redside shiner (*Richardsonius balteatus*), Pacific lamprey (*Lampetra tridentata* and *L. richardsoni*), prickly sculpin (*Cottus asper*), Umpqua chub (*Oregonichthys kalawatseti*), smallmouth bass (*Micropterus dolomieui*), bluegill (*Lepomis macrochirus*), Umpqua pikeminnow (*Ptychocheilus umpquae*), and large-scale sucker (*Catostomus macrocheilus*). Amphibians include the Pacific giant salamanders (*Dicamptodon tenebrosus*), rough-skinned newt (*Taricha granulosa*) and tailed frogs (*Ascaphus truei*). Not all of these species were found in our study streams, however.

Methods

During the period 15 July to 10 August 1993, the ten small streams (Table 1) were sampled for vertebrates using electrofishing. To quantify biota associated with tributary junctions, sampling commenced 50 m upstream from a stream's confluence with another stream or river. We then used a randomly generated number between one and three to determine whether the first, second, or third pool encountered upstream was to be sampled. After this first pool was randomly selected, every third pool was sampled systematically until three or four pools had been sampled. Only pool habitat was sampled, and each pool was treated as a unit of observation. Pools were sampled because they were a more stable habitat type than riffles or runs and were hypothesized to provide refugia for a variety of species in both larger, higher-order streams and smaller, lower-order streams. In addition, pool habitats were the only habitats with depths >0.2 m during the sampling season. All sampled pools were block-netted at the downstream and upstream boundaries. Pool area sampled was calculated as the length (distance between the upper and lower block nets) times the width (mean of widths at one meter intervals between the two block nets)

TABLE 1. Basin characteristics of the ten small streams surveyed for vertebrate biomass. Stream order indicates order of stream at its outlet, followed by order of stream into which it flows. (Source: Umpqua National Forest)

Stream	Elevation (m)	Gradient (%)	Basin Area (ha)	Order (Out— into)	Width (m)
Jackson	866	5.3	1,578	3-4	4.96
Lonewoman	866	4.1	1,966	3-4	4.10
Prong	817	2.8	2,679	3-4	4.69
Squaw	509	3.9	5,850	3-4	5.02
Ash	470	5.9	2,293	3-4	3.86
Budd	457	5.1	384	2-3	2.18
Brownie	439	3.1	607	2-3	2.83
Beaver	396	1.9	9,088	3-4	4.15
Stouts	266	1.7	6,070	3-5	4.97
Days	249	1.0	14,731	3-5	4.30

Each pool was electrofished intensively with three independent passes. One pass consisted of electrofishing from the downstream block-net to the upstream block-net, then back to the downstream block-net. All vertebrates stunned during each pass were collected, identified, measured to the nearest mm (fork length for fishes, total length for salamanders and newts, and snout to vent length for tailed frogs), and weighed to the nearest 0.1 g (wet weight). Analysis was conducted at the species level except for steelhead, which were divided into two age classes, age-0 and age-1 (and older) fish. Age classes of steelhead were determined from length-frequency histograms plotted independently for each stream.

Vertebrate diversities among streams were compared using the Shannon diversity index (Shannon and Weaver 1949);

$$H' = \sum_{i=1}^{n} p_i \log_2 p_i$$

where p_i is estimated from n_i/N (N is the total number of individuals and n_i is the number of individuals from the ith species). A larger H' indicated greater species diversity (Zar 1984).

Population estimates, by species, for each pool were calculated using maximum likelihood methods described by Van Deventer and Platts (1985). Biomass per pool was then estimated by multiplying the average weight of a species sampled in that stream by the estimated number of that species in each pool, expressed as number or biomass per m^2 of pool area.

Comparisons of densities and biomass (per m^2) among streams were made using analysis of variance methods. Analyses compared densities and biomass of individual species and the total catch. Analysis at the species level was conducted only with species captured in at least four of the ten streams. The relationships between elevation, stream gradient, drainage basin area and vertebrate diversity, density and biomass (per m^2) were investigated with simple linear regression and stepwise multiple regression methods . Principal component analysis was used to characterize species associations with the basin. The dominant and subdominant components were determined using varimax rotation on normalized vertebrate density data from the ten streams. Factor loading plots of the species found in at least four streams were employed to determine possible species groupings within the basin.

Results

Twelve different vertebrate species were captured in the ten streams (Table 2). Days Creek and Stouts Creek, the two streams lowest in elevation, had the most species (8), and Beaver Creek and Brownie Creek, the two streams next lowest in elevation each had seven species. Only one species, steelhead, was found in all ten of the streams. Six species: speckled dace, Umpqua dace, Umpqua pikeminnow, Pacific lamprey, redside shiner, and rough-skinned newt were found only in the lower-elevation streams (<439 m). Captures of the other species were scattered throughout the basin. Vertebrate diversity ranged from high of 2.36 in Days Creek, the lowermost stream, to a low of 1.32 in Lonewoman Creek, the uppermost stream.

Vertebrate diversity was significantly ($P<0.05$) higher in streams at lower elevation ($r^2=0.67$, $H'=2.42-0.00113\cdot\text{Elevation}$; Figure 2), lower gradient ($r^2=0.62$, $H'=2.36-0.1553\cdot\text{Gradient}$), and in larger drainage basins ($r^2=0.48$, $H'=1.59+0.0000497\cdot\text{Area}$). The strongest linear relationship was between elevation and vertebrate diversity; higher elevation streams were inhabited by fewer vertebrate species, resulting in lower species diversity (Figure 2). Elevation and gradient combined to explain 86% of the variation in vertebrate diversity among the ten streams ($H'=2.58-0.00078\cdot\text{Elevation}-0.09957\cdot\text{Gradient}$, $P<0.0001$). In both

TABLE 2. Species captured electrofishing ten streams of the South Umpqua Basin during the summer of 1993 (Co: coho salmon; Cu: cutthroat trout; S0: age-0 steelhead; S1: age-1 (and older) steelhead; Sc: sculpin; Sh: redside shiners; Sq: Umpqua pikeminnow; SD: speckled dace; UD: Umpqua dace; La: juvenile lampreys; GS: Pacific giant salamanders; TF: tailed frogs; and RS: rough-skinned newts). An X indicates a species' presence and a dash (–) its absence. Streams are listed top to bottom from highest to lowest elevation.

	Species												
Stream	Co	Cu	S0	S1	Sc	Sh	Sq	SD	UD	La	GS	TF	RS
Jackson	–	X	X	X	X	–	–	–	–	–	X	–	–
Lonewoman	–	X	–	X	X	–	–	–	–	–	X	–	–
Prong	–	–	X	X	–	–	–	–	–	–	X	X	-
Squaw	–	–	X	X	X	–	–	–	–	-	X	–	–
Ash	–	X	X	X	X	–	–	–	–	–	X	–	–
Budd	X	X	X	X	–	–	–	-	–	-	X	–	–
Brownie	X	X	X	X	X	–	–	X	–	X	X	–	–
Beaver	X	–	X	X	X	–	–	X	X	X	X	–	–
Stouts	X	–	X	–	X	X	–	X	X	X	–	–	X
Days	X	–	X	-	X	X	X	X	X	X	–	–	

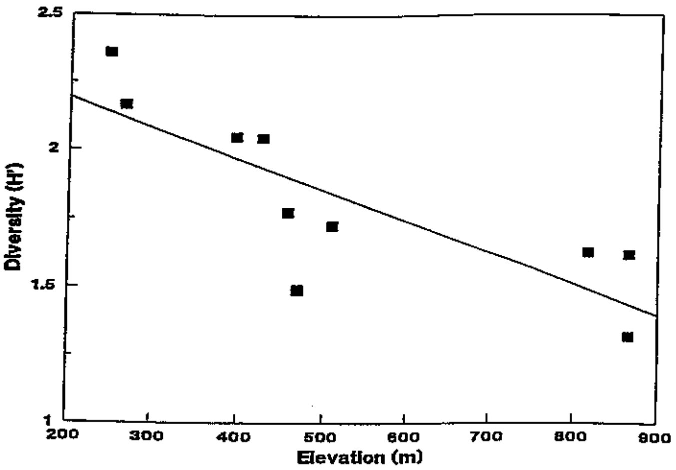

Figure 2. The relationship between stream elevation and vertebrate diversity. (r^2=0.67; P<0.05;H'=2.42–0.00113·Elevation).

cases, lower elevations and lower gradients were associated with higher vertebrate diversity.

Neither individual densities nor total aggregate densities were significantly related to elevation, gradient or basin area (P>0.05). Total densities of vertebrates, which exhibited a small coefficient of variation (30%) among the ten streams, did not differ significantly among the ten streams (P=0.217). Densities ranged from 2.25 vertebrates per m^2 in Squaw Creek to 0.93 per m^2 in Stouts Creek (Table 3). Densities of six of the seven species found in at least four streams did, however, differ significantly (P<0.05) among streams. Pacific lamprey (ammocoetes) was the only species for which density did not differ among streams. Thus, although the total number of vertebrates per m^2 was consistent among streams,

TABLE 3. Density (number per m^2) and biomass (grams per m^2) of vertebrates captured in at least four streams: Co: coho; Cu: cutthroat; S0: age-0 steelhead; S1: age-1 (and older) steelhead; Sc: sculpin; SD: speckled dace; La: lamprey; GS: Pacific giant salamanders; and Tot:total density of all 12 species sampled (including ones not in this table). An asterisk (*) indicates that densities differed among streams (P<0.05) and an inverted V (^) indicates biomass differed among streams (P<0.05). Streams are listed top to bottom from highest to lowest elevation.

	Species								
Stream	Co*^	Cu*^	S0*^	S1*^	Sc*^	SD*^	La^	GS*^	Tot^
Jackson									
(No./m^2)	0.00	0.03	0.63	0.13	0.54	0.00	0.00	0.02	1.34
(grams/m^2)	0.00	0.61	0.29	1.41	0.97	0.00	0.00	0.85	4.13
Lonewoman									
(No./m^2)	0.00	0.09	0.00	0.18	0.84	0.00	0.00	0.05	1.17
(grams/m^2)	0.00	3.21	0.00	2.60	2.13	0.00	0.00	2.27	10.25
Prong									
(No./m^2)	0.00	0.00	0.06	0.43	0.00	0.00	0.00	0.14	0.95
(grams/m^2)	0.00	0.00	0.01	7.71	0.00	0.00	0.00	3.34	11.50
Squaw									
(No./m^2)	0.00	0.00	0.91	0.26	0.84	0.00	0.00	0.24	2.25
(grams/m^2)	0.00	0.00	1.17	4.68	2.75	0.00	0.00	10.33	18.94
Ash									
(No./m^2)	0.00	0.01	0.77	0.10	0.54	0.00	0.00	0.05	1.47
(grams/m^2)	0.00	0.09	1.27	1.65	1.37	0.00	0.00	2.72	7.10
Budd									
(No./m^2)	0.73	0.15	0.21	0.03	0.00	0.00	0.00	0.17	1.29
(grams/m^2)	2.00	2.73	0.29	0.35	0.00	0.00	0.00	3.74	9.20
Brownie									
(No./m^2)	0.86	0.02	0.51	0.02	0.12	0.58	0.21	0.01	1.89
(grams/m^2)	2.26	0.84	0.65	0.82	0.35	0.33	0.30	1.06	6.60
Beaver									
(No./m^2)	0.17	0.00	0.65	0.04	0.07	0.52	0.08	0.01	1.56
(grams/m^2)	0.51	0.00	0.52	0.61	0.16	0.95	0.14	0.10	3.07
Stouts									
(No./m^2)	0.03	0.00	0.02	0.00	0.47	0.05	0.18	0.00	0.93
(grams/m^2)	0.11	0.00	0.18	0.00	1.06	0.36	0.22	0.00	2.81
Days									
(No./m^2)	0.01	0.00	0.06	0.00	0.31	0.49	0.11	0.00	1.07
(grams/m^2)	0.06	0.00	0.25	0.00	0.71	0.71	0.50	0.00	2.65

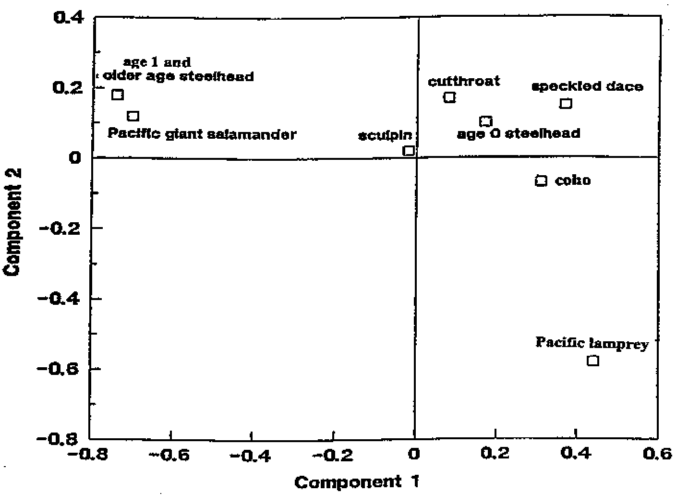

Figure 3. Principal component groupings of the eight species found in at least four streams.

species assemblages differed among streams. For example, in Stouts Creek and Days Creek salmonids accounted for less than 1% of total vertebrate numbers, whereas in Brownie Creek and Budd Creek 73% and 87% of the vertebrates captured were salmonids.

Based on vertebrate densities, factor loadings for the eight groups (seven species with two age classes of steelhead) found in four or more streams indicated three distinct species clusters; 1) age-1 (and older) steelhead and Pacific giant salamander, 2) Pacific lamprey and 3) the remaining four vertebrate species and age-0 steelhead (Figure 3). These two components explained 54% of the total variation in vertebrate density within the basin.

Unlike vertebrate density, vertebrate biomass differed significantly ($P<0.05$) among streams (Table 3). Average vertebrate biomass tended to be higher (but not significantly higher; $P>0.05$) in the upstream rather than the lower elevation streams.

Stream biomass (per m^2) was twice as variable (coefficient of variation = 67%) as vertebrate density. For the five streams with the highest biomasses, two species, Pacific giant salamanders and age-1 (and older) steelhead, together consistently accounted for at least 40% of the total biomass. Prong Creek, for example, which ranked ninth in density of vertebrates, ranked second in biomass because almost all its vertebrates were either Pacific giant salamanders or age-1 (and older) steelhead.

Discussion

Our results indicated that in streams of similar width and order, vertebrate diversity was higher in tributaries of lower elevation, lower gradient and greater drainage basin area. The low-elevation tributaries also tended to flow into river segments that were wider and carried more water than did the headwater tributaries. Higher vertebrate diversity at lower elevations reflected differentially complex species association within these ten rivers. At higher elevations species associations were simple; streams were often dominated by larger salmonid species, sculpins, and Pacific giant salamanders. In the lower elevation streams, species associations were more complex, consisting of up to seven species.

The results support the hypothesis tested here and discussed elsewhere (Osborne and Wiley 1992; Johnson et al. 1995) of the need for the river continuum concept to account for the effects of the location of tributary junctions on species diversity in low-order streams. In this and similar instances, predictions under the river continuum concept (Vannote et al. 1980) should be modified to incorporate main channel influences on species assemblages among small tributaries at different elevations.

Higher vertebrate diversity in lower-elevation streams probably resulted from the higher vertebrate diversity in the mainstem river. Because small streams provide refugia (Frissell et al. 1993; Schlosser 1991) and are repopulated by fish from mainstream segments (Olmsted and Cloutman 1974) they possess many species present in mainstream segments. The relatively few fish species present in the Umpqua River (Snyder 1908) commonly inhabit the mainstem, but only selected ones typically inhabit tributaries. As the number of species within a mainstem segment increases downstream (Horwitz 1978; Platts 1979), the number of species present in low-order tributaries at lower elevations would also be expected to increase.

In addition, these lower-elevation tributaries may have seasonally warmer waters and greater annual variation in other abiotic conditions than occurs in higher elevation streams. This increased variation in the environmental conditions results in optimal conditions, at least during part of the year, for a wider range of species than would less variable conditions (Vannote et al. 1980). Li et al. (1987) reported that more species are typically added to northwestern USA streams as one progresses downstream.

In contrast to diversity, the lack of significant relationships we found between vertebrate density or biomass with elevation, gradient, or discharge, differs from results of several other studies (Platts, 1976; Scarnecchia and Bergersen 1987). Any of a large number of physical and chemical factors (Binns and Eiserman 1979) other than elevation, gradient or drainage basin area evidently determine fish density or biomass in these small streams. Various aspects of stream habitat, as influenced by geomorphology and riparian cover and land use practices, have been implicated in numerous studies to influence biomass and standing crop (e.g., Binns and Eiserman 1979; Lanka et al. 1987). In addition, stream temperatures, which are only partially a function of elevation, have been implicated in affecting both species composition (Roper et al. 1994) and total biomass (Hawkins et al. 1983) in small streams.

Our findings in this river basin indicate that although vertebrate diversity changes with elevation in a predictable pattern, consistent with the river continuum concept, the concept must be modified to consider influences of tributary junctions. Although this result may constitute only a minor deviation from the general predictions of the river continuum concept, it has important implications for conservation. It indicates that if vertebrate diversity within a basin is to be conserved by protecting small streams (Frissell et al. 1993), an array of these streams at a variety of elevations must be afforded protection. Upper streams often serve as thermal refugia in summer. In many cases, however, it is the more accessible, lower-elevation streams having highest biotic diversity that are most subject to human influences and most difficult to protect.

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