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Fish species richness and stream order in Washington State streams

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Synopsis

We sampled fish at pairs of sites of the same stream order on opposite sides of drainage divides in the Cascade Mountains and in the southwest portion of Washington state. Elevation, gradient, drainage area, and stream order were significantly correlated with number of fish species collected at a site. Elevation accounted for the greatest portion of the variation in number of species and stream order for the least, but in low gradient, low elevation streams, stream order was significantly related to number of species. Species richness was greatest in low elevation, low gradient, high order streams. Species richness of a site reflected species richness of the drainage: in paired comparisons, sites in a drainage with a richer ichthyofauna had more fish species than sites in a drainage with fewer species. Addition of species with increasing stream order occurred in most streams, but replacement was more frequent than in other studies relating fish to stream order. The apparently higher frequency of replacement in this study appeared to be a result of headwater introductions of brook charr, *Salvelinus fontinalis,* and a tendency for cutthroat trout, *Salmo clarki,* to occupy headwaters when in freshwater.

Introduction

Kuehne (1962) introduced the Horton-Strahler stream classification (Horton 1945, Strahler 1957) to stream ecology, indicating that its major advantage was that it allowed comparison of different streams by classifying them into stream orders. Fausch et al. (1984) used relationships between stream order and numbers of fish species to develop indices of biotic integrity for use in comparing streams within a region.

In the Horton-Strahler stream classification, first order streams are small streams with no tributaries. Stream order increases by one each time two streams of the same stream order flow together. Thus, stream order is an indicator of stream size (discharge, depth, width). Gradient and elevation decrease and discharge increases with stream order. Within a localized drainage, different ranges of gradients, elevations and discharges are associated with each stream order (Kuehne 1962), but Hughes & Omernik (1981a, 1983) pointed out that certain climatic and geological factors render stream order inappropriate as a basis for ecological comparisons of streams across regional boundaries.

The primary objective of this study was to assess the usefulness of stream order as an indicator of fish species in a climatically and topographically diverse region in which many streams are independent. Most ecological studies using the Horton-Strahler stream classification have been confined to a single, moderately-sized drainage system (e.g. Kuehne 1962, Wilhm & Dorris 1966, Harrell et al. 1967, Harrell & Dorris 1968, Whiteside & McNatt 1972, Lotrich 1973, Platts 1976, 1979a, Evans & Noble 1979). Are the patterns of species richness with stream order constant among drainages as well as within a drainage? Do streams of the same stream order have the same species and the same number of species? Do streams of the same stream order but having different gradients or elevations have the same number of species? We compared species richness in streams of the same stream order but with elevations ranging from near 12 m to over 1500 m and gradients ranging from 0.1% to 15.1%. Low order streams have fewer fish species than higher streams in the same drainage, at least up to fifth or sixth order, except where habitat disturbance has reduced the number of fish species in higher order streams (Kuehne 1962, Harrell et al. 1967, Whiteside & McNatt 1972, Lotrich 1973, Platts 1976, 1979a, Evans & Noble 1979, Fausch et al. 1984). Reduced species richness in low order streams might result from steep gradient, low autochthonous production, small habitat volume, rapid changes in flow and temperature, or limited habitat complexity (Lotrich 1973, Vannote et al. 1980).

Fausch et al. (1984) noted that the relationship between stream order and total number of fish species varies among regions. They developed characteristic maximum-species-richness lines for different watersheds in the Mississippi drainage. Maximum-species-richness lines, which provide a scale for measuring biotic integrity at sites with different potential richness, vary in slope and intercept. Maximum number of species in first order streams (intercept) was generally greater in watersheds with larger total numbers of species. Fausch et al. (1984) suggested physical habitat differences as the most promising explanation for between-watershed variation in maximum-species-richness lines, but they also recognized other zoogeographic factors.

A secondary purpose of our research was to compare the influence of basin richness (number of species in a drainage basin) and physical habitat on site richness (number of species at a site) within a region. We paired sites of the same stream order on opposite sides of drainage divides so that physical conditions (climate, elevation, gradient, stream size) were similar but basin richness differed. If physical conditions, especially those limiting ability of a species to colonize a headwater stream, have a dominant role, then we would expect similar site richness regardless of basin richness (assuming similar distributions of colonizing ability in each fauna). If, on the other hand, physical conditions do not severely limit colonization, then site richness should increase with basin richness.

Methods

Study area

The study area, with approximate location and stream order of each sampling site, is shown in Figure 1. Elevation, gradient, drainage area, drainage basin, and, where available, mean annual discharge are listed for each site in Table 1. We determined gradient between sampling site and 1.6 km downstream from topographic maps.

Wydoski & Whitney (1979) provide an overview of the drainages and physiographic provinces of Washington state. Streams flowing off the crest of the Cascade Mountains are fed largely by snow melt and locally by glaciers. Storm runoff and groundwater flow (Linsley et al. 1975) from abundant precipitation are principal sources of flow in streams originating in the Black Hills, Willapa Hills, and The Rockies. We did not sample any spring-fed streams.

Discussions of the origin and distribution of the fish fauna of the region are provided by McPhail (1967), Reimers & Bond (1967), Wasem (1979), and Wydoski & Whitney (1979). Numbers of fish species in study drainage are listed in Table 2.

Sampling

We sampled each site once during the study (summers and falls, 1980 and 1981) with a 5.7 × 1.3 m seine with 5 mm stretch mesh. We seined until all

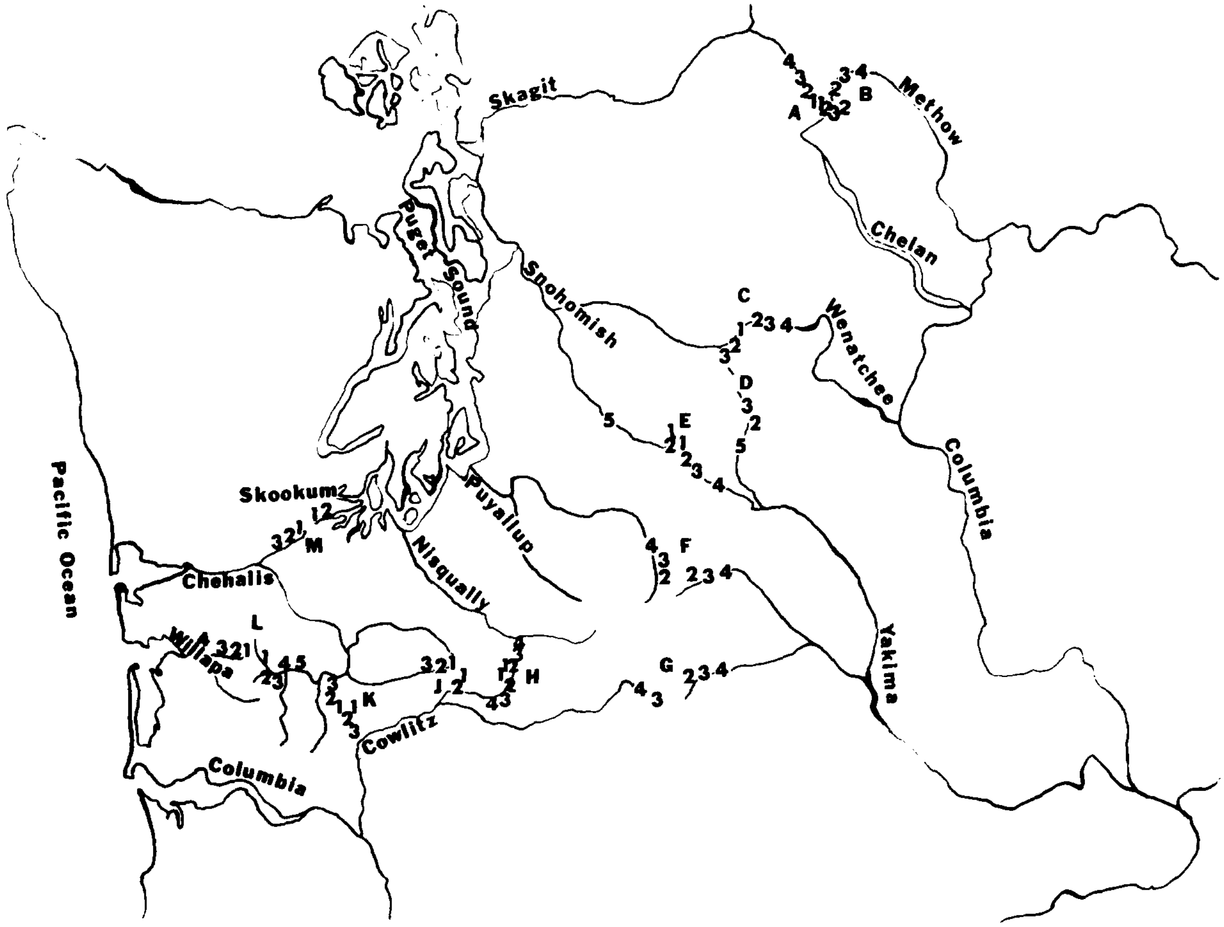

Fig. 1. Locations of sample sites. Numerals indicate stream order at site. Letters A–G identify passes along the crest of the Cascade Mountains: A = Rainy Pass, B = Washington Pass, C = Stevens Pass, D = Deception Pass, E = Snoqualmis Pass, F = Chinook Pass, and G = White Pass. Study areas in The Rockies are: H = Mineral area, and J = Cinebar area. Study areas in the Willapa Hills are: K = Winlock area, and L = Pe Ell area. In the Black Hills, the McCleary area is indicated by M.

habitats we could reach were represented in our sampling at each site and until additional seine hauls yielded no additional species. We identified, counted, and released seine-caught salmonids, but other species were preserved in 10% formalin for later identification. Low (first to third) order sites consisted of up to five or six pool-riffle or pool-cascade sequences, but at higher (third to fifth) order sites we sampled only one or two pool-riffle sequences. We believe the two criteria of ceasing to add new species for the site and sampling all subjectively categorized habitats reduced the chance of failing to detect a species that was present. However, at higher order sites seining was not very effective in deep (>1.3 m) or fast (>1 m sec^{-1}) water. In some cases (Early Winters 3 and 4, Chehalis 4) mask-and-snorkel observations revealed no additional species beyond what we seined, but in other cases (Tilton 2 and 4, Chehalis 5) mask-and-snorkel observations revealed species we had not seined.

In addition to seining, we used the following collection or observation techniques: hook-and-line (Tunnel Creek, Deception Creek, and the Order 2 site on Bridge Creek); mask-and-snorkel (Granite Creek Order 1, Early Winters Orders 3 and 4, Tilton River Orders 2 and 4, and Chehalis River Orders 4 and 5); observation from above

Table 1. Stream order, number of fish species (S), Drainage area (DA), mean annual discharge (Q), elevation (EL), gradient (GR), and drainage basin (DR) for each site. Discharge was obtained from USGS records compiled in Walker & Veatch (1955). Source of other geographical data was USGS topographic maps.

Stream	Stream order	S	DA (km^2)	Q ($m^3\ sec^{-1}$)	EL (m)	GR	DR
Cascade Mountains – crest							
Rainy Pass[a]							
Granite Cr	4[b]	1	62	–	1122	1.7	Skagit
	3[b]	0	13	–	1338	4.2	Skagit
	2[b]	0	5	–	1341	4.2	Skagit
	1[b]	0	1	–	1475	7.6	Skagit
Bridge Cr	2[b]	1	13	–	1378	6.4	Columbia-
	1[b]	1	3	–	1475	6.1	Chelan
Washington Pass[a]							
State Cr	3[b]	1	13	–	1512	7.6	Columbia-
	2[b]	1	10	–	1518	5.7	Chelan
Early Winters Cr	4[b]	1	41	–	1097	1.3	Columbia-
	3[b]	1	26	–	1146	3.2	Methow
	2[b]	0	3	–	1585	15.1	Columbia-Methow
Stevens Pass							
Tunnel Cr	2[b]	1	5	–	878	8.9	Snohomish-
Tye R	1[b]	1	3	–	1219	14.0	Skykomish
Nason Cr	4[b]	1	57	–	853	2.3	Columbia-
	3[b]	1	13	–	1006	3.0	Wenatchee
Stevens Cr	2[b]	1	5	–	1036	3.0	
Deception Pass							
Deception Cr	3[b]	1	62	–	549	7.0	Snohomish-Skykomish
Cle Elum R	5[b, c]	3	414	25.5	689	0.4	Columbia-
	3[b]	1	31	–	1021	0.3	Yakima
Scatter Cr	2[b]	1	8	–	1015	1.7	
Snoqualmie Pass							
Snoqualmie R	5[b, c]	5	970	69.3	121	0.2	Snohomish-
	2[c]	0	10	–	884	8.3	Snoqualmie
unmaned tributary	1[d]	0	?	–	884	8.3	
Yakima R	4[c]	9	153	9.2	732	0.5	Columbia-
Coal Cr	3[c]	2	13	–	805	1.5	Yakima
	2[c]	1	5	–	853	4.9	
	1[c]	1	3	–	884	8.3	
Chinook Pass							
White R	4[c, e]	3	129	–	823	1.7	Puyallup
Silver Cr	3[c]	1	8	–	1341	5.3	
	2[c]	1	3	–	1372	7.6	
American R	4[c]	1	129	–	1020	0.5	Columbia-
	3[c]	0	54	–	1082	1.9	Yakima
Timber Cr	2[c]	0	10	–	1097	3.0	
White Pass							
Clear Fork of Cowlitz R	4[c]	1	65	–	960	2.3	Columbia-
Millridge Cr	3[c]	0	10	–	1250	11.0	Cowlitz
N Fk Tieton Cr	4[c]	2	159	–	884	0.8	Columbia-
Clear Cr	3[c]	1	41	–	914	1.5	Yakima
S Fk Clear Cr	2[c]	1	10	–	1280	16.7	

Table 1. (Continued).

Stream	Stream order	S	DA (km²)	Q (m³ sec⁻¹)	EL (m)	GR	DR
Cascade Mountains – The Rockies							
Mineral Area							
Mineral Cr	4[c]	3	192	10.2	408	0.4	Nisqually
Roundtop CR	3[c]	2	16	–	463	1.5	
Roundtop Cr	2[c]	2	8	–	500	1.3	
Summitt Cr	1[c]	1	4	–	524	2.3	
Tilton R	4[c]	3[f]	363	24.1	235	0.5	Columbia-
	3[c]	5	67	–	314	0.8	Cowlitz
	2[c]	3[f]	21	–	341	1.3	
	1[c]	1	4	–	533	2.3	
Cinebar Area							
Mill Cr	2[c]	3	18	–	268	1.7	Columbia-
	1[c]	1	4	–	402	6.8	Cowlitz
S Fk Newaukum R	3[c]	4	65	–	201	0.8	Chehalis
Kearney Cr	2[c]	3	8	–	232	0.9	
	1[c]	3	3	–	418	4.5	
Willapa Hills							
Winlock Area							
Olequa Cr	3[c]	6[f]	88	3.2	79	0.5	Columbia-
	2[c]	5	39	–	107	0.5	Cowlitz
	1[c]	3	12	–	126	0.5	
Stearns Cr	3[c]	2	70	–	58	0.1	Chehalis
	2[c]	3	23	–	67	0.6	
	1[c]	0	10	–	98	0.9	
Pe Ell area							
Willapa R	4[c]	3[f]	106	5.6	46	0.2	Willapa
Fern Cr	3[c]	3	28	–	69	0.2	
	2[c]	3	10	–	107	1.5	
	1[c]	0	1	–	183	1.9	
Chehalis R	5[c]	5[f]	453	–	85	0.2	Chehalis
	4[c]	5	293	15.3	119	0.5	
Rock Cr	3[c]	2	34	–	143	0.8	
	2[c]	2	16	–	195	1.5	
	1[c]	2	5	–	226	0.8	
Black Hills							
McCleary Area							
Skookum Cr	2[c]	3	44	1.4	12	0.3	Skookum
	1[c]	3	10	–	43	0.5	
Wildcat Cr	3[c]	5	39	–	35	0.5	Chehalis
	2[c]	4	16	–	49	0.6	
	1[c]	4	8	–	98	0.9	

[a] Rainy Pass and Washington Pass are near a triple divide which separates headwaters of Cranite Creek, Bridge and State Creeks, and Early Winters Creek drainages. Three pairings of sites are possible in this area.
[b] Stream order was determined from 1 : 24 000 topographic maps.
[c] Stream order was determined from 1 : 62 500 topographic maps.
[d] Unnamed tributary to South Fork Snoqualmie River at Snoqualmie Pass was assigned a stream order of 1, but it was not shown on 1 : 62 500 topographic map. It might be intermittent stream.
[e] Stream order was determined from a 1 : 50 000 topographic map of Mount Rainier National Park, on which each separately mapped glacial mass with an emerging stream was assigned a stream order of 1.
[f] Number includes species observed but not collected.

surface (Yakima River, Nason Creek, and Willapa River). At six of the 12 sites where we used additional sampling techniques, seining was as effective or more effective than other sampling methods used, based on number of species captured. Seining was ineffective for larger, mobile fish in deep, swift areas. At an Order 3 site on Rock Creek we attribute a difference between seining and electerofishing to different years; a logjam downstream might have been a barrier to coho salmon, *Oncorhynchus kisutch,* the previous fall, which would have explained their absence in our seining collection. As our seining was very effective in that stream and juvenile coho salmon are generally easy to seine, we believe that their absence from our collection was not an artifact. Our sculpin identification was uncertain, but we are confident of the number of species in each collection. Our uncertainties involve *C. gulosus* and *C. perplexus.* Reimers & Bond (1967) noted the variability and overlap of the most distinctive characters of these two species in tributaries of the lower Columbia, including parts of southwest Washington. Numbers of species in our samples were minimum estimates for sites. We undoubtedly missed some fishes. Chum salmon, *O. keta,* and pink salmon, *O. gorbuscha,* spawn in some of the southwest Washington streams we sampled, but our sampling did not coincide with spawning or alevin emergence and outmigration, so we did not collect these fishes.

Statistics

We used nonparametric statistical procedures following Siegel (1956).

Results

We collected 21 fish species in 71 samples (Table 3). Numbers of species collected at each sample site are shown in Table 1. Number of species at a site was generally higher at low elevation, low gradient, large drainage area, and high stream order, in decreasing order of relationship (Kendall's tau, $P<0.01$, 2-tailed; Table 4a). We calculated partial Kendall's tau to control for the influence of elevation on the Kendall's tau values for gradient, drainage, and stream order with number of species. The resulting partial Kendall's tau values for drainage area and gradient decreased, but the magnitude for stream order increased (Table 4b). When we accounted for the relationship between elevation and the other variables with a partial Kendall's tau, stream order had a slightly stronger relationship to number of species than did drainage area (Table 4b).

Table 2. Number of fish species in study drainage systems, based upon this study, Lee et al. (1980), and Wydoski & Whitney (1979). Possible species are those where study drainage is within general range but drainage was not specified in range description.

Drainage	Native species		Introduced species		Recorded	Recorded & possible
	Recorded	Possible	Recorded	Possible	Total	Total
Columbia	52	0	28	1	80	81
Willapa	15	7	2	5	17	29
Chehalis	20	3	4	5	24	32
Skookum	7	11	0	5	7	23
Nisqually	9	12	1	5	10	27
Puyallup	13	11	2	5	15	31
Snohomish	19	4	3	5	22	31
Skagit	17	7	2	5	19	31

Table 3. Numbers of occurrences of fish species in different stream orders.

Species	Stream order	1	2	3	4	5	Total
	Number of collections	15	22	19	12	3	71
Salmo clarki		10	8	8	1		27
S. gairdneri			5	6	4	3	18
Cottus gulosus		2	5	6	3	1	17
C. rhotheus		1	7	4	4	1	17
Oncorhynchus kisutch		3	6	6			15
Salvelinus fontinalis			2	2	3		7
Cottus perplexus		2	3	1			6
C. confusus				1	3	1	5
Catostomus macrocheilus				1	2	2	5
Rhinichthys cataractae					4	1	5
Prosopium williamsoni					3	1	4
Lampetra richardsoni		2	1				3
Salvelinus confluentus				1	2		3
Richardsonius balteatus				1	1	1	3
Lampetra tridentata				1		1	2
Ptychocheilus oregonensis					2		2
Cottus aleuticus			1				1
Gasterosteus aculeatus						1	1
Rhinichthys osculus					1		1
Mylocheilus caurinus						1	1
Oncorhynchus tshawytscha					1		1
Total number of species in each stream order		6	9	12	13	11	21
Maximum number of species in each stream order		4	5	6	9	5	9

Table 4. (a) Kendall rank correlation coefficients (Kendall's tau) between richness and physical attributes of sites. All Kendall's tau values, except that for stream order-elevation, are significant at $P<0.01$ (2-tailed). We ranked highest number of species and largest drainage area as 1, and we ranked lowest stream order, lowest elevation, and lowest gradient as 1. (b) Partial Kendall rank coefficients with elevation partial effect controlled.

	Elevation	Gradient	Drainage area	Stream order
(a) Number of species	0.562 n = 71	0.555 n = 71	0.260 n = 70	− 0.247 n = 71
Elevation		0.564 n = 71	0.254 n = 70	0.018 n = 71
Gradient			0.514 n = 70	− 0.335 n = 71
Drainage area				− 0.784 n = 70
(b) Number of species	NA	0.348	0.146	− 0.310

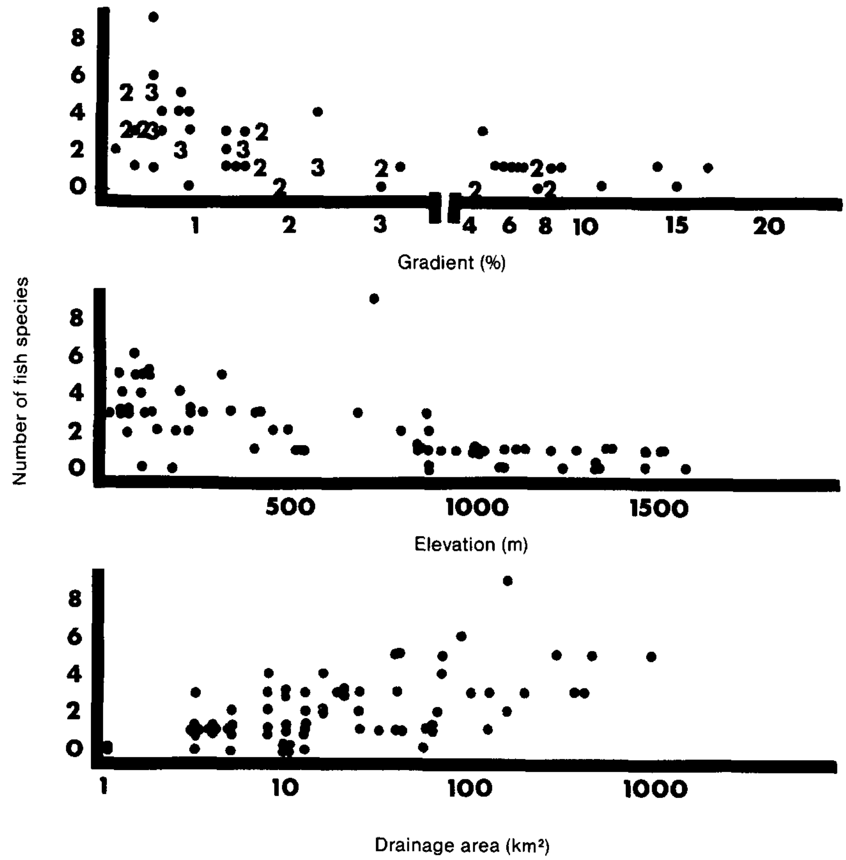

Fig. 2. Numbers of fish species at sites with different gradients, elevations, and drainage areas. Numbers indicate more than one site having the same gradient and number of species.

Elevation

No more than one species, always a salmonid, was collected at any site above 900 m (Fig. 2). We collected fish at all Order 4 sites above 900 m, but in lower order collections above 900 m fish were present at six of nine Order 3 sites, five of eight Order 2 sites, and two of three Order 1 sites. Below 900 m, as many as four species were collected in Order 1 streams, although no fish were collected from two Order 1 streams at 98 m and 183 m. *Cottus gulosus* and *Oncorhynchus kisutch* were collected at low elevations, *C. rhotheus* at middle elevations, and *Salvelinus fontinalis* at higher elevations (Table 5).

Gradient

With a single exception, no more than one species was collected at a site with a gradient exceeding 2% (Fig. 2). The single exception was an artifact of our method of calculating gradient: we collected three species, none of them abundant, at the Order 1 site on the South Fork of Kearney Creek in The Rockies. The site was a marsh with fine mud substrate and fallen trees perched above a steep slope; the slope was included in the calculation of gradient but not in our fish sampling. Twice we collected one species at unusually high gradient sites. In both cases the fishes present probably had been introduced into subalpine lakes less than 1 km upstream. *Salmo gairdneri, C. gulosus, C. rhotheus,* and *O. kisutch* were collected more frequently than expected at low gradient sites (Table 5).

Drainage area

We collected at least one species at all sites with a drainage area ⩾57 km², at least two species at all sites with a drainage area ⩾159 km², at least three species at the six sites with a drainage area ⩾192 km², and five species at two sites with a drainage area ⩾453 km² (Fig. 2). However, the greatest number of species in a single collection was nine from a site with a drainage area of 153 km². *Salmo clarki* was collected at sites with small drainage areas and *O. kisutch* at sites with intermediate drainage areas (Table 5).

Stream order

The mean number of species per site increased from 1.3 at Order 1 sites through 1.7 at Order 2 sites, 1.8 at Order 3 sites, 2.7 at Order 4 sites, and 4.3 at the Order 5 sites. No fishes were collected at several Order 1, 2, and 3 sites. We collected as few as one species at several Order 4 sites. We collected at least three species at each Order 5 site. We collected nine species at an Order 4 site (Fig. 3). *Catostomus macrocheilus* and *Cottus confusus* were associated with higher stream order (Table 5). No species was collected more than expected in low order streams.

Table 5. Chi-square values were calculated to test the null hypothesis that each species was randomly distributed among elevation ranges, among gradient ranges, among ranges of drainage area, and among stream orders. In cases where chi-square values were significant, probabilities (0.01 or 0.05) are listed for the combination of variable and species, and + or − indicates a range where number of collections in which fish was observed was greater or less, respectively, than expected if null hypothesis held. (A + or − is tallied only if that range contributes >2 to the chi-square value.) NA indicates that species was collected in too few collections to use chi-square test. Sample size (n) indicates number of collections.

Species:		*Salmo clarki*	*Salmo gairdneri*	*Cottus gulosus*	*Cottus rhotheus*	*Oncorhynchus kisutch*	*Salvelinus fontinalis*	*Cottus perplexus*	*Cottus confusus*	*Catostomus macrocheilus*
Variable		n = 27	n = 18	n = 17	n = 17	n = 15	n = 7	n = 6	n = 5	n = 5
Elevation				0.01	0.01	0.01	0.05	NA	NA	NA
150 m	n = 18			+		+				
151–600 m	n = 17				+					
601–900 m	n = 11			−		−				
900 m	n = 25			−	−	−	+			
Gradient			0.005	0.01	0.01	0.01			NA	NA
<1.0%	n = 28		+	+	+	+				
1.0–2.0%	n = 14									
2.1–5.0%	n = 12		−	−	−	−				
>5.0%	n = 17		−	−	−	−				
Drainage area			0.05			0.05		NA	NA	NA
<5 km²	n = 16		+			−				
6–10 km²	n = 13									
11–25 km²	n = 18					+				
>100 km²	n = 11		−			−				
Stream order			0.05	0.05					0.01	0.01
1	n = 15		+	−						
2	n = 22									
3	n = 19									
4 & 5	n = 15		−	+					+	+

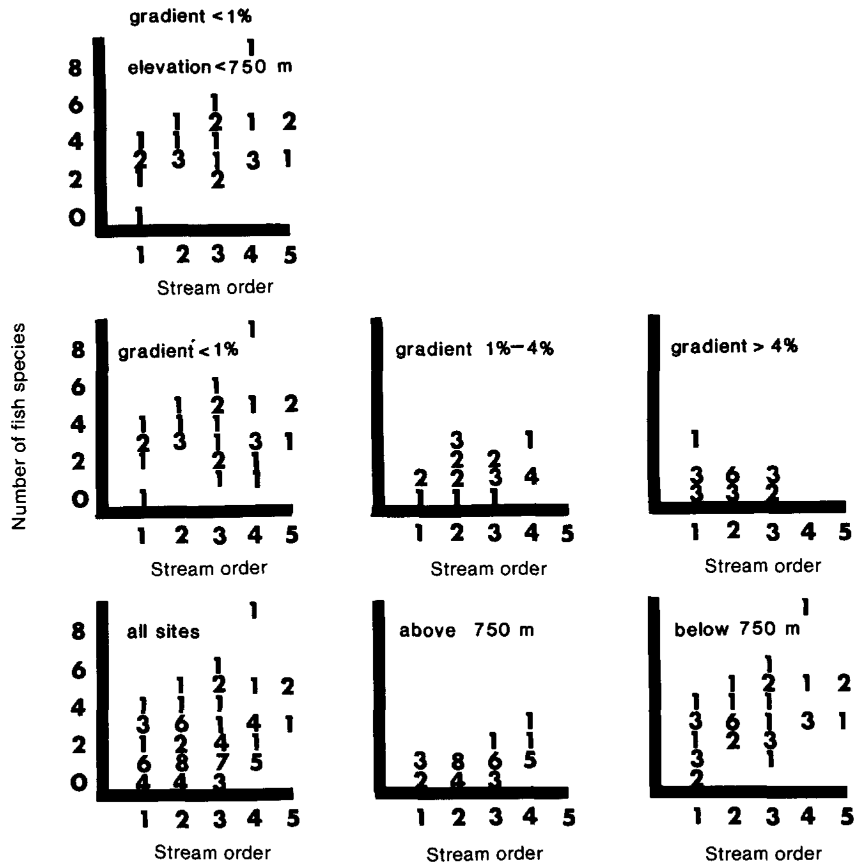

Fig. 3. Numbers of fish species at sites of different stream order at different ranges of elevation and/or gradient. Numbers indicate numbers of sites having the same stream order and number of species.

Basin richness

In 14 of 26 paired site comparisons, sites from richer basins had more species than sites from basins with fewer species; in 6 cases sites from the richer basin had fewer species (Table 6). D_s is an index of the difference between number of fish species in streams of the same stream order but different drainage richness. D_s is significantly positive (sign test, one-tailed $P = .007$), indicating that streams in drainages with larger numbers of species are likely to have more species than similar streams in drainages with few species. However, this relationship was not apparent in streams draining the crest of the Cascade Mountains: sites in species-rich basins had more species in 5 cases, fewer species in 3 cases, and the same number of species in 3 cases.

Discussion

Species richness of a stream reach was correlated to varying degrees with different physical variables of that stream reach (Table 4). Elevation showed the highest correlation among the four variables we examined; stream order and drainage area showed the lowest correlations. However, partial rank correlation with partial effect of elevation controlled, indicated that stream order and number of species were nearly as strongly correlated as gradient and number of species. Species richness of the drainage was also related to species richness of a particular stream reach within that drainage.

Washington first order streams have similar numbers of fish species to first order streams in other parts of the United States except Gulf coast

Table 6. Streams of same stream order on opposite sides of divides compared. If D_s is positive, there are more species at site in species-rich drainage. $D_s = S_r - S_p$, where S_r is number of fish species collected in member of pair from drainage with greatest number of species, and S_p is number of species from other member of pair.

Region – Pass or divide area	Stream order of pair	D_s
Cascade Mountains – crest		
Rainy and Washington passes		
Granite – Bridge creeks	2	+1
	1	+1
Granite – State creeks	3	+1
	2	+1
Granite – Early Winters creeks	4	0
	3	+1
	2	0
composite	4	0
	3	+1
	2	+0.67
	1	+1
Stevens Pass	2	0
Deception Pass	3	0
Snoqualmie Pass	2	+1
	1	+1
Chinook Pass	4	−2
	3	−1
	2	−1
Cascade Mountains – The Rockies		
Mineral area	4	0
	3	+3
	2	+1
	1	0
Cinebar area	2	0
	1	−2
Willapa Hills		
Winlock area	3	+4
	2	+2
	1	+3
Pe Ell area	4	+2
	3	−1
	2	−1
	1	+2
Black Hills		
McCleary area	2	+1
	1	+1
Number of pairs where $D_s>0$		
all pairs, including actual data for Rainy and Washington passes		14
all pairs, including composite data for Rainy and Washington passes		16
Number of pairs where $D_s<0$		
all pairs, including actual data for Rainy and Washington passes		6
all pairs, including composite data for Rainy and Washington passes		6
Total number of pairs		
including actual data for Rainy and Washington passes		29
including composite data for Rainy and Washington passes		26

streams, which have a very rich ichthyofauna, and Ontario streams, but Cascade Mountain streams have fewer species at all stream orders sampled than streams in other regions (Table 7). However, among Washington streams, the number of species in a stream order varies severalfold even in different portions of the Columbia drainage. Idaho, with similar environments and ichthyofauna, is most similar to Washington streams in number of species at different stream orders. Third and fourth order streams in Illinois and Kentucky show a greater rate of species addition with stream order than Washington streams despite similar species richness in first order streams. Streams in the Dakotas, Oklahoma, and central Texas are similar in species richness to Washington streams, although fourth order streams in Oklahoma and central Texas are richer than those in Washington.

Among the studies listed in Table 7, physical habitat appears to limit number of species. Fewer species are found in high elevation-high gradient streams or streams in cold or arid regions. Most species per stream order were found in Evans & Noble's (1979) study in east Texas, where elevations and gradients are low and temperature and precipitation are high. Mahon et al. (1979) found little change in either number of species or gradient in Speed River, Ontario. Among Washington streams, Black Hills streams are lowest in elevation and gradient, temperature is moderated by maritime climate, rainfall is high, and they had the greatest number of species at a stream order.

Stream order, elevation, gradient, drainage area, and species richness

Stream order is related to varying degrees with other physical attributes of a stream reach (e.g., drainage area, discharge, depth, width, elevation, gradient, maximum velocity, permanence, substrate particle size). Because stream order is relatively easy to determine from topographic maps (but, see Hughes & Omernik 1981a, 1983), and, because it reflects other physical variables which could influence presence or absence of aquatic species, it has been suggested as a basis for comparing streams in biological studies (Kuehne 1962, 1970). If these relationships are valid, then stream order should be correlated with and useful for predicting species numbers or presence of particular species within a region.

In streams of southwest Washington and the Cascade Mountains, we found a significant Kendall rank correlation between number of fish species at a site and stream order. However, elevation and gradient were more strongly correlated with number of species than was stream order (Table 4). We graphed the number of species at different stream orders within different ranges of elevation and gradient in Figure 3; in the ranges of elevation (below 750 m) and gradient (less than 1%) where number of species varied the most, number of species increased with stream order (Kendall's tau = 0.42, P = 0.004). In most cases no more than one fish species was found above 750 m (34 of 37 cases) or where gradient exceeded 1% (34 of 43 cases).

We conclude that one reason stream order was not more highly correlated with fish species richness in our study was the geographic heterogeneity of our study area. Hughes & Omernik (1981b) emphasized that stream comparisons should be made only within a resonably homogeneous region. Fausch et al. (1984) developed separate analyses of the relationships between fish species richness and stream order in each of several relatively homogeneous regions. Our study area encompassed areas of both low and high topographic relief within a small geographic area (~26,000 km^2; Fig. 1) and included several distinct ecoregions (Bailey 1976) or natural provinces (Wydoski & Whitney 1979). Some of the greatest extremes in gradient and elevation within our study area (high and steep – Washington Pass; low and flat – Olequa Creek) are in the same drainage, the Columbia. Platts (1979a, b) recognized that landtypes, as well as stream order, within a physically heterogeneous region were related to fish species richness and abundance.

Addition of species with increasing stream order occurred along most streams within a basin (considering the entire Columbia, Chehalis, or Snohomish as three systems of basins rather than as

Table 7. Number of fish species in streams of different stream order in different parts of the United States and Canada. First number indicates mean number of species. Range of numbers of species is listed in parentheses if more than one sample per stream order.

Study location	Stream order						Reference
	1	2	3	4	5	6	
Washington	1.4 (0–4)	1.8 (0–5)	2.0 (0–6)	2.7 (1–9)	4.3 (3–5)	–	this study
Cascade Mountains crest	0.6 (0–1)	0.7 (0–1)	0.8 (0–2)	2.4 (1–9)	4.0 (3–5)	–	this study
The Rockies	1.5 (1–3)	2.7 (2–3)	3.7 (2–5)	3.0	–	–	this study
Willapa Hills	1.2 (0–3)	3.2 (2–5)	3.2 (2–6)	4.0 (3–5)	5.0	–	this study
Black Hills	3.5 (3–4)	3.5 (3–4)	5.0	–	–	–	this study
Idaho	1.0	4[1]	6[1]	9[1]	7[1]	–	Platts 1979a
North & South Dakota	–	–	3.0	4.7 (3–6)	6.0 (3–10)	11.8 (7–14)	Fausch et al. 1984
Illinois	4.0 (3–5)	–	11.8 (1–19)	15.5 (4–21)	17.4 (8–31)	19.8 (3–35)	Fausch et al. 1984
Oklahoma	–	–	2.3 (1–5)	8.3 (6–11)	10.5 (5–13)	9.2 (5–13)	Harrell et al. 1967
Texas (east)	22.0	22.0	29.7 (28–31)	32.0 (31–33)	–	–	Evans & Noble 1979
Texas (central)	1.0 (0–4)	2.6 (0–5)	4.8 (1–2)	8.2 (5–12)	12.0	–	Whiteside & McNatt 1972
Kentucky	1.0	5.9 (3–11)	12.3 (9–17)	18.5 (12–25)	–	–	Kuehne 1962
Kentucky	1.0	8.0	15.0	–	–	–	Lotrich 1973
Ontario	7.5[2]	8.7[2]	10.0[2]	10.1[2]	–	–	Mahon et al. 1979

[1] Platts (1979a) listed average numbers of individuals per species per site rather than numbers of species, so only maximum numbers can be listed for Idaho.

[2] Mahon et al. (1979) listed mean number of species per stream order.

three single basins), but replacement of species occurred in more than half the basins (Table 8). In two basins we found no change in species with change in stream order. Previous studies of fish species composition with stream order have shown addition of species to be much more important than replacement (Shelford 1911, Kuehne 1962, Harrell et al. 1967, Sheldon 1968, Whiteside & McNatt 1972, Lotrich 1973, Platts 1979a). The high frequency of replacement in this study is largely a result of apparent restriction of cutthroat trout to headwaters in several basins. Cutthroat trout were captured in headwaters but were replaced in lower reaches by other trout, usually steelhead, in eight basins. Replacement of cutthroat trout by steelhead in larger streams was reported by Hartman & Gill (1968). Cutthroat trout were collected most frequently in Order 1 streams. As some of the cutthroat trout sampled in Order 1 streams were probably anadromous, they must have traversed higher order downstream reaches where we did not capture them. Failure to collect cutthroat trout in migration routes, construction of dams which stop anadromy, and introduction of cutthroat trout into alpine and subalpine lakes and streams may account for many of these apparent cases of replacement. In two other basins (Cle Elum and Tieton) introduced brook charr were found in headwaters but dropped out at higher order sites where other species occurred. It is possible, but unlikely, that

Table 8. Addition and replacement of species with increasing stream order within a drainage basin.

Drainage	Addition	Replacement	No change
Columbia			
Methow	+		
Chelan			+
Wenatchee			+
Yakima	+	+[a]	
Cle Elum	+	+[b]	
American	+		
Tieton	+	+[b]	
Cowlitz	+		
Tilton	+	+[a, c]	
Mill	+		
Olequa	+		
Willapa	+	+	
Chehalis			
Rock	+	+	
Stearns	+		
Newaukum	+	+[a, d]	
Wildcat	+	+[a, d]	
Skookum		+[a, d]	
Nisqually	+	+[a, c]	
Puyallup	+	+[a, c]	
Snohomish			
Snoqualmie	+		
Skykomish		+[a, e]	
Skagit	+		
Total	18	12	2

[a] Cutthroat trout (*Salmo clarki*) in upper reaches.
[b] Introduced brook charr (*Salvelinus fontinalis*) in upper reaches.
[c] Cutthroat trout probably anadromous before dams.
[d] Cutthroat trout probably anadromous.
[e] Cutthroat trout probably introduced in headwaters.

no natural examples of replacement occur in our study streams. If that were the case, streams of the Cascade Mountains and southwest Washington would be similar to streams in New York (Sheldon 1968), Kentucky (Kuehne 1962, Lotrich 1973), Oklahoma (Harrel et al. 1967), central Texas (Whiteside & McNatt 1972), and Idaho (Platts 1979a). However, Hartman & Gill's (1968) information that coastal cutthroat trout are fugitive species relative to the larger, more fecund, more crowding-tolerant steelhead is consistent with our finding of replacement in Washington streams, and Evans & Noble (1979) indicated that some east Texas stream fishes occurred only in lower order sites of their study.

Elevation is the variable most highly correlated with fish species richness in this study (Table 5); low elevation streams had more fish species than high elevation streams. Wildcat Creek and Skookum Creek, which are essentially coastal plain streams, had more species than most mountain streams of similar stream order. Platts (1976) found a similar strong influence of elevation upon fish communities in Rocky Mountain streams, and Minshall & Kuehne (1969) found that elevation had a stronger influence than stream order on benthic invertebrate communities in an English mountain stream system. Elevation probably influences stream communities in several ways: (1) barriers downstream are more probable as elevation increases, (2) gradient generally increases with elevation, and (3) temperatures are reduced for longer at higher elevations.

Waterfalls and cascades, which are found more often at higher than at low elevations (Leopold 1962, Leopold et al. 1964), vary in their effectiveness as barriers to migration and dispersal depending upon height, configuration, flow, and species of fish. In southwest Washington, adult steelhead leap waterfalls that are about 4 m high on the Kalama River (Bruce Crawford, personal communication). Michael (1983) reported a probable case of cutthroat trout passing a series of log jams that was a barrier to steelhead and coho salmon in an Olympic Peninsula stream. Mason & Machidori (1976) reported that obstructions 30 cm high were barriers to prickly sculpin, *Cottus asper,* and 45 cm were barriers to coastrange sculpin, *C. aleuticus*. Barriers change with time. Reimers & Bond (1967) discussed apparent changes in sculpin distribution in southwest Washington and northwest Oregon in response to changes in effectiveness of barriers.

Gradient probably influences fish communities by (1) increasing barrier frequency, and (2) controlling suitability of physical habitat components such as water velocity and substrate composition. Gradient and elevation were highly correlated, but the partial correlation between number of species and gradient with elevation effects controlled suggests that elevation-independent effects of gradient have some influences on Washington fish communities.

In this study, the correlation between drainage area and stream order is fairly strong, but drainage area is more strongly correlated with species richness than is stream order (Table 4). This finding supports the contention of Hughes & Omernik (1981a) that watershed area should be included in a combination of several watershed characteristics to replace stream order in stream classification.

Thompson & Hunt (1930) found a positive relationship between drainage area and numbers of species in Illinois streams. Moeller et al. (1979) found a strong positive relationship between drainage area and dissolved organic transport, an important factor at the base of stream food chains, in river systems in Oregon, Idaho, Michigan, and Pennsylania. Cushing et al. (1980) concluded that watershed area is a useful characteristic for segregating groups of streams with physical-chemical similarities.

Basin richness and site richness

Basin richness in Washington streams is a product of past glaciation, past and present climate, geological history of the region, dispersal patterns of different fishes, and, possibly, species-area relationships. Puget Sound and its tributary streams were recently glaciated, which, together with small area of individual drainage basins, accounts for low numbers of fish species in Puget Sound streams. Secondary freshwater fishes (salmonids, gasterosteids, and cottids) dominate Puget Sound streams. The Chehalis basin is larger, lower gradient, and was not glaciated; these factors contribute to its greater species richness compared to Puget Sound streams (McPhail 1967). The Willapa basin was not glaciated but has a small drainage area. Much of the large Columbia basin was not glaciated, and pluvial lakes in this basin may have supported a rich ichthyofauna (Gilbert 1976, Smith 1981).

Paired stream samples support the hypothesis that species richness of a drainage influences species richness at a site in the drainage. In paired site comparisons, sites from richer basins have more species than sites in basins with fewer species; site richness is related to basin richness (Table 4). However, the Cascade Mountain crest pairs did not show this relationship. The two sides of the Cascade crest did not differ consistently in number of species per stream order even though east slope streams are part of the Columbia drainage, the most species-rich drainage in Washington. Cascade crest streams had the highest gradients and elevations among streams studied. In these steep mountain streams, high gradient limits dispersal from downstream as discussed above. Other factors associated with high altitude (low production, low temperature) or with high gradient might limit colonization by those fish that do reach such sites.

In streams not originating along the Cascade crest, site richness is related to basin richness, indicating that factors associated with low stream order do not place a uniform limit on site richness. Instead, the size of the pool of potential colonizers influences the number of species at a site.

The relationship of site richness to basin richness may appear trivial, but other relationships are possible. Two examples, one involving replacement, the other involving addition of species with increasing stream order but no replacement, are outlined here.

If two similar sized basins have the same number of species per stream order, one basin could accumulate more species through replacement. For example, two second order basins, each with one species in first order streams and two species in second order streams, will differ in drainage richness if there is replacement in the first basin and only addition in the second. With replacement, first order streams would have species A and the second order stream would have species B and C, for a drainage richness of three. With addition but no replacement, first order streams would have species X and the second order stream would have species X and Y, for a basin richness of two.

Different sized basins could have different basin richness but similar site richness without replacement. Larger basins have more streams of any order than smaller basins. All streams of the same stream order do not have the same species. For example, a small basin might have species A in one first order stream, species B in another first order stream, and both A and B (or A, B, and C) in a second order stream, with a basin richness of two (or three). A larger basin might have species P in one first order stream, Q in another, R in another, and S in still another. Second order streams in the larger basin might have species P and Q (or P, Q, and T) in one and R and S (or R, S, and U) in another. In this example site richness is the same at sites of the same stream order in different basins, but basin richness is two (or three) in the smaller basin and four (or six) in the larger basin.

Initially we asked several questions about stream order and fish communities. Washington streams of the same stream order vary in number of fish species depending upon elevation, gradient, and basin richness; however, when steep mountain streams are excluded from consideration, number of fish species increases with stream order. In Washington streams, maximum-species-richness lines of the type developed by Fausch et al. (1984) would have utility as benchmarks for measuring biotic integrity only if steep mountain streams were disregarded. If maximum-species-richness lines were developed for Washington streams, different lines would be needed for different basins, but the basins would have much smaller areas than those of Fausch et al. (1984). Zoogeographic factors, including past physical habitat differences among basins, account for differences between basins in maximum-species-richness. In steep mountain streams, physical conditions appear to have limited colonization to salmonids capable of leaping waterfalls that are barriers to other fishes and capable of inhabiting cold, steep streams. (Some salmonids have colonized steep mountain streams via intentional introduction; thus their recreational value to people was the 'attribute' that allowed them to pass barriers.) In these steep mountain streams the influences of stream order and basin richness on species richness appears negligible.

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