

The structure of food webs along river networks

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Do changes in the species composition of riverine fish assemblages along river networks lead to predictable changes in food-web structure? We assembled empirical “fish-centered” river food webs for three rivers located along a latitudinal gradient in the South Saskatchewan River Basin (SSRB) that differ in land-use impacts and geomorphology but flow through similar mountain, foothill, and prairie physiographic regions. We then calculated 17 food-web properties to determine whether the nine river food webs differed according to physiographic region or river sub-basin. There were no statistically significant differences in the 17 food-web properties calculated among the rivers. In contrast, fish species richness, connectance, the proportion of herbivores, and the proportion of cannibals changed longitudinally along the river network. Our results suggest that regional changes in river geomorphology and physicochemistry play an important role in determining longitudinal variation in food-web properties such as fish species richness and connectance. In contrast, the overall structure of river food webs may be relatively similar and insensitive to regional influences such as zoogeography. Further explorations of river and other food webs would greatly illuminate this suggestion.

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Several fundamental insights into the ecology of flowing waters suggest exploring longitudinal changes in food webs along river networks (Vannote et al. 1980). First, to the extent that upstream processes in rivers consistently determine downstream processes, this global mechanism may cause food-web structure to change predictably along river networks longitudinally from headwater streams to river mouths. Also, consistent changes along river networks in physicochemical variables such as temperature and nutrients, and biotic variables such as photosynthetic sources and community composition may create predictable food-web patterns (Vannote et al. 1980, Minshall et al. 1983). Beyond physicochemical variation, physiographic variation in, for example, geomorphology or current velocity may generate longitudinal patterns in river food webs. Finally, deviations

from predictable changes in food-web structure could signal strong land-use effects such as anthropogenic disturbances that significantly alter the biota of streams and rivers (Allan and Flecker 1993, Johnson et al. 1995). Despite the importance of such alterations, land-use effects on the structural properties of food webs are rarely studied.

To determine whether the structure of food webs changes along river networks or whether regional effects such as zoogeography or land-use changes at sub-basin scales effect potential food-web patterns, we assembled fish dominated food webs for the north (Red Deer), central (Bow) and south (Oldman) headwater sub-basins of the South Saskatchewan River Basin (SSRB). These rivers flow through three similar mountain, foothill, and prairie regions before draining into the South Saskatch-

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ewan River and are similar in their composition and richness of fish species. Comparisons of how food-web structure changes across regions provides an intriguing approach to illuminating regional and local influences on food webs. Such an approach also provides a scientifically powerful alternative to logistically difficult experiments studying, for example, how food webs are affected by land-use and history.

Methods

River sub-basins in the SSRB

The South Saskatchewan River Basin (SSRB) includes the sub-basins of the Red Deer, Bow, Oldman, and South Saskatchewan River systems (Fig. 1). These basins begin in the Rocky Mountains and generally flow eastward through foothill and prairie regions. The combined watershed is 121 095 km². Agriculture is the largest consumptive use of water in the SSRB. While there are considerable differences in land-use impacts affecting the three sub-basins (see below), each river has impoundments, which coupled with fish stocking, habitat degradation, and extirpations may have resulted in homogenization of fish fauna (Paul and Post 2001).

The northern Red Deer River flows for 708 km from its headwaters to the Alberta-Saskatchewan border. This sub-basin's area is South Saskatchewan's largest but contributes to only 20% of its annual flow. From its origin in Banff National Park, it flows northeasterly through foothills and parkland to the City of Red Deer and then turns sharply to the south flowing through Dinosaur National Park before joining the South Saskatchewan River. Land-use in the prairie region of the Red Deer is utilized primarily for cattle ranching. Prior to the construction of the Dickson Dam upstream of the City of Red Deer, the fish fauna below Red Deer was composed of primarily cool-water species such as walleye and mountain whitefish, a cold-water species.

The central Bow River flows for 498 km from its headwaters in Banff National Park to its confluence with the Oldman River at Grand Forks. The Bow River contributes the most (43%) water to the South Saskatchewan. It originates in forested mountains and transitions from a foothill to a prairie stream before it reaches the City of Calgary. The Bow River has 11 hydroelectric dams and irrigation is the largest consumptive water user. From Banff National Park to Carseland, the Bow River fish fauna are primarily cold-water species, including mountain whitefish and rainbow trout. Brown trout are found primarily upstream of the Carseland weir. From the Carseland weir to Bassano the fish fauna changes from a cold-water community to a cool-water community. However, downstream of Bassano dam, fish production is severely limited by the massive water diversion (90%), high water temperatures (29°C) which

exceed the tolerance limits of cool-water fish species, low dissolved oxygen concentration during low discharges, and highly variable pH factors which combine to devastate the fish community.

The southern Oldman River flows 450 km from its headwaters in the Livingstone Range of the Rocky Mountains to its confluence with the Bow River at Grand Forks. Land-use in the Oldman Basin includes forestry, recreation, agriculture, and oil and gas development. The basin also supports intensive livestock feeding operations, particularly north of Lethbridge. The Oldman joins the Crowsnest and Castle Rivers in the foothills and then flows east through semi-arid grassland to join with the Bow River. The Oldman has three southern tributaries, the Belly, Waterton, and St. Mary's Rivers that contain mixed warm- and cold-water fish communities.

Despite their physiographic similarity, the three rivers are physically very different. The Red Deer is dominated by gravel substrate north of the City of Red Deer, and by sand south of Finnegan. Its upper reaches are set in a broad forested valley and its lower reaches cut deep below the surrounding arid prairie as it flows through badlands. In contrast, the Bow and Oldman are stream-cut in wide valleys with gravel substrates throughout their length. The Bow and Oldman rivers differ primarily in their headwater valleys and foothills. While the Bow flows through a forested valley in the mountains, the Oldman flows through unforested grass-covered mountain valleys that closely resemble the foothills.

Food web construction

We constructed separate food webs for each river sub-basin and for different physiographic regions within each sub-basin according to elevation. Physiographic regions (Fenneman 1946) were chosen to delineate regional boundaries longitudinally as physiography affects the surrounding landforms, habitat quality, disturbance patterns, and upstream-downstream linkages (Swanson et al. 1988). Different physiographies within drainages have also been shown to support distinctive fish faunas (Hocutt and Wiley 1986, Jenkins and Burkhead 1994). We defined mountain stream, foothill stream, and prairie stream physiographic regions.

Mountain streams flow through a glacial montane ecoregion. In the mountain regions forestry, hydroelectric developments, natural gas exploration and development, and recreation are the main land-uses. Foothill streams flow through a boreal ecoregion of gently rolling hills and parkland. Forestry, agricultural activity, and oil and gas exploration and production are the main land-uses. The prairie streams flow through grassland. This ecoregion has been modified the most

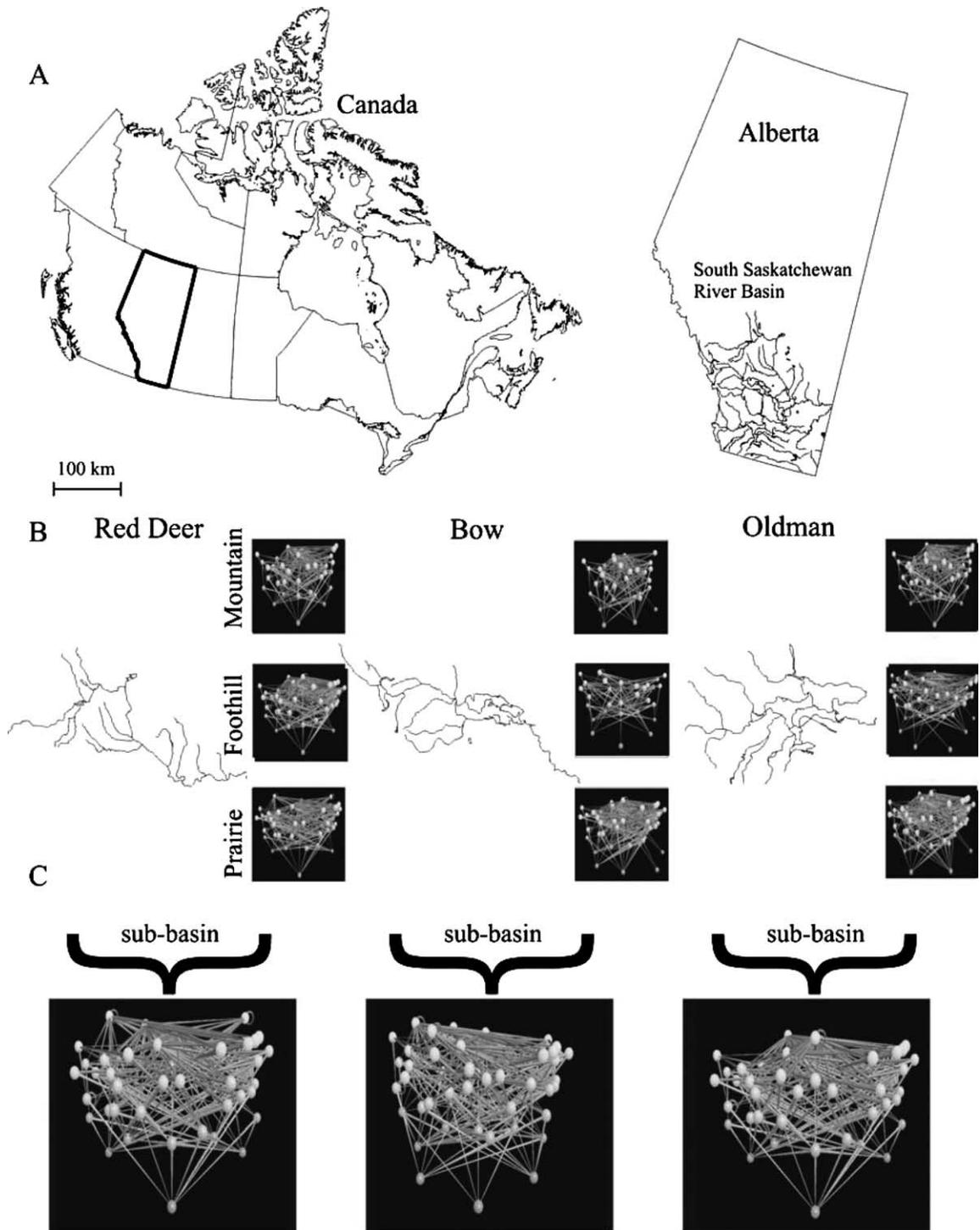


Fig. 1. Map of the South Saskatchewan River Basin (SSRB) and visualization of river food webs. Panel A shows a map of Canada and Alberta with the drainages of the SSRB. Panel B shows the sub-basins of the SSRB: the Red Deer, the Bow, and the Oldman and how food web structure shifts longitudinally from mountain to prairie streams for each sub-basin. Panel C shows how food web structure differs across physiographic regions for the Red Deer, Oldman, and Bow Rivers.

and is characterized by intensive agriculture and urbanization.

Our binary food webs describe who eats whom among “fish-centered” networks (Winemiller 1990) that include all 34 fish species present in the SSRB. Lower trophic taxa such as primary producers and consumers were aggregated into the following larger taxonomic groups: aquatic insects, gastropods, amphibians, crustaceans, bivalves, terrestrial insects, zooplankton, worms, leeches, detritus, POM, macrophytes, decomposing organic matter (see Appendix). Fish species belonging to each food-web were based on fish species ranges in Nelson and Paetz (1992). Fish records were verified using catch data from grey literature sources (e.g. Longmore and Stenton 1981). Species diets were determined from a review of the literature (e.g. Vander Zanden et al. 1997). The presence and absence of taxa across rivers and in different physiographic regions was determined using range estimates and habitat information from numerous sources (e.g. Thorp and Covich 1991, Russell 1993, Scotter and Ulrich 1995, Giller and Malmqvist 1999, Acorn and Sheldon 2000, Russell and Bauer 2000). The unevenness of the webs with the fishes being resolved to species and the rest of the web being either absent (e.g. microbes), or highly aggregated, causes food-web patterns to be dominated by changes in the fish community composition rather than changes at lower trophic levels. Thus, our references to changes in food-web structure refer more specifically to changes in the fish portion of the food web.

The food webs were constructed by employing several key assumptions. First, presence and absence data for fish species were aggregated according to physiographic

region and river basin. Thus, if a species had been recorded at one location, for example in one mountain stream in the Bow, it was assumed to be present in the whole mountain region area of the Bow. This minimized exclusion bias that can occur due to inadequate sample size. Second, all taxa were assumed to be present regardless of seasonal or temporal bias. Third, all feeding links present across all ontogenetic stages were included for each fish species.

Food-web properties and statistical analysis

The analysis focused on a suite of 17 food-web properties that describe species’ trophic habits, linkage complexity, and food chains (Williams and Martinez 2000, Bersier et al. 2002; Table 1). Food web properties were analyzed using software developed for previous food-web studies (e.g. Williams and Martinez 2000, Williams et al. 2002). We used Kruskal-Wallis ANOVA by ranks to determine whether there were greater differences within river sub-basins by physiographic region than between river sub-basins. Spearman R rank correlations was used to examine relationships among food-web properties. Due to data limitations we could not make statistical comparisons of the differences in food-web properties for each physiographic region across the three rivers. Thus, when comparing food-web properties across the three rivers to determine if food web properties changes according to land-use, we used all three physiographic regions in each analysis.

Table 1. Definition of the 17 food web properties calculated for food webs in the SSRB.

Food web property	Definition of food web property
Species properties	
Taxa richness	Number of all taxa compartments in the web.
Fish species richness	Number of fish species in the web.
% Top	Fraction of species with prey but no predators.
% Intermediate	Fraction of species with both prey and predators.
% Basal	Fraction of species with predators but no prey.
% Herbivores	Fraction of species which are strictly herbivore.
Link properties	
Linkage density	Link/Species ratio (L/S), the number of all trophic links in the web (L) divided by S .
Connectance	Directed connectance (L/S^2), ranges from 0 (no species preys on any species) to 1 (every species preys on every other species including itself).
Chain properties	
Maximum trophic level	Trophic level (i.e. position that an organism occupies in a food web starting with primary producers as trophic level 1) of the top predator in the web.
Mean trophic level	Mean trophic level of all taxa in a web.
Trophic SD	The standard deviation of trophic level.
Consumer trophic level	Mean trophic level of all intermediate species in the food web.
Chain length	Mean number of links in every possible food chain or sequence of links connecting top species to basal species.
Chain length SD	The standard deviation of chain length.
Omnivory properties	
Direct omnivory	Fraction of taxa that feed directly on more than one trophic level.
Consumer direct omnivory	Fraction of intermediate species that feed on more than one trophic level.
Cannibalism	Fraction of taxa that feed directly on its own species.

Table 2. Shown are the 16 food web properties calculated for each of the nine food webs assembled. A separate food web was assembled for each physiographic region (M = Mountain, F = Foothill, P = Prairie) within each river sub-basin (B = Bow, O = Oldman, R = Red Deer).

River basin	Bow River Basin			Oldman River Basin			Red Deer River Basin				
	M	F	P	M	F	P	M	F	P	R	
Physiographic region											
Fish species richness	13	17	28	14	19	29	14	23	31	34	
Taxa richness	31	32	40	36	39	43	34	41	40	45	
Maximum trophic level	4.41	4.35	4.60	4.41	4.44	4.67	4.41	4.67	4.67	4.67	
% Top	6.45	15.63	12.50	5.56	2.56	11.63	8.82	7.32	12.50	11.11	
% Intermediate	80.65	68.75	77.50	86.11	82.05	79.07	82.35	85.37	80.00	82.22	
% Basal	12.90	15.63	10.00	8.70	15.38	9.30	8.82	7.32	7.50	6.67	
% Herbivore	9.68	9.38	7.50	11.11	7.69	6.98	11.76	7.32	7.50	8.89	
Connectance	0.13	0.12	0.12	0.12	0.10	0.11	0.13	0.11	0.12	0.11	
Links/species	4.13	3.69	4.80	4.47	3.90	4.81	4.32	4.49	4.78	5.04	
Chain length	4.43	4.23	4.47	4.48	4.68	4.48	4.46	4.48	4.48	4.78	
Chain length SD	1.04	0.98	1.02	1.09	1.17	1.02	1.07	1.13	1.02	1.14	
Trophic level	3.04	2.86	3.25	3.12	2.96	3.28	3.13	3.37	3.31	3.36	
Trophic level SD	1.04	1.04	1.02	0.96	1.03	1.00	0.96	0.98	0.97	0.97	
% Cannibalism	0.06	0.13	0.10	0.06	0.10	0.09	0.06	0.12	0.08	0.11	
Direct omnivory	0.68	0.66	0.70	0.69	0.67	0.70	0.68	0.71	0.70	0.71	
Consumer direct omnivory	0.78	0.78	0.78	0.76	0.79	0.77	0.74	0.76	0.76	0.76	
Consumer mean trophic level	3.34	3.21	3.50	3.37	3.31	3.51	3.34	3.56	3.50	3.53	

^a Food webs for the three river sub-basins are composite webs including all three physiographic regions.

Results

Fish species richness increased longitudinally from mountain to prairie streams with low variability for mountain and prairie streams (mountain, mean 13.6 ± 0.57 SD, foothills, mean 19.6 ± 3.05 SD, prairie, mean 29.3 ± 1.52 SD; Tables 2 and 3). Fish species richness was more variable across the foothill physiographic region, ranging from 29 in the Red Deer to 17 in the Bow. The Oldman had an intermediate fish species richness of 23.

Fish species richness and connectance increased longitudinally across physiographic regions (Table 3). Fish species richness was positively related to taxa richness ($R = 0.85$, $p = 0.004$), indicating that significant changes according to physiographic region were primarily a result of changes in the species richness of the fish communities. However, fish species richness was unrelated to connectance ($R = -0.58$, $p = 0.103$). Fish species richness and connectance were unrelated to the proportion of top species in the web, which in these food webs were all predatory fish, as well as the proportion of intermediate species.

The only other food web properties that were significantly different according to physiographic region were the proportion of herbivores and the proportion of cannibals. Herbivory was highest in the mountain streams and was negatively related to fish species richness ($R = -0.85$, $p = 0.004$). Cannibalism was highest in the foothills and was strongly related to connectance ($R = 0.68$, $p = 0.04$).

Prominent differences across rivers by physiographic regions include 1) high fish species richness in the foothills region of the Red Deer ($S = 23$) in comparison with the Bow ($S = 17$) and the Oldman ($S = 19$), 2) high proportions of top predators in the foothill region of the Bow (15.62%) in comparison with the Red Deer (7.32%) and the Oldman (2.56%), and 3) higher connectance in the Bow for all three physiographic regions compared to the other two river basins. While we were unable to test each of these food web properties statistically, the patterns suggest that differences across the three river sub-basins in geomorphology or land-use may also affect food-web properties especially in the foothills regions.

Discussion

One of the clearest results of our analysis is that physiographic regions affected food-web structure primarily by altering fish species richness and connectance. As we discuss below, the structural correlates of this variation are profound but differences between sub-basins are much less apparent. Physiographic region affected 4 of the 17 empirical food-web properties,

Table 3. Kruskal-Wallis ANOVA results for variation in food web structure for a) variation between river basins, and b) variation between physiographic regions across basins.

Source of variation	DF	n	F	p
A) River basin				
Taxa richness	2	9	2.039	0.361
Fish species richness	2	9	0.695	0.707
Maximum trophic level	2	9	2.000	0.368
% Top	2	9	2.622	0.270
% Intermediate	2	9	3.289	0.193
% Basal	2	9	5.067	0.079
% Herbivore	2	9	0.157	0.925
Connectance	2	9	1.422	0.491
Links/species	2	9	0.622	0.733
Chain length	2	9	4.622	0.099
Chain length SD	2	9	2.489	0.288
Trophic level	2	9	2.756	0.252
Trophic level SD	2	9	4.622	0.099
Cannibalism	2	9	0.622	0.733
Direct omnivory	2	9	1.367	0.505
Consumer direct omnivory	2	9	4.782	0.092
Consumer mean trophic level	2	9	1.422	0.491
B) Physiographic region				
Taxa richness	2	9	4.392	0.111
Fish species richness*	2	9	7.261	0.027
Maximum trophic level	2	9	4.095	0.129
% Top	2	9	2.779	0.249
% Intermediate*	2	9	3.200	0.202
% Basal	2	9	0.622	0.733
% Herbivore*	2	9	6.006	0.050
Connectance*	2	9	6.489	0.039
Links/species	2	9	5.600	0.061
Chain length	2	9	0.800	0.670
Chain length SD	2	9	2.400	0.301
Trophic level	2	9	2.400	0.301
Trophic level SD	2	9	1.156	0.561
Cannibalism*	2	9	7.200	0.027
Direct omnivory	2	9	2.420	0.298
Consumer direct omnivory	2	9	1.931	0.381
Consumer mean trophic level	2	9	2.400	0.301

* indicates significant difference.

including fish species richness and connectance. These consistent longitudinal shifts in food-web properties appear to reflect the degree to which fish species richness is affected by riverine geomorphology and physicochemistry as the rivers flow through mountain, foothill, and prairie regions. The terrain surrounding mountain streams in the SSRB is characterized by forested valleys, often with little or no cultivation. Foothill streams are surrounded by wide forested valleys and cultivated plains, while prairie streams are surrounded by cultivated and urban plains. In each sub-basin large-scale physical variables such as depth and area, and chemical conditions such as temperature and nutrient loading generally increase longitudinally from mountain streams to prairie streams. These changes in physicochemical conditions according to physiographic region exert a strong effect on the species composition of riverine fish communities with cold-water species dominating mountain streams, cold- and cool-water species in foothills regions, and primarily cool-water species found in prairie regions. Physicochemical conditions exert strong effects on the species composition of riverine fish communities

(Vannote et al. 1980), and are related primarily to river morphometry, hydrodynamics and temperature (Ryder and Pesendorfer 1989). However, not only does the fish community composition change in a predictable manner longitudinally, but the fish species richness and connectance of the food webs also change predictably according to physiographic region.

We found an increase in fish species richness from mountain to prairie streams with low variability in mountain and prairie streams and higher variability in foothill streams. Fish species richness generally increases longitudinally in river systems (Sheldon 1968) as a function of water volume and productivity (Angermeier and Schlosser 1989) and has also been shown to increase with basin area, a correlate for river size (Allan and Flecker 1993). These regional factors have been shown to be more important in regulating stream fish diversity than local factors such as habitat complexity (Angermeier and Winston 1998). For example, Angermeier and Winston (1998) showed that regional diversity was the best predictor of local diversity for stream fish in Virginia. The higher variability in fish species richness across foothill physiographic regions may be due to greater differences across the rivers in land-use and geomorphology between foothill regions of the river basins than for either mountain or prairie regions. In the foothill regions of the Bow and the Oldman, the primary land-use is ranching while in the foothill region of the Red Deer land-use is more varied with a combination of agriculture and forestry.

Connectance increased from mountain to foothill to prairie streams. This result was expected given strong longitudinal control of trophic patterns in fish communities and the fact that more links increase the probability that consumers are themselves resources for other consumers. Increases in connectance from mountain to prairie streams may also be related to longitudinal changes in productivity. For example, Thompson and Townsend (2005) found that connectance was higher in high productivity grassland stream webs than in forested webs. Connectance has also been shown to be highest in webs with large proportions of intermediate and omnivorous species (Dunne et al. 2004). While connectance was unaffected by the proportion of intermediate or omnivorous species in the river food webs, it was negatively related to the proportion of cannibals and positively related to the proportion of herbivores suggesting that variability in connectance in these river webs is primarily due to changes the trophic relationships between the fish species.

Comparisons with other food webs

Connectance and linkage density are generally highest in webs with large proportions of intermediate and

omnivorous species (Dunne et al. 2004). In comparison with other published webs, connectance in the empirical river food-webs (mean 0.118, range 0.1–0.133) was slightly lower than terrestrial (0.03–0.31), lake/pond (0.12–0.32), or marine (0.06–0.27) food webs, but was more similar to stream (0.07) and estuarine (0.04–0.1) webs (Dunne et al. 2004). However, it is important to note that if we had included more highly resolved meiofaunal and macrofaunal taxa the connectance of the river food webs would likely have been even lower. For example, a recent highly resolved tropical stream food web in Brazil which included all food web compartments including fishes had an overall connectance of 0.05 (Motta and Uieda 2005). The distribution of taxa between top, intermediate, and basal levels in the river food webs were more similar to lake and pond webs that have higher proportions of intermediate species than other stream webs. This discrepancy may be expected from the lack of fishes in other stream food webs (Dunne et al. 2004). In contrast, chain length in the river food-webs was more similar to fishless stream food webs (3.1–3.2) than to lake or pond webs (4.0–10.7) (Dunne et al. 2004).

Conclusion

Regional influences such as zoogeographic history are often cited as determinants of biodiversity patterns in stream fish communities (Angermeier and Winston 1998). For example, fish communities in low elevation streams in eastern North America are more diverse than in western North America (Mahon 1984, Moyle and Herbold 1987). In the SSRB however, while the specific composition of the fish communities differed between sub-basins, overall food-web structure was remarkably consistent between river sub-basins and only changed consistently across physiographic regions. This means that differences in river food webs might be viewed as generally expected changes driven by longitudinal processes affecting fish species richness and connectance along the river network. A similar result was found by Thompson and Townsend (2003) when they compared the food web structure of food webs in pine-forest streams in New Zealand with pine-forest streams in Maine and North Carolina. They found structural similarities between the stream food webs regardless of location (Thompson and Townsend 2003).

In river ecology, the emphasis on longitudinal patterns and processes embodied by the river continuum concept (Vannote et al. 1980) and nutrient spiraling (Newbold et al. 1981) have long been considered unifying concepts. Within this longitudinal continuum there are important discontinuities (Ward and Stanford 1983) such as dams that act to reset to biotic communities along gradients.

Physiographic regions within drainages have been previously shown to support distinctive fish faunas (Hocutt and Wiley 1986, Jenkins and Burkhead 1994, Angermeier and Winston 1998). However, few if any published studies have previously attempted to describe longitudinal variations in food-web structure within a drainage basin. In river networks, upstream-downstream linkages, the longitudinal nature of the patterns and processes, and strong physical forcing on the biota argue strongly for more thorough descriptions of how food-web structure changes along river networks. Our results suggest that these processes may lead to some consistent changes in fish species richness, connectance, and other highly correlated food-web properties as rivers flow through different physiographic regions. Further explorations of river and other food webs would greatly illuminate this suggestion.

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