Longitudinal Zonation of Pacific Northwest (U.S.A.) Fish Assemblages and the Species-Discharge Relationship

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Fish ecologists often use species-discharge relationships (SDRs) to understand how species richness varies with aquatic habitat availability, but few SDR studies have considered whether the reported SDRs are scale-dependent, or attributed the SDR to a specific causal mechanism. Here, we assessed whether the SDR is scale-dependent by using individual river reaches, rather than complete river basins, as sampling units in a SDR analysis. We also determined whether the SDR is a function of among-reach habitat diversity. To do so, we first tested for longitudinal zonation along three major Pacific Northwest (U.S.A.) rivers. Our zonation tests consistently detected 'lower,' 'middle,' and 'upper' river fish assemblages, each of which was characterized by common patterns in adult habitat use, feeding guild structure, and reproductive behavior, and was associated with predictable habitat conditions. When these longitudinal zones were used as sampling units in a SDR analysis (i.e., total discharge and species richness within each zone), we detected strong linear relationships between discharge and species richness (log_{10} data). Because individual zones predicted species richness more effectively than complete basins, we conclude that the SDR is scale-dependent. And we infer that among-zone habitat shifts are an important determinant of the SDR, as the slope of the SDR is a function of the differential richness found in each zone.

SPECIES-discharge relationships (SDRs), which are analogous to terrestrial species-area relationships, but focus explicitly on aquatic habitats and their inhabitants (Matthews, 1998), are valuable tools in the study and conservation of freshwater fish diversity (Xenopoulos et al., 2005). For example, in a global analysis of 166 rivers, Oberdorff et al. (1995) found river discharge to be the most effective predictor of fish species richness. Likewise, Xenopoulos and Lodge (2006) reported significant linear relationships between discharge and fish richness in Upper Mississippi River drainages and southeastern (U.S.A.) drainages, then used these SDRs to predict the numbers of species that would become vulnerable to extinction if specific flow reductions were to occur, thereby diminishing aquatic habitat availability. These studies illustrate the importance of documenting SDRs in basic and applied fish research. However, they are also subject to two shortcomings of the basic species-area relationship method (Connor and McCoy, 1979; Drakare et al., 2006). First, Oberdorff et al. (1995) and Xenopoulos and Lodge (2006) do not clarify whether the reported SDRs are scale-dependent; both studies use large, complete-basin taxa lists as their basic sampling units, without testing the effects of smaller (i.e., sub-basin scale) sampling units. Second, they do not attribute the SDRs to any particular causal mechanism (McGuinness, 1984; Gotelli and Graves, 1996).

A means of overcoming both of these limitations was devised by Buckley (1982), while studying the plant diversity of a West Australian archipelago. On each island, Buckley (1982) summed the total surface area of each of several habitat types, and noted the total number of plant species occurring within each habitat. He then used these area measurements and the associated plant richness values as sampling units in a species-area analysis, finding that the habitat-specific data predicted species richness more effectively than complete island data (i.e., the total area and richness of each island, regardless of intra-island habitat variability). Buckley (1982) therefore demonstrated that the species-area relationship for West Australian plants is scale-dependent, as the slope, fit, and significance of the habitat-specific regression model differed from the complete island model. He also established a causal link between habitat diversity and the species-area relationship: larger islands were inhabited by more species because they featured a greater diversity of habitat types (Buckley, 1982; Gotelli and Graves, 1996). This was a significant discovery because it showed that island diversity is not necessarily driven by immigration and extinction rates, as suggested by the Theory of Island Biogeography (MacArthur and Wilson, 1967). Rather, it can be a function of intra-island habitat diversity (Gotelli and Graves, 1996).

Here, we use an approach similar to Buckley's (1982) to determine whether habitat-specific data, at the sub-basin scale, will reveal a significant SDR for fish assemblages in three Pacific Northwest (U.S.A.) rivers. First, we test for longitudinal zonation along each of the three rivers. Longitudinal zonation occurs when fish assemblages with distinct taxonomic and functional characteristics are distributed along longitudinal river gradients, in association with specific types of longitudinally-oriented habitats (Hawkes, 1975; Vannote et al., 1980; Schlosser, 1987). A classic example is Huet's (1959) description of Western European rivers, which contain discrete 'trout,' 'grayling,' 'barbel,' and 'bream' zones. Balon and Stewart (1983) detected 'headwater,' 'foothill,' 'floodplain,' and 'exit' zones within an African river (Luongo River, Zaire). Ibarra and
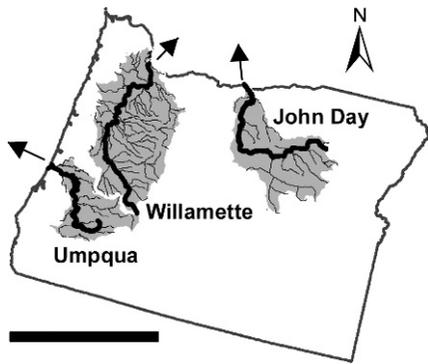
Fig. 1. Locations of the three study basins in Oregon. River courses that were converted to longitudinal profiles are shown as heavy black lines. The Willamette course flows from June Lake (43.39°N, 122.13°W) to the Middle Fork Willamette River, to the mainstem Willamette River. The Umpqua course flows from Last Creek (43.17°N, 122.75°W) to Boulder Creek, to the South Umpqua River, to the mainstem Umpqua River. The John Day course flows from Hidaway Creek (45.08°N, 118.58°W) to Camas Creek, to the North Fork John Day River, to the mainstem John Day River. Arrows indicate the direction of flow. Scale bar length is 250 km.

Fig. 2. Longitudinal profiles of the Willamette, Umpqua, and John Day Rivers. Dashed vertical lines reflect the approximate locations of longitudinal zone boundaries (i.e., demarcations between lower, middle, and upper zones).

Stewart (1989) observed four fish zones in a South American river (Napo River, Ecuador). Zonation studies have been more equivocal in North American rivers, with some authors reporting discrete zones (Burton and Odum, 1945; Maurakis et al., 1987), others reporting a gradual downstream accumulation of species (i.e., species additions, rather than replacements; Sheldon, 1968; Evans and Noble, 1979), and some reporting mixed results (Rahel and Hubert, 1991; Matthews, 1998). But regardless of whether longitudinal zones are truly saltatory, or occur through incremental additions, it is clear that some degree of subdivision is necessary to accurately characterize local fish assemblages within large river systems (Angermeier and Winston, 1999; Olden et al., 2006). And the zonation approach has generally served this purpose well (Huet, 1959; Hawkes, 1975; Matthews, 1998).

Next, we apply the results of our longitudinal zonation tests to a sub-basin scale SDR analysis. Because these zones consist of distinct biotas and habitats, we hypothesize that they are analogous to Buckley's (1982) habitat units, and therefore appropriate for use in a habitat-specific SDR analysis: each drainage basin is an independent 'island' (Hugueny, 1989), and each longitudinal zone is a distinct habitat type with a characteristic fish fauna. To perform this SDR analysis, we estimate river discharge within each zone. Discharge is used in lieu of other measures of aquatic habitat 'size,' such as two-dimensional surface area (i.e., channel length × mean channel width), because it is a particularly effective predictor of fish species richness (Livingstone et al., 1982; Oberdorff et al., 1995; Xenopoulos et al., 2005). Discharge also regulates many of the functional processes (e.g., habitat diversity and complexity, habitat selection, and trophic dynamics) that govern fish assemblage structure (Poff and Allan, 1995; Lamouroux et al., 1999, 2002). We then regress these discharge estimates against the observed fish species richness within each zone to create a sub-basin scale (i.e., zone-specific) SDR. Ultimately, this process allows us to test whether the SDR for Pacific Northwest fishes is scale-dependent and to determine whether fish species richness is causally linked to habitat diversity.
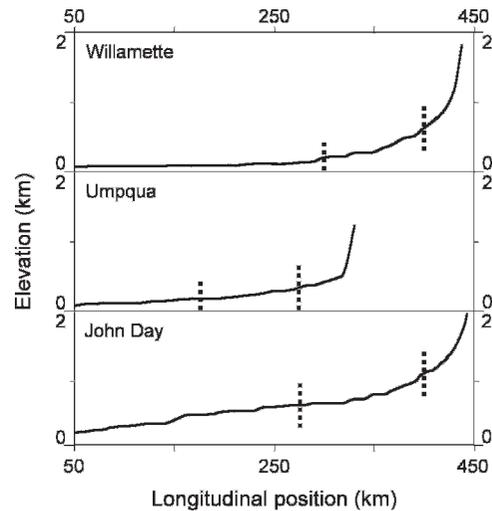
MATERIALS AND METHODS

Study area and data compilation.—We examined fish assemblages in the Willamette, Umpqua, and John Day river basins (Fig. 1). In each basin, we selected a single, discrete river course, which flowed from a headwater tributary to either a Columbia River confluence (Willamette and John Day) or the Pacific Ocean (Umpqua). These river courses (Fig. 1) were queried from the U.S. Geological Survey's (USGS) National Hydrography Dataset (U.S. Geological Survey, 2000) and superimposed on 30-m USGS National Elevation Dataset (Gesch et al., 2002) grids to create longitudinal river profiles (Fig. 2). Spatial operations were performed with ArcInfo (Environmental Systems Research Institute, Redlands, CA).

Fish assemblage data were compiled from the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) database, including 429 geo-referenced point samples, distributed throughout the three study basins. All EMAP samples were collected between June–August (1983–2003; all data pooled) with standardized methods (i.e., single-pass backpack electrofishing in wadeable streams and single-pass boat electrofishing in non-wadeable rivers; Hughes et al., 2002; Peck et al., 2006). Abundance data were employed in each of the longitudinal zonation tests to maximize analytical power (Rahel, 1990). We also used geo-referenced, presence–absence records (2624 localities; 76 recognized species) from the Oregon State University ichthyology collection to ensure that our species counts within each longitudinal zone were complete (see 'Species-discharge relationship').

Longitudinal zonation.—We characterized fish assemblage structure along each river profile by superimposing the geo-referenced EMAP samples onto their respective river localities, then pooling them within equal-interval, 50-km segments (Horwitz, 1978; Matthews, 1998). These segments allowed us to account for non-uniform spatial distributions and minimized spatial autocorrelation bias (Ludwig and Cornelius, 1987; Hofer et al., 1999). Equal-interval river

segments were identified by their downstream boundaries; for example, segment '150' represents river kilometers 150–199, moving in the upstream direction. The 0-km segment was removed from each river to minimize the confounding influences of downstream assemblages (i.e., Columbia River fishes in the Willamette and John Day, and Pacific estuarine fishes in the Umpqua). Also, we did not have data to fill the 150-km and 250-km segments on the Umpqua River, or the 250-km segment on the John Day River. These data gaps constrained our ability to identify the precise locations of some longitudinal zone boundaries. They did not, however, preclude us from detecting longitudinal zonation; whenever data gaps occurred between segments with significantly different fish assemblages, we interpolated a longitudinal zone boundary at the midpoint between those segments.

Because EMAP samples were unevenly distributed among the equal-interval segments, we standardized the data within each segment (Gotelli and Colwell, 2001). For each river, we 'rarefied' the fish data by superimposing individual EMAP samples upon the longitudinal profile, then pooling samples within 50-km equal-interval segments. The total number of individuals within each segment was summed from the per-sample totals, and a standard number of rarefied individuals was randomly selected from each segment, as determined by the segment with the fewest total individuals. All rarefied samples reached an asymptotic 'probability of interspecific encounter' (PIE) evenness score, and were therefore considered reliable indicators of local fish assemblage structure (Gotelli and Graves, 1996). Hierarchical cluster analyses (Bray-Curtis similarity, average linkage) and nonmetric multidimensional scaling (NMDS; Bray-Curtis similarity, city-block distance) were then used to examine longitudinal zonation patterns. Segments that were joined by a ≥75% similarity clustering criterion, and which aggregated in NMDS plots, were assumed to comprise distinct longitudinal zones, while zone boundaries were inferred from clusters that were <75% similar, and which did not aggregate in NMDS plots. Rarefaction and PIE evenness calculations were performed with EcoSim 7.0 (Gotelli and Entsminger, Acquired Intelligence Inc. and Kesey-Bear, http://www.garyentsminger.com/ecosim/index. htm), and cluster analyses and NMDS ordinations were performed with SYSTAT 11.0 (SYSTAT Software, Inc., Richmond, CA).

Finally, we used mean similarity tests to assess the significance of the longitudinal zonation results (Van Sickle and Hughes, 2000). To perform these tests, we randomly selected five independent EMAP samples (i.e., samples that were not included in the rarefied datasets) from within each of the longitudinal zones. These samples were used to calculate average Bray-Curtis similarities within each longitudinal zone, as well as the grand mean of all within-zone averages (W_{avg}). We then calculated average between-zone similarities (B_{avg}) for each river, and compared these values with the W_{avg} values. Strong zonation was indicated by W_{avg} values that exceeded B_{avg} values, thereby demonstrating that assemblage structure was similar within zones, but dissimilar among zones (Van Sickle and Hughes, 2000). Monte-Carlo simulations (1,000 iterations per river) were then used to perform significance tests. In each iteration, the independent samples were randomly shuffled among longitudinal zones, and the W_{avg} and B_{avg} values were recalculated. P-values were then estimated as the number of iterations in

which

$$(W_{avg} - B_{avg})_{\text{simulated}} \geq (W_{avg} - B_{avg})_{\text{empirical}}.$$

These simulations tested the null hypothesis of 'no longitudinal structure' (Van Sickle and Hughes, 2000). Mean similarity tests were performed with MEANSIM 6.0 (Van Sickle, U.S. Environmental Protection Agency, http://www.epa.gov/wed/pages/models/dendro/mean_similarity_analysis.htm).

Zone characteristics.—After confirming the significance of the zonation results, we used species-level descriptions of primary adult habitats, feeding guilds, and reproductive habits to compare the functional characteristics of each ichthyofaunal zone (Hughes et al., 1998; Zaroban et al., 1999; Wydoski and Whitney, 2003). By applying these descriptions to the abundance data used in zonation analyses, we were able to determine whether conspicuous patterns in behavior and resource use occurred among zones and basins. We also documented the following habitat characteristics for each longitudinal zone. Mean channel slope within each longitudinal zone was interpolated from the longitudinal profiles (Fig. 1). Mean August discharge, which coincided with EMAP sampling, was estimated at the mid-point elevation of each longitudinal zone with linear regression models. Discharge models were created for each river by selecting all USGS gauging stations along each of the four river profiles with 40 years of continuous data on record, then regressing mean August discharges ($\log_{10}$ data) against their respective gauge elevations (independent variable). Linear models of the Willamette ($n = 9$), Umpqua ($n = 4$), and John Day ($n = 4$) rivers accounted for 99.1, 82.1, and 78.5% of the August flow variability, respectively. Mean wetted channel width was measured directly from USGS aerial photos (1-m resolution, taken on dates when local discharge was within ±25% of the 40 year average). Mean August maximum air temperature, which is strongly correlated with water temperature in western U.S. rivers (Rahel and Hubert, 1991), was estimated for each longitudinal zone by superimposing the longitudinal profiles on continuous-coverage, PRISM grids (2.5 arc-minute cells, provided by the Spatial Climate Analysis Service at Oregon State University, http://www.ocs.oregonstate.edu/prism/). Total channel length within each longitudinal zone was estimated by querying all river segments that occurred between the minimum and maximum elevations of each longitudinal zone (interpolated from Fig. 2), then summing their lengths. Finally, we estimated the total discharge within each longitudinal zone by multiplying the mean August discharge results (km² water · km river channel · s⁻¹) by the total channel length (km) within each zone. Note that these discharge estimates were, in effect, instantaneous water volumes. We maintained the 'discharge' label, however, for consistency with the current literature.

Species-discharge relationship.—To determine the species richness of each longitudinal zone, we supplemented the full EMAP dataset with geo-referenced records from the Oregon State University ichthyology collection. Species' occurrences were documented within each zone using three criteria: only empirical data were used (i.e., anecdotal references were not included); species status in Nelson et al. (2004) was the criterion for all species designations (suspected, but unverified species and sub-species were
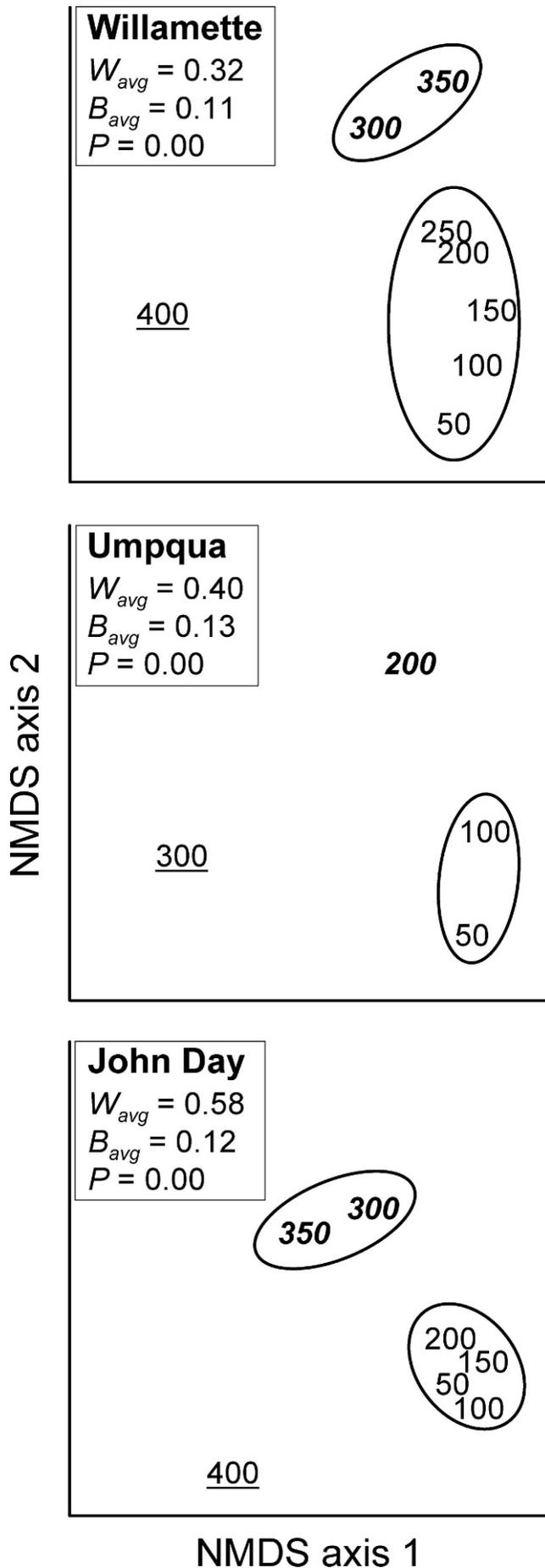
excluded); and anomalous documentations of non-native species were excluded (e.g., a single record of Florida Gar, *Lepisosteus platyrhincus*). After tallying the number of species in each zone, we regressed these zone-specific richness values against their respective total discharge values ($\log_{10}$ data) to generate a SDR (Rosenzweig, 1995). This process was performed with both a complete species dataset and a native species only dataset (i.e., non-native species removed).

RESULTS

Longitudinal zonation.—Cluster analyses and NMDS ordinations revealed three distinct zones in each basin (Fig. 3). These results were supported by mean similarity tests, which showed that rarefied fish samples within zones were consistently more similar than samples among zones (i.e., $W_{avg} > B_{avg}$) and which confirmed the statistical significance of the zonation patterns (Fig. 3). Each of these zones was, in turn, characterized by a predictable suite of functional, assemblage-level characteristics. For example, species that preferred benthic (e.g., Chiselmouth, *Acrocheilus alutaceus*) and water column habitats (e.g., Northern Pikeminnow, *Ptychocheilus oregonensis*), which were common in the lower and middle zones, were replaced in the upper zones by cryptic, hiding species (e.g., Reticulate Sculpin, *Cottus perplexus*; Fig. 4A). Top predators (e.g., Smallmouth Bass, *Micropterus dolomieu*), omnivores (e.g., Largescale Sucker, *Catostomus macrocheilus*), and herbivores (e.g., Bridgelip Sucker, *Catostomus columbianus*) were abundant in the lower zones, but were gradually replaced in the middle and upper zones by invertivores (e.g., Speckled Dace, *Rhinichthys osculus*; Fig. 4B). Also, active nest guarders (e.g., *M. dolomieu*) and vegetation spawners (e.g., Redside Shiner, *Richardsonius balteatus*) in the lower and middle zones were largely replaced by non-guarding cavity nesters (e.g., *C. perplexus*) in the upper zones, while lithophilic (i.e., gravel-spawning) species were common in all zones (Fig. 4C).

A predictable succession of physical habitat characteristics was also observed among the lower, middle, and upper zones (Table 1). Along all profiles, mean channel slope increased gradually from lower to middle zones, then more abruptly from middle to upper zones. Mean August discharge increased rapidly from upper to lower zones. Mean wetted channel width and mean August maximum air temperature also increased downstream, though at slower, approximately linear rates. Total channel length was more variable, increasing upstream in the Umpqua and John Day Basins, but downstream in the Willamette. Total discharge did, however, increase in the downstream direction in all basins (Table 1). In general, the lower zones in each basin were large, warm, low gradient habitats, while the upper zones were small, cool, high gradient environments (Carter and Resh, 2005; Stanford et al., 2005).

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Fig. 3. Nonmetric multidimensional scaling (NMDS) ordinations of the Willamette, Umpqua, and John Day River segments. Points within each plot are identified by their respective longitudinal positions (e.g., point '100' represents the 100-km through 149-km segment). Segments that were at least 75% similar in cluster analyses (i.e., within the same zone) are circled. Mean within-zone similarities (W_{avg}), mean between-zone similarities (B_{avg}), and mean similarity test *P*-values are shown for each river. Lower, middle, and upper zone segments are indicated by plain, bold-italic, and underscored characters, respectively.
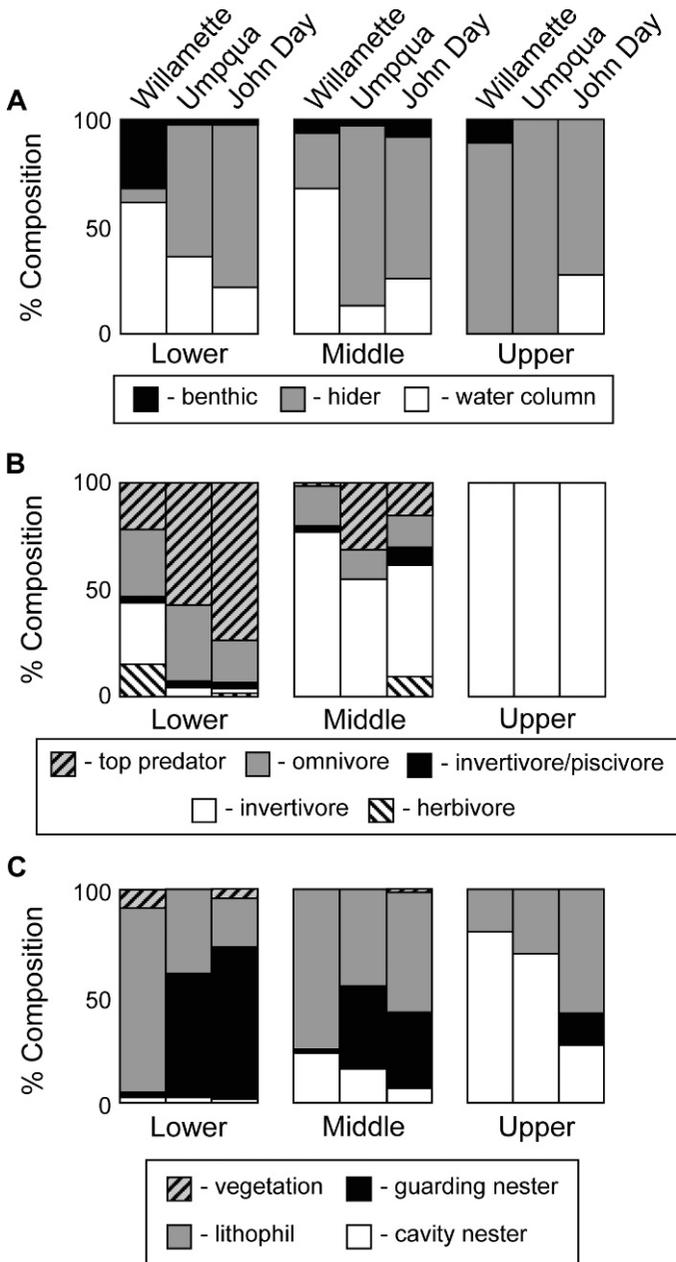
Fig. 4. Functional characteristics of the lower, middle, and upper zone fish assemblages in each of the study basins, including (A) primary adult habitats, (B) feeding guilds, and (C) reproductive habits. All data are expressed as percentages. In each panel, longitudinal zone membership is shown on the primary (lower) x-axis, while basin identity is shown along the secondary (upper) x-axis.

Species-discharge relationship.—Sixty-seven fish species (38 native and 29 non-native species) were assigned to at least one of the 12 longitudinal zones (Appendix 1). Of these, 13 (eight non-natives) were endemic to a single basin and zone. The majority of species were, however, cosmopolitan: 45 species occurred in more than one basin, and 50 occurred in at least two of the three longitudinal zones. When total (i.e., native and non-native) species richness within each zone ($\log_{10}$ data, dependent variable) was regressed against the discharge estimate in each zone ($\log_{10}$ data, independent variable), it exhibited a linear, highly significant SDR (Fig. 5A; $P < 0.01$, $r^2 = 0.94$) with a slope (z) of 0.19. The native species only SDR (Fig. 5B) was also highly significant

Table 1. Environmental Characteristics of the Lower, Middle, and Upper Zones of the Willamette, Umpqua, and John Day Rivers.

Environmental variable	Willamette			Umpqua			John Day		
	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Elevation range (m)	35–180	181–608	609–1805	55–127	128–254	255–1181	183–605	606–1037	1038–2010
Mean channel slope (%)	0.09	0.43	3.39	0.08	0.20	2.72	0.19	0.43	3.35
Mean August discharge ($m^3 \cdot s^{-1}$)	150.45	30.28	0.03	14.02	3.85	0.01	4.39	0.93	0.05
Mean wetted channel width (m)	138.8	48.5	13.3	106.8	40.8	12.0	71.2	36.6	7.4
Mean August max air temp. (°C)	27.8	26.7	25.3	28.9	28.5	21.7	29.7	29.1	25.6
Total channel length (km)	8146	6949	6243	1471	2169	5318	1815	5046	9050
Total discharge ($km^3 \cdot s^{-1}$)	1225.57	210.42	0.19	20.62	8.35	0.05	7.97	4.69	0.45

($P < 0.01$), though with a lower coefficient of determination ($r^2 = 0.80$) and lower slope ($z = 0.13$).

DISCUSSION

Although SDRs for freshwater fish assemblages are increasingly well-documented (Oberdorff et al., 1995; Xenopoulos et al., 2005; Xenopoulos and Lodge, 2006), few studies have examined the SDR at sub-basin scales (but see Angermeier and Schlosser, 1989). We used longitudinal zones as independent, sub-basin sampling units and discovered remarkably strong SDRs for Pacific Northwest fishes (Fig. 5A, 5B). This is an important result for two reasons. First, it demonstrates that the SDR is scale-dependent: when the complete-basin method (i.e., total species richness within each basin regressed upon average discharge at the mouth of each basin) of Xenopoulos and Lodge (2006) was applied to nine other Pacific Northwest basins (Rogue, Siuslaw, Alsea, Tillamook, Nehalem, Sandy, Deschutes, Umatilla, and Grande Ronde; unpubl. data), the SDR was no longer significant ($P = 0.26$, $r^2 = 0.18$, $z = 0.14$). Second, it allows us to associate the SDR with a causal mechanism. Because the SDR is most apparent when zone-specific data are used, we can infer that it is largely a product of among-zone habitat diversity (Buckley, 1982; Gotelli and Graves, 1996).

Our SDR analyses also illustrate the success of non-native fishes in western (North America) rivers (Li et al., 1987; Gido and Brown, 1999). Both the all species (Fig. 5A) and native species only (Fig. 5B) SDRs were significant, but the slope of the all species SDR was much steeper, due to high numbers of non-native species in the middle (mean no. = 9.7) and lower (mean no. = 13.3) zones (see Appendix 1 for complete species lists within each zone). One mechanism driving non-native fish invasions in the Pacific Northwest has been the proliferation of artificial impoundments (Li et al., 1987). Impoundments create lentic habitats that favor many of the warmwater species found in eastern lakes and rivers (e.g., Smallmouth Bass and Walleye, *Sander vitreous*), and are an important vector for their establishment in Pacific Northwest rivers (Wydoski and Whitney, 2003). We do not believe, however, that impoundments are sufficient explanation for our SDR results, as none of the EMAP samples were collected from impoundments. Furthermore, non-native species are numerically dominant throughout much of the middle and lower John Day River (unpubl. data), yet the John Day has no major dams.

An alternative explanation for the large number of non-native fishes is that the region is not 'saturated' with species: harsh environmental conditions (e.g., volcanism and cyclic periods of flooding and desiccation) throughout the Tertiary and Quaternary Periods eliminated approximately one-half of the region's ancestral ichthyofauna (Smith, 1981; McPhail and Lindsey, 1986; Minckley et al., 1986). These extinctions may, in turn, have opened many ecological niches, which non-native fishes are now beginning to fill. This hypothesis is consistent with the general observation that rivers with low native diversity, such as those in the western U.S.A., tend to have the highest numbers of non-native fishes (Ross, 1991; Gido and Brown, 1999), and the fact that interspecific competition with non-native species has not, as yet, precipitated widespread native extirpations in the Pacific Northwest (unpubl. data; see also Li et al., 1987; Moyle and Light, 1996; Gido and Brown, 1999).

One mechanism that is frequently invoked to explain SDRs (and species-area relationships in general) is the
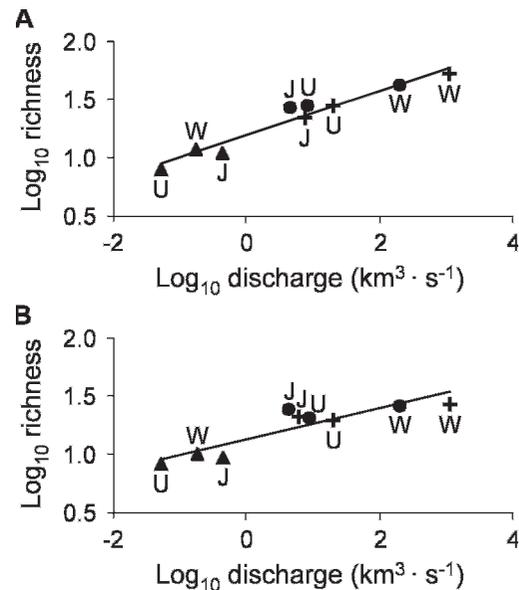
Fig. 5. Species-discharge relationships for (A) all species data (i.e., native and non-native species) and (B) native species only. Uppercase letters indicate river basins: W = Willamette; U = Umpqua; J = John Day. Triangles, circles, and crosses represent upper, middle, and lower zones, respectively.

Theory of Island Biogeography (McGuinness, 1984; Gotelli and Graves, 1996). Island Biogeography asserts that the SDR is the result of a dynamic equilibrium between immigration (increasing richness) and extinction (decreasing richness), in which larger islands have richer biotas because they tend to have lower density-dependent extinction rates (MacArthur and Wilson, 1967). That is, larger areas tend to have more species because they can support more individuals. Island Biogeography also predicts that the slope of the SDR should reflect the average rate of immigration, with steeper slopes indicating longer distances (i.e., lower immigration rates) between islands (Rosenzweig, 1995). Several fish studies have documented limited evidence of an Island Biogeography mechanism. For example, Oberdorff et al. (1997) demonstrated the importance of immigration by showing that fish species richness was higher in tributaries that shared species than in comparably sized, but isolated rivers in Western Europe and North America. When we used longitudinal zones as sampling units, however, we found that the Pacific Northwest fish SDR is parsimoniously explained by among-zone habitat diversity (Fig. 5). We therefore conclude that Island Biogeography is not necessary to account for the SDR in Pacific Northwest rivers.

Whether the slopes of our SDRs indicate a fundamental immigration/extinction dynamic is currently speculative (Connor and McCoy, 1979; McGuinness, 1984; Gotelli and Graves, 1996), but we do emphasize two points regarding the observed slopes. First, as indices of among-zone beta diversity (Rosenzweig, 1995; Drakare et al., 2006), the slopes can be used to estimate the rate of increase (or decrease) in fish species richness among upper, middle, and lower zones. This observation has important implications for the conservation of biological diversity in Pacific Northwest rivers (see below). Second, the slope of the all species SDR (Fig. 5A) approximates the average slope ($z \approx 0.17$) that Drakare et al. (2006; see their fig. 1e) calculated in their meta-analysis of non-nested (i.e., samples collected within a spatially non-

overlapping framework, such as longitudinal zones) stream data. This congruence suggests that species richness may be governed by similar mechanisms in other lotic assemblages. We therefore hope that our results will encourage further investigation of the SDR, using a zonal perspective.

We also suspect that our methods are broadly applicable, given the similarity between our longitudinal zonation results and the patterns found in other North American (Burton and Odum, 1945; Rahel and Hubert, 1991), South American (Ibarra and Stewart, 1989), African (Balon and Stewart, 1983), and European rivers (Hawkes, 1975; Ibarra et al., 2005). In each of these systems, 2–4 distinct, longitudinally oriented fish assemblages were identified along large river gradients. Schlosser (1987) explained this common pattern with a habitat heterogeneity and stability model: the most upstream zones are comprised of 'colonizing' species, which are resilient to the unstable flow regimes of headwater streams. Species richness is generally constrained in these zones by a lack of structural and trophic complexity. By contrast, the downstream zones, which offer persistent refugia (e.g., deep pools and backwater habitats) from environmental perturbations, are structurally and trophically diverse, and tend to support 'stable,' species-rich assemblages. Our zonation results are highly compatible with Schlosser's (1987) model. Primary adult habitats, functional feeding groups, and reproductive behaviors were most diverse in the lower zones, and least diverse in the upper zones (Fig. 5). This longitudinal trend corresponded with downstream increases in habitat availability (i.e., increasing discharge; Table 1), stability (Rathert et al., 1999; Torgersen et al., 1999), and species richness (Appendix 1). Together, these results suggest that assemblage-level responses to aquatic habitat diversity and stability were key determinants of the observed zonation (Schlosser, 1987; Poff and Allan, 1995; Matthews, 1998; Lamouroux et al., 2002).

One potential limitation of our zonation analysis is the coarseness of the sampling design. The 50-km segments constrained our ability to determine whether specific environmental features (e.g., dams or waterfalls) coincided with zone demarcations, and prevented us from detecting finer-scale changes in assemblage structure (Jackson et al., 2001). For example, using individual point samples, Hughes and Gammon (1987) identified three, rather than two (Fig. 2), fish assemblages between river kilometers 50–300 on the Willamette River. This disparity likely reflects differential sensitivity to microhabitat availability, which is a key determinant of fish assemblage structure (Gorman and Karr, 1978; Matthews, 1998; Lamouroux et al., 1999). Individual point samples should be less prone to obscure species-habitat relationships than composite samples, and we suspect that microhabitat-scale studies would reveal additional species richness trends (Gorman and Karr, 1978). For instance, Angermeier and Schlosser (1989) found that fish species richness is significantly correlated with the volume of individual pools in Illinois streams, but not with the volume of riffle habitats.

Disparate analytical methods could also explain why zonation studies in North American rivers have often reported gradual downstream transitions, rather than discrete zone boundaries. When Rahel and Hubert (1991) used point sample data to test for longitudinal zonation along Horse Creek (Wyoming), they observed mostly gradual, downstream species additions, with a single distinct boundary between high gradient, coldwater streams and low

gradient, warmwater rivers. Their analysis was, however, vulnerable to two statistical biases. First, it did not ensure an equal sampling effort among sites (i.e., their point sample data were not rarefied; Gotelli and Colwell, 2001). Second, it did not account for spatial autocorrelation (i.e., their samples were not uniformly spaced along the longitudinal profile; Legendre, 1993). Our method (rarefied data within 50-km segments), which accounted for both of these problems, was a logistical compromise between data availability and the need to make robust, statistically valid comparisons at large spatial scales (Rahbek, 2005). It also revealed patterns that were nearly identical to Li et al.'s (1987) conceptual model of Pacific Northwest fish zonation. We are therefore confident that the 50-km segments were well-suited to our objective, which was to characterize zonal assemblage structure and species richness across large expanses (>300 km) of river habitat.

As climate change and anthropogenic disturbances continue to encroach on natural environments, the species-area relationship is becoming an increasingly important component of conservation planning (Rosenzweig, 1995; Botkin et al., 2007). For instance, Xenopoulos and Lodge (2006) showed how the slope of the SDR could be used to estimate the number of species that are likely to be extirpated as increasing demands for freshwater reduce in-stream flows. They were particularly concerned about obligate large river fishes (e.g., Paddlefish, *Polyodon spathula*), which are not likely to survive in systems with substantially diminished flows (Xenopoulos and Lodge, 2006). We agree with the logic of Xenopoulos and Lodge (2006), suggesting that the slopes of our SDRs (0.19 for all species; 0.13 for native species; Fig. 5A, 5B) should be considered in regional conservation planning. And we point out that several Pacific Northwest fishes are found exclusively in large river (i.e., lower zone) habitats (e.g., Green Sturgeon, *Acipenser medirostris*, and White Sturgeon, *Acipenser transmontanus*), and may therefore be especially vulnerable to diminished flows (Wydoski and Whitney, 2003). However, we also acknowledge the cautions of Angermeier and Winston (1999), who explained why it is prudent to incorporate sub-basin units (zonal or otherwise) in conservation planning, and of Botkin et al. (2007), who explained why SDRs should account for habitat diversity before being used to forecast species extinctions. The zone-specific SDR method presented here addresses both of these concerns. It also allows us to recognize scale-dependence in the SDR, and to identify among-zone habitat diversity as a causal mechanism. It is therefore a tool with considerable potential in aquatic research and management.

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Appendix 1

Functional categories and longitudinal zone membership for Oregon fishes. Native status, primary adult habitat, feeding guild, and reproductive habit descriptions are from Hughes et al. (1998), Zaroban et al. (1999), and Wydoski and Whitney (2003). Species presences within the lower, middle, and upper zones are indicated by capital letters: W = Willamette; U = Umpqua; J = John Day. [a]Indicates a non-native species. [b]Primary adult habitats: benthic (Be); water column (Wc); hider (Hi). [c]Feeding guilds: invertivore/piscivore (IP); herbivore (He); invertivore (In); omnivore (Om); filterer (Fi); top predator (Tp). [d]Reproductive habits: lithophil/gravel (Li); cavity nester (Cn); vegetation (Ve); live-bearer (Lb); guarding nonlithophil nester (Gn); guarding lithophil (Gl); psammophil/sand (Ps).

Species	Functional categories[b,c,d]	Longitudinal zone		
		Lower	Middle	Upper
Acipenser transmontanus	Be, IP, Li	W		
Acrocheilus alutaceus	Be, He, Li	W, J	W, J	
Alosa sapidissima[a]	Wc, In, Li	W, U		
Ameiurus catus[a]	Be, IP, Cn	W		
Ameiurus melas[a]	Hi, IP, Cn	W, J	W, J	
Ameiurus natalis[a]	Hi, IP, Cn	W, U	W, U	
Ameiurus nebulosus[a]	Hi, IP, Cn	W, U	W, U	
Carassius auratus[a]	Be, Om, Ve	W	W	
Catostomus columbianus	Be, He, Li	J	J	
Catostomus macrocheilus	Be, Om, Li	W, U, J	W, U, J	
Catostomus occidentalis	Be, Om, Li	U	U	
Catostomus platyrhynchus	Be, He, Li	W, J	W, J	
Cottus aleuticus	Be, In, Cn	W		
Cottus asper	Be, IP, Cn	W, U, J	W, U, J	
Cottus bairdii	Be, In, Cn		W, J	W, J
Cottus beldingii	Hi, In, Cn	W, J	W, J	W, J
Cottus confusus	Be, In, Cn		W, J	W, J
Cottus gulosus	Hi, In, Cn		W, U	W, U
Cottus perplexus	Hi, In, Cn	W, U	W, U	W, U
Cottus rhotheus	Hi, IP, Cn	W, U, J	W, U, J	
Ctenopharyngodon idella[a]	Wc, He, Ve	W		
Cyprinus carpio[a]	Be, Om, Ve	W, J	W, J	
Fundulus diaphanus[a]	Wc, In, Ve	W		
Gambusia affinis[a]	Hi, Om, Lb	W, U	W, U	
Gasterosteus aculeatus	Hi, In, Gn	W, U	W, U,	
Ictalurus punctatus[a]	Hi, IP, Cn	W, J		
Lampetra richardsoni	Hi, Fi, Li	W, U, J	W, U, J	W, U, J
Lampetra tridentata	Hi, Fi, Li	W, U, J	W, U, J	W, U, J
Lepomis auritus[a]	Wc, IP, Gn	W	W	
Lepomis cyanellus[a]	Wc, IP, Gn	W, U	W, U	
Lepomis gibbosus[a]	Wc, IP, Gn	W, U	W, U	
Lepomis gulosus[a]	Wc, IP, Gn	W	W	
Lepomis macrochirus[a]	Wc, IP, Gn	W, U	W, U	
Lepomis microlophus[a]	Wc, IP, Gn	W	W	
Micropterus dolomieu[a]	Hi, Tp, Gl	W, U, J	W, U, J	
Micropterus salmoides[a]	Hi, IP, Gn	W	W	
Misgurnus anguillicaudatus[a]	Hi, Om, Ve	W		
Mylocheilus caurinus	Wc, In, Li	W, J	W, J	
Notemigonus crysoleucas[a]	Wc, Om, Ve	W		
Oncorhynchus clarkii	Hi, In, Li	U	W, U, J	W, U, J
Oncorhynchus kisutch	Wc, In, Li	W, U, J	U	
Oncorhynchus mykiss	Hi, In, Li	W, U, J	W, U, J	W, U, J
Oncorhynchus mykiss redband	Hi, In, Li	J	J	J
Oncorhynchus tshawytscha	Wc, In, Li	W, U, J	W, U, J	
Oregonichthys crameri	Hi, In, Ve	W	W	
Oregonichthys kalawatseti	Hi, In, Ve	U	U	
Perca flavescens[a]	Wc, IP, Ve	W		
Percopsis transmontana	Hi, In, Li	W	W	
Pimephales promelas[a]	Be, Om, Cn	W		
Platichthys stellatus	Be, In, Ps	W		
Pomoxis annularis[a]	Wc, IP, Ve	W	W	
Pomoxis nigromaculatus[a]	Wc, IP, Ve	W, U	W, U	
Prosopium williamsoni	Be, In, Li	W, J	W, J	

Appendix 1
Continued.

Species	Functional categories[b,c,d]	Longitudinal zone		
		Lower	Middle	Upper
Ptychocheilus oregonensis	Wc, Tp, Li	W, U, J	W, U, J	
Ptychocheilus umpquae	Wc, IP, Li	U	U	
Rhinichthys cataractae	Hi, In, Li	W, U, J	W, U, J	
Rhinichthys evermanni	Hi, In, Li	U	U	
Rhinichthys falcatus	Hi, In, Li	W, J	W, J	
Rhinichthys osculus	Hi, In, Gl	W, U, J	W, U, J	
Richardsonius balteatus	Wc, In, Ve	W, U, J	W, U, J	
Salmo trutta[a]	Hi, In, Li		W, J	W, J
Salvelinus confluentus	Hi, In, Li		W, J	W, U, J
Salvelinus fontinalis[a]	Hi, In, Li			W, J
Sander vitreous[a]	Wc, IP, Li	W		
Thaleichthys pacificus	Wc, In, Li	W		
Tinca tinca[a]	Wc, In, Ve	W		