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Influence of Rare Species on Electrofishing Distance When Estimating Species Richness of Stream and River Reaches

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Abstract.—The electrofishing distance needed to estimate fish species richness at the stream or river reach scale is an important question in fisheries science. This distance is governed by the shape of the species accumulation curve, which, in turn, is influenced by a combination of factors, including the number of species, their overall abundances, habitat associations, the efficiency of the sampling method, and the occurrence of rare species. In this study we document the influence of rare species on the species accumulation curves from stream and river sites in data sets from five dispersed regions of the USA. Spatial discontinuity (i.e., a noncontinuous distribution within reaches) was observed in four of the five data sets, and the four data sets contained numerically rare species represented by one or two individuals (termed singletons and doubletons, respectively). Numerically rare species were typically proportionally rare (i.e., <1% of the total number of individuals captured), but proportionally rare species were not always numerically rare and were dependent on the total number of fish captured. Species richness asymptotes were reached at shorter electrofishing distances when singletons and doubletons were removed. The number of singletons and doubletons in the samples remained relatively constant with increasing sampling effort (i.e., sampling distance and total abundance). Simulation modeling indicated that individual aggregation within species was not a plausible reason for spatially discontinuous species distributions. When accurately detecting the presence of species is a sampling goal, the presence and prevalence of numerically rare species may need to be considered in determining sampling protocols.

Fish species richness is frequently used to quantify the effect of environmental changes (Xenopoulos and Lodge 2006) and assess biological condition at stream and river sites (Karr et al. 1986; Simon 1998; Whittier et al. 2007; Pont et al. 2009). In general, the number of fish species captured initially increases sharply with the sampling distance, and incrementally more sampling yields diminishing returns in observing additional new species (Lyons 1992; Angermeier and Smogor 1995; Paller 1995; Erős et al. 2008). This pattern results in a

classic asymptotic species accumulation curve. Inadequate sampling efforts (i.e., shorter reach distances) tend to underestimate true species richness of sites, but excessive sampling precludes an efficient use of limited resources. Sampling effort at a reach is typically considered appropriate at a distance at which most of the observed species (90–95%) are captured (Angermeier and Smogor 1995; Patton et al. 2000; Hughes et al. 2002; Dauwalter and Pert 2003a; Reynolds et al. 2003).

Many studies have investigated the distance required to estimate species richness in stream and river reaches and have differed greatly in the linear electrofishing distances recommended (22–85 mean stream widths

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[MSW]; Lyons 1992; Angermeier and Smogor 1995; Paller 1995; Patton et al. 2000; Hughes et al. 2002; Reynolds et al. 2003; Meador 2005; Utrup and Fisher 2006; Dos Anjos and Zuanon 2007; Hughes and Herlihy 2007; Maret et al. 2007). The variability of electrofishing effort requirements potentially results from the interplay of multiple factors such as the number of species (Cao et al. 2001; Meador 2005), fish habitat associations (Angermeier and Winston 1998; Lamouroux et al. 1999), overall abundances (Angermeier and Schlosser 1989; Cao et al. 1998; Nichols et al. 1998), and the occurrence of rare species (Paller 1995). In addition to intrinsic attributes of fish assemblages, extrinsic factors also influence species accumulation, including gear efficiency and selectivity (Meador and McIntyre 2003), reach selection by fisheries workers (Yant et al. 1984; Balkenbush and Fisher 1999; Hughes et al. 2002), and sampling protocols (Meador 2005; Kimmel and Argent 2006). In many studies, additional new species were frequently captured with increased sampling, and the species accumulation curves did not asymptote (Angermeier and Smogor 1995; Paller 1995; Hughes et al. 2002).

Spatially discontinuous distributions of organisms slow species accumulation and influence the shape of species accumulation curves (Angermeier and Smogor 1995; Chazdon et al. 1998; Cao et al. 2001). Therefore, it is of interest to quantify the degree of spatial discontinuity in fish data. A factor causing spatial discontinuity may be selection or avoidance of particular habitat by fish (Angermeier et al. 2002). Many stream fishes are shown to be associated with certain habitat units (e.g., riffles or pools; Angermeier and Winston 1998; Lamouroux et al. 1999; Peterson and Rabeni 2001; Erős et al. 2008), and often habitat units are not equally represented in all stream reaches.

Another plausible reason for spatial discontinuity is the presence of rare species (Angermeier and Smogor 1995; Angermeier et al. 2002). Fish species can be rare in samples because their required habitats are rare in the reach sampled (see previous paragraph), because their population density is genuinely low, or because they were inadequately sampled by an inefficient sampling technique (Novotný and Basset 2000). The occurrence of many rare species, while a few are common, is observed in biological assemblages across taxa and ecosystems (Magurran and Henderson 2003). The ratio of rare to common species influences the shape of the species accumulation curve (Novotný and Basset 2000; Thompson and Withers 2003). Electrofishing data from rivers and streams often includes rare species represented by one or two individuals (e.g., Hughes et al. 2002), termed singletons or doubletons, respectively. Singletons and doubletons have been used

as an indicator of rarity in terrestrial assemblages (e.g., tropical insects; Novotný and Basset 2000), but have not been used in stream fish data. This is potentially important as singletons and doubletons represent numerical rarity, as opposed to proportional rarity. To date, stream studies have only used proportional rarity to assess the effect of rare species on species accumulation (Paller 1995; Cao et al. 1998).

As the lists of alien and imperiled freshwater fishes continue to expand (Lomnicky et al. 2007; Jelks et al. 2008), knowing where fish species occur and do not occur is becoming a critical component of ecosystem management. If the objective is to accurately record species richness at a particular stream reach, an adequate sampling effort might require long electrofishing distances or multiple passes (Paller 1995; LaVigne et al. 2008a; Flotemersch et al., in press). If the objective is to maximize species richness detection at a watershed or region, the sampling design must consider the balance between the local reach distances and the number of reaches when costs are fixed (Smith and Jones 2005; LaVigne et al. 2008a; Smith and Jones 2008). Regardless of the spatial scale, it is fundamental to understand the rate of species accumulation at the local reach scale.

We present empirical data from stream and river sites from five states of the USA to explore two objectives: (1) document the level of spatial discontinuity in each case study, and (2) determine if the observed spatial discontinuity resulted from aggregation of common species into subreaches versus the sporadic occurrence of rare species. Our predictions were that (1) spatial discontinuity will be generally observed in fish assemblages across species-rich and species-poor regions, (2) spatial discontinuity will be caused by the occurrence of rare species rather than the aggregation of common species, and (3) numerically rare species, represented by singletons and doubletons, will decrease with increasing sampling effort when constrained to the reach scale (i.e., 40–100 MSW).

Methods

Study streams.—Parallel analyses on the effect of spatial discontinuity on species accumulation curves were conducted on five data sets representing a range of geographic regions, stream size, and species richness across North America. These data sets included wadeable streams in Connecticut (Y. Kanno and J. C. Vokoun, unpublished data), eastern Wyoming (Patton et al. 2000), and Arkansas (Dauwalter and Pert 2003a), and nonwadeable rivers in Idaho (Maret et al. 2007) and Oregon (Hughes et al. 2002; Table 1). A brief description of each data set is provided below.

Connecticut data included 19 wadeable stream sites

TABLE 1.—Characteristics of the stream and river sites in the five U.S. localities used in this study. The average electrofishing distance to capture 90% of the observed species reported here may differ from that in the source publications because of variations in analytical methods. The values in parentheses are ranges; VVP = variable voltage pulsator.

Locality	Sampling method	Mean stream widths (MSW) sampled	Average electrofishing distance (MSW) to capture 90% of observed species	Mean observed species richness per site	Mean number of singletons and doubletons per site
Species-poor wadeable streams					
Connecticut	One pass backpack electrofishing	50	30	10 (6–16)	3 (0–8)
Wyoming	One pass VVP electrofishing	Eight discontiguous 50-m-long units[a]	18	10 (6–13)	0
Species-poor nonwadeable rivers					
Idaho	One pass boat electrofishing	40	24	9 (6–14)	2 (0–7)
Oregon	One pass raft electrofishing	100	70	10 (6–16)	3 (0–7)
Diverse wadeable streams					
Arkansas	One pass backpack electrofishing	75	45	18 (9–26)	4 (2–8)

[a] Patton et al. (2000) alternately sampled 16 continuous 50-m-long units by electrofishing and seining. Only the electrofishing data were used in this study.

sampled between 15 June and 17 August 2007 in Northeastern Highlands and Northeastern Coastal Zone ecoregions. Stream widths ranged from 2.8 to 10.6 m. A mixture of pool–riffle–run sequences was the most typical habitat sampled with gravel, pebble, and cobble substrate. Fish were sampled using a Model LR-24 pulsed-DC backpack electrofisher (Smith-Root, Inc., Vancouver, Washington). Electrofishing extended 50 MSW, and each stream site was divided into 10 continuous subreaches of equal lengths. A crew of three people conducted one-pass electrofishing, proceeding upstream by sampling all available habitats. Species composition and catches were recorded separately for each subreach. Species richness was low across streams in Connecticut (an average of 10 species per site [range = 6–16]; Table 1). Total abundance averaged 315 individuals per site.

Patton et al. (2000) sampled nine sites in the Great Plains ecoregion of eastern Wyoming, wetted widths ranging from 2.5 to 10.2 m. Study sites were on low-gradient streams, dominated by fine substrates and homogeneous pool–run habitat. At each site, Patton et al. (2000) sampled 16 continuous 50-m-long subreaches alternating between single-pass electrofishing and seining. For consistency with other data sets, only the electrofishing data were used in this study (i.e., eight subreaches per stream). Patton et al. (2000) did not collect any species by seining that were not collected by electrofishing. The sites were species poor (having a mean of 10 species per site [range = 6–13]) and had the highest mean individual catch per stream width among our data sets (1,448 individuals per site; Table 1).

Fifteen stream sites (MSW = 3.3–10.5 m) in the Ozark Highlands ecoregion of Arkansas were sampled by single-pass backpack electrofishing (Dauwalter and Pert 2003a). Sampling extended to 75 MSW at each site, and fish were processed at every 5 MSW (15 subreaches per site). The Ozark Highlands were never glaciated, and the stream sites were relatively species rich (mean of 18 species per site [range = 9–26]; Table 1). The average abundance was 972 individuals per site.

A data set from nonwadeable rivers came from Maret et al. (2007) who employed single-pass boat electrofishing to sample river reaches in the Snake River Plain and Idaho Batholith ecoregions of Idaho. River sites had an average mean channel width of 8–193 m. Twelve sites that were sampled for 40 MSW were used in our analyses, and each was subdivided into 10 continuous subreaches (four MSW per subreach). The sites supported few species (mean of nine species per site [range = 6–14]), and total abundance averaged 300 individuals per site (Table 1). Electrofishing was concentrated near riverbanks. Collections alternated between the riverbanks after sampling two consecutive subreaches, where possible.

Additional nonwadeable rivers were sampled in eight Oregon mountain and plains ecoregions by Hughes et al. (2002). Thirty-two river reaches with at least five species were used in the analyses, and stream widths ranged from 10 to 150 m (Table 1). Data were collected through use of an electrofishing raft by

TABLE 1.—Extended.

Locality	Mean number of species with < 1% relative abundance per site	Mean total individual abundance per site	Mean individual abundance per stream width	Reference
Species-poor wadeable streams				
Connecticut	2 (0–8)	315 (112–607)	6 (2–12)	This study
Wyoming	1 (0–4)	1,448 (278–4,552)	21 (3–77)	Patton et al. (2000)[a]
Species-poor nonwadeable rivers				
Idaho	2 (0–4)	300 (82–692)	8 (2–17)	Maret et al. (2007)
Oregon	2 (0–8)	265 (153–631)	3 (2–6)	Hughes et al. (2002)
Diverse wadeable streams				
Arkansas	9 (2–14)	972 (288–1,737)	13 (4–23)	Dauwalter and Pert (2003a)

sampling continuously along one randomly selected bank for 100 MSW. Each river site was divided into 10 continuous subreaches (each subreach = 10 MSW), and fish identity and catch were recorded separately for each subreach. Similar to Idaho rivers, Oregon rivers had low species richness (mean of 11 species per site [range = 6–16]) and low total abundance (mean of 265 individuals per site).

Data analyses.—A sequence of identical analyses was run on the five data sets to address the two objectives. First, the level of spatial discontinuity was documented by plotting relative abundance for each species at each site against the number of subreaches occupied by each species at each site (Angermeier and Smogor 1995; Paller 1995). Spatial discontinuity was defined as the absence of a species from a subreach or subreaches when the species was present in the larger total reach sampled (Angermeier and Smogor 1995). In the five data sets used, subreaches were systematically delineated as multiples of average stream widths or a uniform length (50 m in the Wyoming data), and each subreach was represented either by a single habitat type or a mixture of channel units (e.g., a combination of

pool, riffle, and run in streams, or inside and outside bends of rivers). The linear, distance-based definition of subreaches was justified because sampling protocols typically specify exact sampling distances, often relative to stream size (Meador et al. 1993; Lazorchak et al. 1998; Flotemersch et al. 2006; Peck et al. 2006). Also, habitat types are categorized and measured differently among researchers, resulting in considerable assessment error (Roper and Scarnecchia 1995; Poole et al. 1997; Whitacre et al. 2007). Following Angermeier and Smogor (1995), we categorized the distribution of species into three levels of spatial discontinuity. Categories represented the percentages of subreaches occupied by fish species at each reach, and included 30% or less (high discontinuity), 31–70% (medium discontinuity), and greater than 70% (low discontinuity).

Simulation of aggregation levels of individuals was conducted to address our second objective. If many of the species present in a reach are confined to a few subreaches (i.e., aggregation is high), species accumulation curves will approach asymptotes more slowly than if species are less aggregated or continuously

TABLE 2.—Number of fish species occurring in selected percentages of subreaches in the five study localities. The numbers of fish species are sums of all the fish species at all sites at each locality (i.e., species were counted more than once).

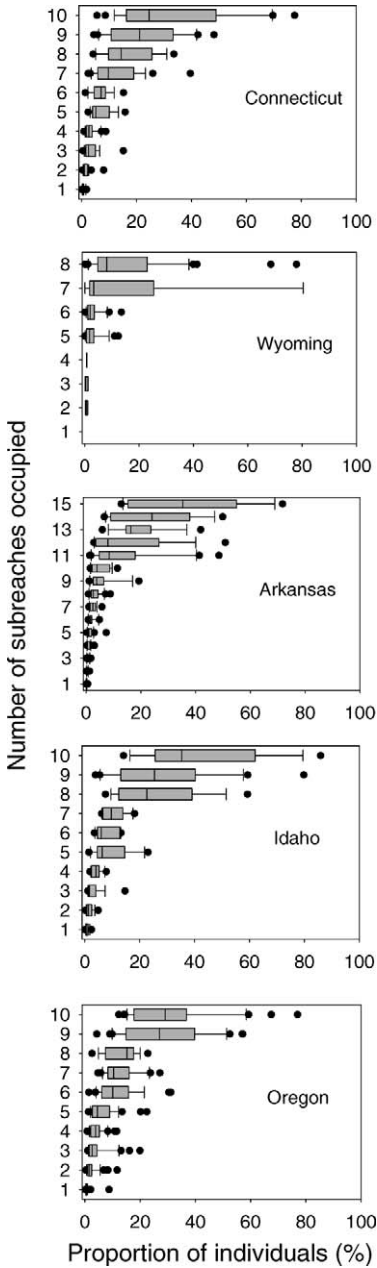| Locality	Percent of subreaches occupied			Number of sites sampled	Number of subreaches sampled	Number of channel widths per subreach
	≤30	31–70	>70			
Connecticut	75	62	52	19	10	5
Wyoming	4	24	60	9	8	11 (5–20)
Arkansas	128	87	58	15	15	5
Idaho	63	37	36	12	10	4
Oregon	71	62	38	32	10	10

FIGURE 1.—Relationships between proportional abundance and the number of subreaches occupied by all species at all study sites in Connecticut, Wyoming, and Arkansas streams and Idaho and Oregon rivers. The box dimensions represent the interquartile ranges, the lines within the boxes the medians, and the whiskers the 90th and 10th percentiles. Filled circles are observations outside the 10th and 90th percentiles. The degree of spatial discontinuity decreases along the y-axis.

distributed. Three levels of individual aggregation were simulated and compared with the empirical data. Simulations represented high aggregation, moderate aggregation, and a completely random distribution of individuals, within species, among subreaches. Using the shuffle option in Program EstimateS (Colwell 2005), the three aggregation levels were executed by setting "patchiness" parameters at 0.9, 0.5, and 0. The program reassigns individuals, within species, to subreaches with a given probability of aggregation, while maintaining relative and absolute abundance of species in a sample (Chazdon et al. 1998). For example, when the patchiness parameter is set to 0.9, the first individual of a species is randomly assigned to a subreach, and the second individual of this species is assigned to the same subreach as the first one with a probability of 0.9, and to a randomly selected subreach with a probability of 0.1. The third individual is similarly assigned to the same subreach as the second with the same 0.9 probability and to a randomly selected subreach with 0.1 probability. This reassignment method continues until all individuals of that species are reassigned. When the patchiness parameter is set to 0, subreach affiliations of individuals are completely randomized among all subreaches, removing any aggregation present in the original data. Because this approach influences species with multiple individuals only, singletons do not affect simulation outcomes and the influence of doubletons is limited; therefore, it is an appropriate method to quantify aggregation of the more common species without the confounding effect of numerically rare species. Each level of simulated aggregation was executed with 200 randomizations of subreach order without replacement, and species accumulation curves were constructed by averaging proportions of species richness observed across all study sites at each sequential subreach. These curves were then compared with a curve constructed with the empirical subreach data structure, in which subreach order was similarly randomized in Program EstimateS.

We documented if the observed spatial discontinuity resulted from the sporadic occurrence of rare species by removing rare species from the data sets. Because rare species can be defined numerically and proportionately, we reconstructed species accumulation curves with two methods: (1) removal of singletons and doubletons, and (2) removal of species with less than 1% relative abundance in each stream or river reach (Paller 1995; Fischer and Paukert 2009). Species accumulation curves were derived with 200 randomizations of subreach order without replacement in Program EstimateS (Colwell 2005).

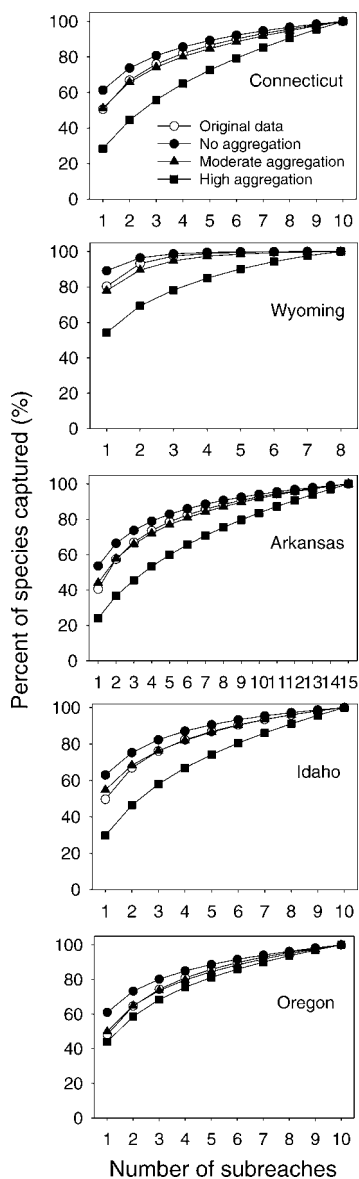Finally, the occurrence of singletons and doubletons

FIGURE 2.—Original species accumulation curves and curves simulated with three different levels of individual aggregation in Connecticut, Wyoming, and Arkansas streams and Idaho and Oregon rivers. Each symbol represents the mean percentage of species captured in a particular number of subreaches. Simulations of no, moderate, and high aggregation were performed by setting the "patchiness" parameters at 0, 0.5, and 0.9, respectively, using the shuffle option in Program EstimateS (Colwell 2005). Each simulated species accumulation curve was constructed with 200 randomization runs without replacement. Note that subreach length differs among the five regions (Connecticut, 5 mean stream widths [MSW]; Wyoming, 50 m [the mean of 11 MSW]; Arkansas, 5 MSW; Idaho, 4 MSW; and Oregon, 10 MSW).

was examined in relation to increasing linear sampling distances. The orders of the empirical subreach data were randomized (200 runs) without replacement in Program EstimateS, and the number of singletons and doubletons was plotted as a function of increasing subreach number (which represented sampling distance). Because total abundance increased with linear distance, this analysis also described the occurrence of singletons and doubletons as a function of increasing fish abundance. Wyoming data were excluded from this portion of data analyses because no singletons or doubletons were collected.

Results

Spatially discontinuous distributions of some fish species were observed in all five regions (Figure 1). Species with both low proportional abundance and few subreaches occupied appeared in the lower left of each panel in Figure 1, although Wyoming sites had notably fewer species showing this pattern. Proportional abundances of fish species varied when species were collected from many subreaches (upper portion of each panel of Figure 1). No proportionately abundant species were confined to few subreaches (i.e., there were no species in any reach that were plotted in the lower right). This indicated that proportionately abundant species tended towards more continuous distributions among the subreaches.

Data from Connecticut, Arkansas, Idaho, and Oregon were similar in that more species were discontinuously distributed, as many species occurred at few subreaches (Table 2). For example, in Connecticut, fish species occurred at three or fewer subreaches among a possible 10 subreaches in a total of 75 occasions (mean of four species per site). To the contrary, distributions of most species were spatially continuous in the Wyoming reaches as the majority of species were collected from more than 70% of subreaches.

A nearly consistent pattern across study regions was observed in the simulations of individual aggregation within species (Figure 2). The percent of species captured increased faster (i.e., in fewer subreaches) at the lowest level of aggregation. Similarly, the highest level of aggregation resulted in the slowest increase in the percent of species captured for all data sets. In the four regions except Wyoming, the empirical species accumulation curves lay nearest the moderately aggregated (0.5-probability) simulation curve. The empirical species accumulation curve was between the moderately aggregated and the completely random simulation curves in the Wyoming data.

The effect of rare species removal differed among regions (Figure 3), as the Wyoming and Arkansas data
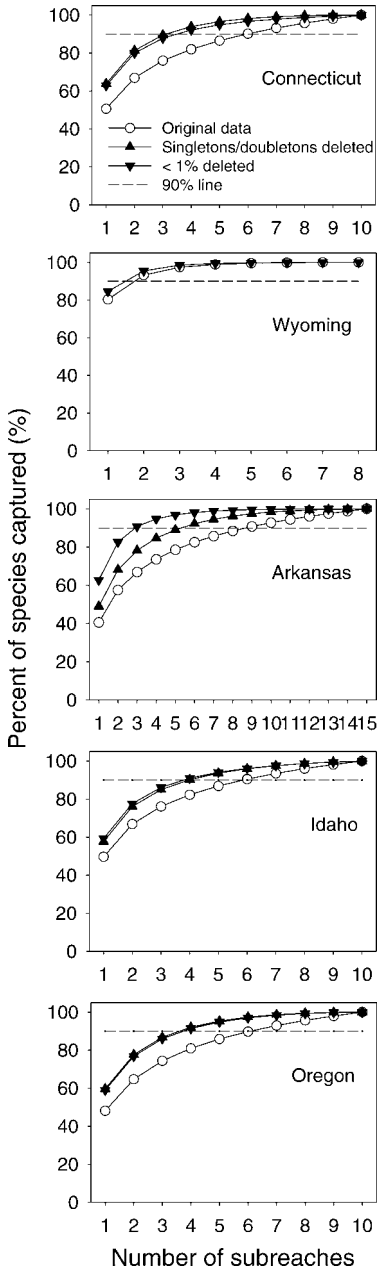
FIGURE 3.—Influence of rare species on species accumulation curves in Connecticut, Wyoming, and Arkansas streams and Idaho and Oregon rivers. Except for Wyoming, three species accumulation curves are shown in each panel: one with the original data, one with singletons and doubletons removed from the data set, and one with species with less than 1% relative abundance removed from the data set (there were no singletons or doubletons at the Wyoming sites). See Figure 2 for additional details.

appeared individually distinctive while the Connecticut, Idaho, and Oregon data were similar. Species accumulation curves were nearly identical between the two methods of rare species removal for Connecticut, Idaho, and Oregon. In these regions, the removal of rare species shortened the sampling distance to capture 90% of species richness from six subreaches (30 MSW for Connecticut, 24 MSW for Idaho, and 60 MSW for Oregon) to four subreaches (20 MSW for Connecticut, 16 MSW for Idaho, and 40 MSW for Oregon). The similarity of the two methods was a function of the total number of singletons and doubletons being nearly identical to that of species with less than 1% relative abundance. Proportional rarity is dependent on total individual abundances, and the mean total abundance was 315, 300, and 265 individuals per site in Connecticut, Idaho, and Oregon, respectively (Table 1).

For the Arkansas sites, an average of nine subreaches (45 MSW) was originally required to capture 90% of species, but six subreaches (30 MSW) were sufficient with the removal of singletons and doubletons (Figure 3). Removal of proportionately rare species further decreased the electrofishing distance requirement to three subreaches (15 MSW). In the Arkansas data, numerically rare species were a subset of proportionately rare species. Specifically, the mean total abundance was 972 fish per site; therefore, when rare species were defined as those with less than 1% relative abundance, more species qualified as rare (species represented by one to nine individuals, on average). This was naturally greater than the number of singletons and doubletons.

Finally, the species accumulation curve from Wyoming was little influenced by the removal of species with less than 1% relative abundance, and there were no singletons or doubletons (Figure 3). Ninety percent of species richness was reached after sampling a mean of two subreaches (18 MSW) whether or not species with less than 1% relative abundance were deleted. The mean number of individuals of proportionately rare species was nine per site (range = 3–30), indicating that, in general, there were as many individuals of these species as there were subreaches. Therefore, proportionately rare species did not differ much in spatial discontinuity from more common species.

The number of singletons and doubletons remained relatively constant with increasing sampling effort (i.e., sampling distance and total abundance) except in Arkansas (Figure 4). The Arkansas data set produced a unique pattern; the number of the numerically rare species initially increased up to four subreaches (20 MSW), leveled off, and gradually declined after seven subreaches (35 MSW).
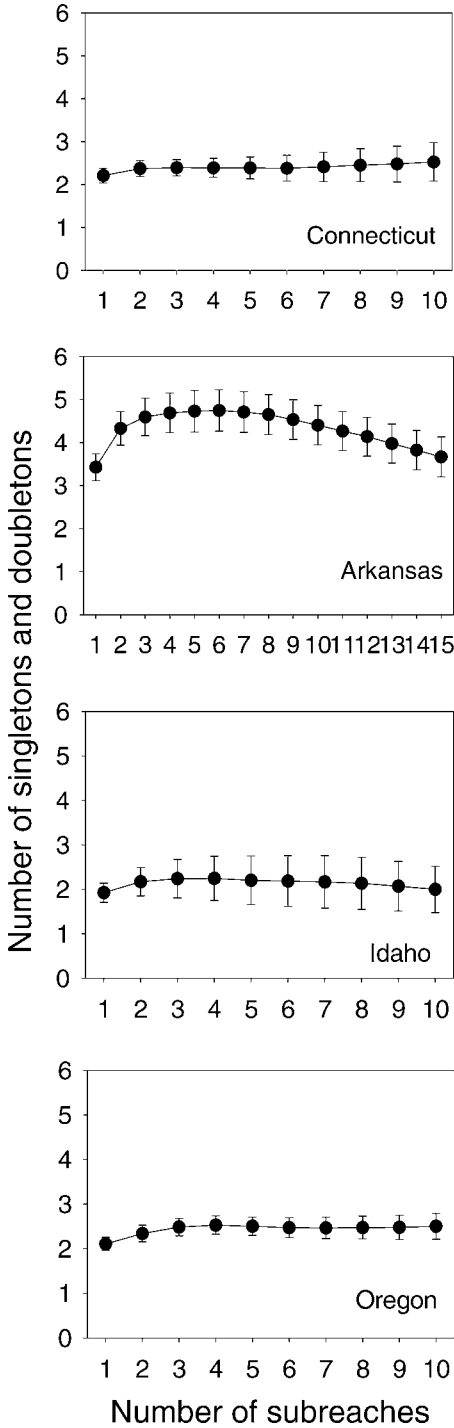
FIGURE 4.—Mean number of singletons and doubletons in Connecticut and Arkansas streams and Idaho and Oregon rivers as a function of the number of subreaches sampled; the error bars represent SEs. There were no singletons or doubletons in the Wyoming data.

Discussion

Species accumulation curves derived from reach-scale electrofishing showed initial sharp increases, followed by gradual addition of new species as reported by the original studies. It is important to note that, except for the Wyoming data, species accumulation curves did not become asymptotic, and new species were often observed near the termination of sampling. Therefore, more sampling effort is likely to record additional new species at many of the sites across these regions, as has been reported by Cao et al. (2001), Hughes et al. (2002), and Dauwalter and Pert (2003a). This observation suggests that the initial total reach length selected for sampling was an important source of the variability among previous studies that recommended sampling distances needed to accurately estimate species richness (Lyons 1992; Paller 1995; Patton et al. 2000; Hughes et al. 2002; Reynolds et al. 2003; Maret et al. 2007). There was a tendency that the recommended sampling distance increased with increasing initial total reach length in these studies (Table 3). The pattern was rather striking; except in cases in which sampling efficiency was very high (Wyoming; Patton et al. 2000) or very low (Oregon; Hughes et al. 2002), 90–95% of observed species richness has been captured at 0.57–0.68 times the total distance sampled.

Detection of additional new species with increasing linear distance resulted from spatial discontinuity of fish distributions. Previous studies quantified spatial discontinuity from species-rich streams (Angermeier and Smogor 1995; Paller 1995), and our analyses showed that this was perhaps a common pattern that was observed similarly from species-poor regions. We caution that the degree of spatial discontinuity is affected by sampling efficiency (Angermeier and Smogor 1995) and the spatial grain of subreaches, and these elements differed across the five data sets we analyzed. For example, the least amount of spatial discontinuity was recorded in the Wyoming data, and it may partly be explained by both the highest sampling efficiency and the longest subreaches relative to stream width among the five data sets. The Oregon data were characterized by low capture efficiency due partly to low conductivity and low nutrient waters, the fast river current, and low electrofisher power settings to avoid harming highly valued, listed salmonid populations (Curry et al. 2009). Results were based on single-pass electrofishing in subreaches that were systematically delineated as multiples of average stream widths or a uniform length. While authors have defined subreaches in other ways (e.g., channel unit habitats; Angermeier and Smogor 1995), we maintain that single-pass electrofishing of predetermined distances is the most

Table 3.—Summary of studies that have examined the relationship between sampling distance and species richness at the stream or river reach scale in North America.

Locality	Electrofishing sampling method	Total distance sampled (MSW)	Average distance to achieve a given criterion (MSW)	Criterion	Ratio of distance to achieve criterion to total distance sampled	Reference
Connecticut	One pass backpack	50	30	90% observed species richness	0.60	This study
Idaho	One pass boat	40	24	90% observed species richness	0.60	Maret et al. (2007)
Wyoming	One pass VVP	88	22	90% observed species richness	0.25	Patton et al. (2000)
Oregon	One pass raft	100	85	95% observed species richness	0.85	Hughes et al. (2002)
Oregon	One pass backpack	70	40	90% observed species richness	0.57	Reynolds et al. (2003)
Virginia	One pass electric seine	72	41	90% observed species richness	0.57	Angermeier and Smogor (1995)
Wisconsin	One pass barge	47	32	95% observed species richness	0.68	Lyons (1992)
Arkansas	One pass backpack	75	45	90% observed species richness	0.60	Dauwalter and Pert (2003a)
South Carolina	Seven pass backpack, barge, or boat	87	96	100% estimated species richness	NA	Paller (1995)

frequently used method in standard fish surveys (Meador et al. 1993; Lazorchak et al. 1998; CEN 2003; Flotemersch et al. 2006).

As predicted, spatial discontinuity was caused by the occurrence of rare species and not by the aggregation of more common species into subreaches. The sampled distributions of fish species tended towards a moderate level of aggregation across the study regions (the Wyoming data deviated slightly from this pattern), regardless of differences in species richness and overall abundances. Individual aggregation was not considered a driver of spatial discontinuity in streams in Virginia, even when data were collected at the finer spatial scale of channel mesohabitat units (Angermeier and Smogor 1995). In our five data sets, fish species were never proportionately abundant and found in few subreaches, despite differences in the length of subreaches. Therefore, the definitions of subreach length used did not preclude useful analyses and interpretations. More research into the effects of larger subreach definitions and varying spatial scale on analyses of spatial discontinuity and sampling requirements in stream fishes is needed.

Rare species influenced species accumulation curves to the extent that their spatial distributions were discontinuous. Numerically rare species, represented by singletons or doubletons, always produced spatial discontinuity, but distributions of proportionately rare species were not always spatially discontinuous, as was the case in the Wyoming data. The definition of rare species was important because numerical and proportional rarity identified different numbers of species in some of the fish assemblages and therefore affected species accumulation curves differently, as observed in the Arkansas data. Singletons or doubletons were the species with the highest degree of spatial discontinuity, so it followed that their removal generally resulted in the majority of remaining species being captured at shorter sampling lengths. In agreement with previous findings (Angermeier and Smogor 1995; Paller 1995; Angermeier et al. 2002), we concluded that spatial discontinuity was the primary factor affecting the distance requirements to accurately estimate species richness in river and stream reaches. When spatial discontinuity was observed, it resulted from the sporadic occurrence of numerically rare species.

Contrary to our prediction, the number of singletons and doubletons did not decrease with increased sampling distance and increased individual abundance. It is important to note that singletons or doubletons persisted even in species-poor reaches in Connecticut, Idaho, and Oregon, as well as the more species-rich streams of Arkansas. We do not presume that any particular singleton or doubleton species is inherently numerically rare, just that it was sampled as such, because detection probabilities typically differ among fish species (Bayley and Peterson 2001). This is particularly true when singletons or doubletons are those species that are less susceptible to electrofishing (e.g., small ictalurids). In theory, singletons and doubletons should eventually disappear after sufficiently large numbers of fish are collected (Walther and Moore 2005). Yet, as in other biological surveys (Mao and Colwell 2005; Walther and Moore 2005), stream and river surveys often contain singletons and doubletons, and they play a disproportionately important role in

species richness counts. The patchy distribution of rare species is problematic for those who estimate sufficient sampling effort by stopping sampling when no new species are collected or when a randomization-based data evaluation method is not used.

Adequacy of site electrofishing distance is often addressed in terms of sampling goals. With regards to species detection, our results, along with previous work (Paller 1995; Cao et al. 2001), indicate that longer sampling distances are likely to result in detection of more new species, even at the reach scale. The question then becomes how much additional sampling is justifiable at the reach scale under resource and time constraints faced by natural resource agencies (Hughes and Peck 2008). Smith and Jones (2008) found that it was beneficial to sample more shorter reaches than fewer longer reaches to maximize species inventory at the watershed scale in Michigan streams. However, they noted that this pattern may not be general, and sampling longer reaches might be better in watersheds with high travel costs or lower species turnover among reaches (i.e., low among-site diversity [beta diversity] within the watershed). Though varying sampling effort and gear confounds direct regional comparisons, species accumulation rates at the reach scale differed among the five regions examined, and they may differ even among streams within the same region (Lyons 1992; Angermeier and Smogor 1995; Patton et al. 2000). This makes it difficult to recommend a single generic sampling distance that can be applied across regions. The adequacy of sampling distances for estimating species richness probably needs to be considered by region or possibly by stream, depending upon the prevalence of numerically rare species. Nonetheless, a greater level of gear and distance standardization is needed across the continent so that in future among-region comparisons, analysts can better separate differences in sampling effort from differences in species accumulation curves (Cao et al. 2001, 2007; Bonar et al. 2009). More research is needed on temporal variability of rare species among samples and if the known presence of rare species could be used to inform sampling distances. Regardless, increasing sampling effort through employment of a statistical site-scale sampling design, greater electrofishing efficiency and intensity, additional gears, and more sites in addition to longer sampling distances would increase the chance of finding numerically rare species in many instances (LaVigne et al. 2008a, 2008b). Finally, recent observations that index of biotic integrity scores stabilize within relatively short sampling distances (Dauwalter and Pert 2003b; Reynolds et al. 2003; Hughes and Herlihy 2007; Maret et al. 2007) should be balanced with the acknowledgment that these routine monitoring efforts are increasingly the only current fish distribution data being collected in many regions. As stream fishes become increasingly threatened (Jelks et al. 2008) and as alien fish species increasingly disperse (Lomnicky et al. 2007), the need to achieve accurate records of species occurrences may serve to emphasize the role of numerically rare species in determining sampling protocols.

Acknowledgments

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