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Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams

MARK R. VINSON

United States Department of the Interior,
Bureau of Land Management Aquatic Monitoring Center,
Department of Fisheries and Wildlife, Utah State University,
Logan, Utah 84322-5210 USA

CHARLES P. HAWKINS

Department of Fisheries and Wildlife, Ecology Center,
and Watershed Science Unit, Utah State University,
Logan, Utah 84322-5210 USA

Communities vary in the number of taxa they harbor. Ecologists wonder why and try to discover what factors influence taxa richness. Resource managers wonder why and try to determine 1) what effects management practices have on biotic richness, 2) what we need to do to conserve biotic diversity, and 3) if we can use observed differences in richness as a measure of the biotic integrity of communities. In all cases, we make the implicit and sometimes brash assumption that we can really measure the number of taxa in a community. Although measuring taxa richness might appear straightforward, accurate measurement has been extraordinarily difficult; and despite years of effort, no universally accepted methods for its measurement have emerged. The essential problem is that we can never completely census a taxonomic assemblage or entire community; we rely instead on estimates that describe some portion of the real taxa richness of an assemblage. The problem of knowing what percent of the taxa present have been collected is exacerbated when investigators fail to explicitly define their universe of interest (i.e., the spatial bounds of the community or communities in question). Comparisons of taxa richness among studies that used different sampling and subsampling methods are especially difficult and should be viewed skeptically.

The difficulty of obtaining accurate measurements of richness is due to the collector's curve phenomenon (after Colwell and Coddington 1995): the number of taxa encountered in a sample increases asymptotically as functions of both the area sampled and the number of individuals in the sample. Collector's curves are statistical phenomena related to both sampling and ecological processes. Bigger sampling areas tend to have more types of habitats and thus more species. Larger numbers of individuals per sample increase the likelihood that new taxa will be encountered. The relationship between taxa number and area sampled has been recognized for more than 75 y (Arrhenius 1921), and that between the number of individuals and the number of taxa in a sample for almost 50 y (Preston 1948). These relationships show that we should somehow standardize estimates of richness by area and by number of individuals identified when comparing taxa richness among sites, whether for biomonitoring purposes or ecological investigations. Although ecologists often control for the area sampled, controlling simultaneously for the number of organisms collected is impossible. Furthermore, in studies of small, numerous organisms such as aquatic invertebrates, we often subsample the field collection and potentially corrupt the area control. Because we can seldom conduct a complete census of a group of organisms of interest, we must therefore base inferences regarding taxa richness on either raw, nonstandardized estimates or adjusted estimates interpolated from the raw samples. Much work has been directed toward methods for either extrapolating the true taxa richness from raw counts (Colwell and Coddington 1995) or standardizing comparisons by interpolating the richness expected for a standard number of individuals (Sanders 1968, Heck et al., 1975, Simberloff 1979, James and Rathbun 1981).

Benthologists are not immune to these problems, although we have infrequently addressed them explicitly (e.g., Stout and Vandermeer

1975, Minshall et al. 1985, Douglas and Lake 1994). Richness data reported by benthologists are especially prone to problems associated with variation in individual counts. Although we frequently collect samples with 100s if not 1000s of individuals, we usually homogenize these samples and then sort, count, and identify a small subset of the original sample. In an attempt to both standardize and reduce collection and processing costs, a relatively small number of individuals is used to represent the assemblage. For example, the United States Environmental Protection Agency's rapid bioassessment protocols (RBPs) are based on the random selection of 100, 200, or 300 individuals from a sample (Plafkin et al. 1989). The United States Geologic Survey's National Water-Quality Assessment (NAWQA) program and many state and federal monitoring programs also develop taxa lists based on subsamples of the original sample. In most surveys, samples are collected from <2 m^2 of stream bottom, and these data are used to represent a much larger universe—i.e., an entire reach or stream. Considering the increasingly frequent use of richness measures in water-quality monitoring and assessment (Resh and McElravy 1993), the adequacy of these sampling and subsampling techniques for representing the sampled assemblage should be carefully scrutinized before they are generally accepted and implemented.

In this paper we use an extensive database of aquatic macroinvertebrate collections from streams in several ecoregions (sensu Omernik 1987) to explore some of these problems. We use these data to determine if our ability to detect differences in richness among ecoregions is sensitive to variation in sample area and number of individuals subsampled. In doing so, we describe empirical relationships between taxa richness, sample area, and number of individuals in a subsample. We conclude by 1) suggesting that the information content extracted from samples can be optimized by conducting 2-phase sorting of samples, and 2) making a plea for greater standardization in sampling and sample treatment.

Methods

Data collection, processing, and compiling

We used the macroinvertebrate database compiled and maintained by the Bureau of Land Management (BLM) Aquatic Monitoring Center, (US Department of the Interior) in Logan, Utah. This database includes 2224 benthic stream riffle samples collected from 20 ecoregions within the United States: Coast Range (N = 251), Cascades (118), Sierra Nevada (329), Eastern Cascades Slopes and Foothills (20), Columbia Basin (63), Blue Mountains (112), Snake River Basin (135), Northern Basin and Range (155), Southern Basin and Range (97), Northern Rockies (133), Montana Valley and Foothill Prairies (13), Middle Rockies (29), Wyoming Basin (59), Wasatch and Uinta Mountains (23), Colorado Plateaus (166), Southern Rockies (201), Arizona/New Mexico Plateau (1), Northwestern Great Plains (24), Central Appalachians (149), and Alaska (146). Our intent in this paper was not to analyze why differences in richness exist among groups of samples from these ecoregions; instead our objectives were 1) to examine if differences existed and 2) to illustrate the need for adequate subsampling and sample rarefaction procedures when drawing conclusions about metrics based on taxa richness.

All samples had been sent to the Center for processing and had thus been treated similarly. Most samples were collected with Surber-type samplers or fixed-area kicknets from streams on lands administered by either the BLM or the (US Department of Agriculture) Forest Service (see Angradi and Vinson 1995 for details). The data available from each sample included location of the sample (ecoregion and state) and area of the sample (m^2). Sample processing followed Cuffney et al. (1993). For 912 samples, a 1-phase subsampling procedure was used. Samples were processed by pouring the entire sample into a 250-μm-mesh sieve and then taking a series of sequential subsamples until at least 250 individuals had been removed. Each subsample was processed in its entirety. For the remaining 1312 samples, a 2-phase sorting method was used. For these samples, the entire sample was first poured into an enamel pan and searched for approximately 10 min; large, rare organisms that could be lost during subsequent sample splitting were removed and stored separately. After this "large–rare" search, the rest of the sample was subsampled as described above. If there were fewer than 250 organisms in a sample no subsampling was done (N = 484 for 1-phase, N = 565 for 2-phase processing). All unsubsampled samples were grouped with data

from the 1-phase subsampling method. Therefore the sample sizes are 1477 for 1-phase processing (912+565) and 747 (1312−565) for 2-phase processing. Individuals in both the large–rare and the combined subsamples were usually identified to the genus level, and the counts for each taxon were entered into a database; overall density, taxa richness, and various metrics were estimated.

Data analysis

For the purposes of this paper, we have assumed that samples were taken from a random set of riffle habitats within each ecoregion. In reality the data from each ecoregion represent samples from different reaches within the same stream and different streams. Although the assumptions of random sampling may not have been strictly met, sample sizes were sufficiently large and locations varied enough to illustrate how sample area and subsampling procedures affect our ability to detect differences among categories of grouped data.

Data from the 19 ecoregions with sample sizes > 10 (N = 2223) were analyzed as follows. We first generated box plots of the raw richness estimates by ecoregion and then used ANOVA to determine if there were statistically significant differences in mean sample richness among ecoregions. We then determined if differences in area sampled and number of individuals identified were associated with estimates of richness. The effect of sample area was examined by generating separate collectors curves for samples of <0.1 m², 0.1–0.5 m², 0.5–1.0 m², and >1.0 m². The potentially confounding effect of number of individuals in the sample was analyzed by applying a rarefaction technique (Eq. 1, Hurlbert 1971) to all samples and calculating the expected number of taxa (ET) for 50, 100, 150, 200, 250, and 300 individuals. Hurlbert's (1971) equation computes the expected number of taxa [denoted here by $E(T_n)$] in a random sample of size n, from a population of N individuals distributed among T taxa

$$E(T_n) = \sum_{i=1}^{T}\left\{1 - \left[\binom{N - n_i}{n} \Big/ \binom{N}{n}\right]\right\} \quad (1)$$

where n_i is the number of individuals of the ith species.

We then selected those samples that met the following 3 criteria for additional analysis: 1) samples were all taken from 0.09–0.1 m² areas and samples had sufficiently high numbers of individuals to calculate values of ET50 through at least ET200, 2) only the 1-phase subsampling (i.e., no large–rare search) had been used or the entire sample had been sorted and identified, and 3) there were at least 10 samples in an ecoregion after applying criteria 1 and 2. This process reduced the data set to 180 samples from 7 ecoregions. Prior to conducting ANOVAs, we used Bartlett's test to test for homogeneity of variance among ecoregions for counts, raw richness, ET200, ET150, ET100, and ET50. In all cases except counts ($p < 0.001$), variances were not significantly different ($0.20 \leq p \leq 0.63$). Because we could not homogenize variances in counts with transformations, we excluded these data from further analyses. Separate ANOVAs on raw richness, ET200, ET150, ET100, and ET50 were then conducted, and the Tukey-Kramer HSD test was used to determine all significant ($p < 0.05$) pairwise differences between ecoregions. We then compared how much variation (r^2) in each measure was associated with ecoregion, and if the number of significant pairwise differences (SPWDs) changed depending on the richness measure used. We used the number of SPWDs as a measure of the sensitivity of the data to detect differences among groups of samples. We determined if the type of sorting procedure used affected estimates of richness by constructing and comparing collectors curves for samples processed with 1- and 2-phase sorting.

Results and Discussion

Box plots showed that richness appeared to vary substantially among the sample groups from different ecoregions (Fig. 1). Streams in the Coast Range group appeared to have the most taxa ($\bar{x}$ = 34.3) and streams in the Alaska group the fewest taxa ($\bar{x}$ = 16.9). An ANOVA implied there were significant differences among the ecoregions, with 45% of the variation in sample richness associated with ecoregion (Table 1). However, both the area sampled and the number of individuals within a sample varied among ecoregions. The steepness of the collector's curves increased with sample area (Fig. 2); taxa richness from sampling areas >1.0 m² was about 1.7 times greater than that from the small-

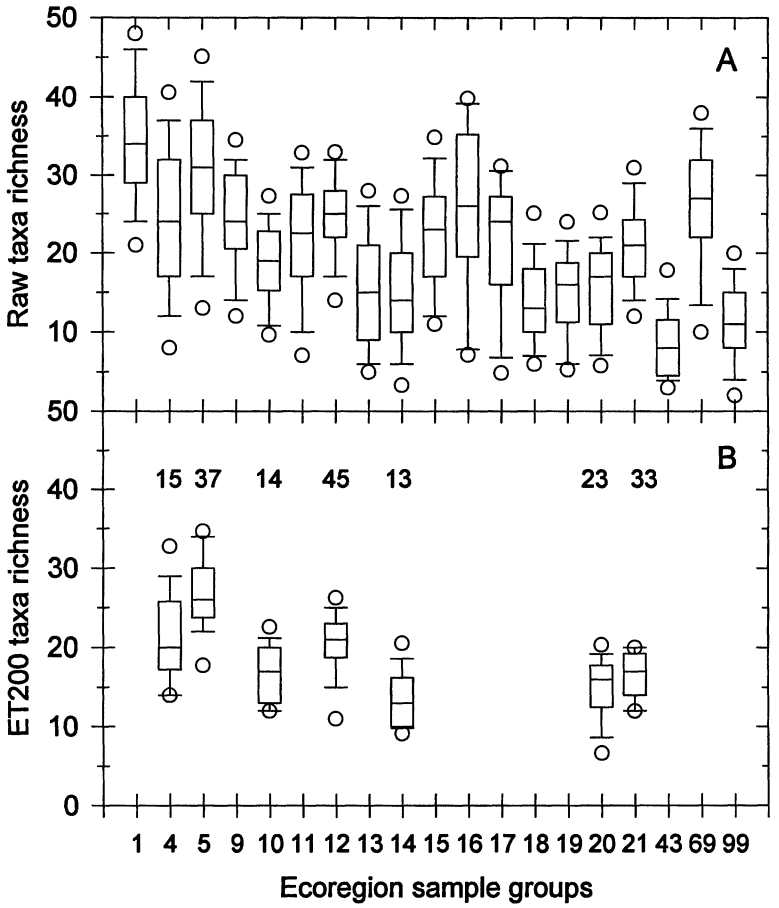

FIG. 1. A.—Box plots showing the apparent differences in taxa richness between samples collected from 19 different ecoregions. Ecoregions are coded following Omernik (1987) as follows: Coast Range (1), Cascades (4), Sierra Nevada (5), Eastern Cascades Slopes and Foothills (9), Columbia Basin (10), Blue Mountains (11), Snake River Basin/High Desert (12), Northern Basin and Range (13), Southern Basin and Range (14), Northern Rockies (15), Montana Valley and Foothill Prairies (16), Middle Rockies (17), Wyoming Basin (18), Wasatch and Uinta Mountains (19), Colorado Plateaus (20), Southern Rockies (21), Northwestern Great Plains (43), and Central Appalachians (69). Samples from Alaska were assigned a code of 99 because Omernik (1987) did not classify Alaska. See text for sample sizes. B.—Box plots of the number of taxa expected in samples of 200 individuals (ET200) for those ecoregions meeting the 3 criteria of similar sample area, similar subsampling procedure, and samples size >10 (see text). Sample sizes are shown above each box plot. For each box plot, horizontal lines represent, from top to bottom, the 10th, 25th, 50th, 75th, and 90th percentiles. The top and bottom open circles represent the 5th and 95th percentiles.

est sampling areas for samples where >400 individuals were identified. Among all 2223 individual samples, the number of individuals sorted ranged from 62 to 4313 with a $\bar{x}$ of 375 ($\bar{x}$ = 435 for samples that were subsampled). The fewest ($\bar{x}$ = 244) individuals were identified from Wyoming Basin samples and the most ($\bar{x}$ = 476) from samples taken from the Southern Basin and Range.

When we examined only the 7 ecoregion sample groups that met the 3 criteria of <0.1 m^2 sample area, estimates of ET200, and a minimum of 10 samples, significant differences still existed among sample groups in both $\bar{x}$ sample richness and counts of individuals (Table 1). Ecoregion was associated with 50% of the variation in sample richness and 13 of the 21 pairwise differences were significant.

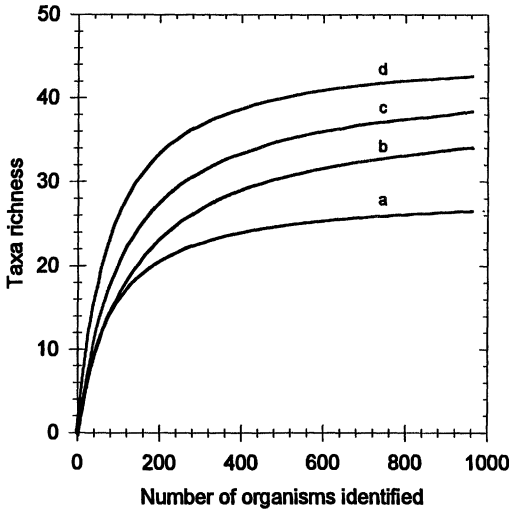

FIG. 2. Collector's curves showing the relationship between number of taxa and number of organisms identified per sample for 4 different-sized sampling areas. Curves are: a = 0.09–0.1 m², n = 1423; b = 0.1–0.5 m², n = 291; c = 0.5–1.0 m², n = 437; and d = >1.0 m², n = 73. Each line represents the approximate shape of the relationship as described by a hyperbolic function (Y = ax/(b + x)), where a = maximum richness and 0 richness occurs at 0 count.

The ANOVAs on the rarefied richness estimates produced results similar to those observed for raw richness (Table 1), although the box plots showed that subtle shifts in median richness relative to other ecoregions occurred with rarefaction (cf. Fig. 1A and 1B). Fifty-two percent of the variation in ET200 was associated with ecoregion, an increase of only 2% over that obtained with raw richness values. The number of SPWDs for the ET200 data did not differ from that for raw richness. If we assume that the standardized ET200 estimate represents the most accurate estimate of real differences in richness between eooregions, these results imply that use of raw richness values would have led to a correct conclusion for all pairwise comparisons. As the rarefied number of individuals used to make comparisons was decreased from 200 to 50, variation in richness associated with ecoregion dropped from 52% to 43% and the number of significant pairwise differences dropped from 13 to 12. These results also have some interesting implications. Considering that, when done properly, fixed-count subsampling is a mechanical form of rarefaction, use of 100–200 individuals may provide data that are equally sensitive in detecting differences among treatments or comparisons. However, use of rarefied estimates based on <150 individuals may result in loss of sensitivity as collector's curves converge with decreasing sample sizes thereby reducing one's ability to detect real differences among collections (A. L. Sheldon, University of Montana, personal communication). For our data, ANOVAs based on ET100 or ET50 detected about 5% fewer pairwise differences among ecoregions than did ANOVAs based on richness estimates standardized to 150 individuals (Table 1).

Taxa richness increased rapidly with number of individuals examined up to 200 organisms and increased at a much slower rate between 200 and 1000 individuals (Fig. 3). Estimates of richness were substantially higher in samples with 2-phase subsampling (large–rare search) than for samples with 1-phase subsampling for samples with >250 individuals (Fig. 3). Using the 2-phase sorting procedure increased the

TABLE 1. Results of ANOVAs testing the relationships between ecoregion sample groups on raw richness, number of organisms identified (counts), and rarefied richness measures for 19 ecoregion sample groups and for 7 ecoregion sample groups that satisfied 3 criteria. SPWD = the number of statistically significant (p < 0.05) pairwise differences among the 7 ecoregions. See text for details.

Data set	Variable	n	p	r^2	SPWD
19 Ecoregions	Counts	2223	<0.001	0.09	—
	Raw richness	2223	<0.001	0.45	—
7 Ecoregions	Raw richness	180	<0.001	0.50	13
	ET200	180	<0.001	0.52	13
	ET150	180	<0.001	0.51	13
	ET100	180	<0.001	0.48	12
	ET50	180	<0.001	0.43	12

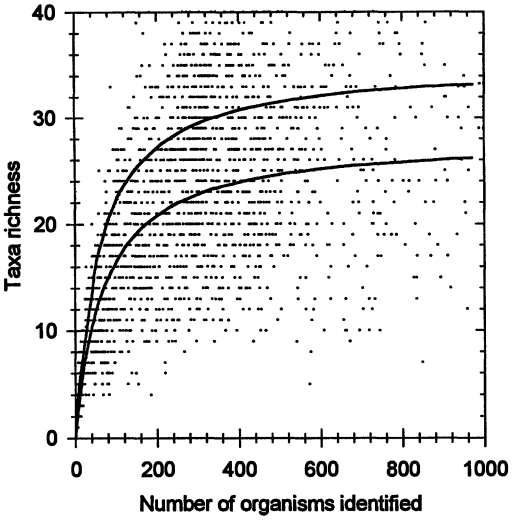

FIG. 3. Collector's curves showing the relationship between number of taxa and number of individuals per sample for samples processed with 2-phase sorting that included a large–rare search (top line) and 1-phase sorting without a large–rare search (lower line). All data points are plotted to show the actual variability in the data and the 2 lines represent the best fit to a hyperbolic function. N = 747 for large–rare search and 1477 for without large–rare search.

number of taxa by about 7 for subsamples with >300 individuals. These differences represented about 29 and 27% increases in estimates of richness for counts of 300 and 1000 respectively. Taxa included by the large–rare search tended to be large and potentially ecologically important taxa such as Decapoda, *Tipula* (Diptera), *Dicosmoecus* (Trichoptera), *Cordulegaster* (Odonata), *Doroneuria* (Plecoptera), and *Pteronarcys* (Plecoptera), all of which were found >50% more frequently during the large–rare searches.

Conclusions and Recommendations

We believe these results have important implications for the collection of data in both basic and applied studies. First, it is clear from the taxa–area relationships that comparison of richness among streams will be difficult unless standard sampling areas are used. Although we recognize that the size of the area sampled will often need to be tailored to the objectives of specific projects, use of a standard sampling quadrat would greatly facilitate subsequent synthesis. Considering the typically high heterogeneity of streams, we suggest that collecting a series of pooled 0.1 m² or larger samples is a better approach than a single sample from an equal area. Regardless of the procedure used, however, it is critical that the total area sampled and subsequent manipulations of samples are reported. For example, because of the taxa–area and collector curve relationships, the richness estimated from 5–0.1-m² samples pooled before sorting and subsampling will be different from that estimated by either 1) taking the mean of the richness values from the same 5, but independently sorted, samples or 2) pooling the taxa encountered in the 5 separate samples.

Do small, fixed-count samples provide an acceptable tradeoff between reducing sample processing costs while maintaining biological information (Barbour and Gerritsen 1996) or is the tradeoff unacceptable (Courtemanch 1996)? The answer lies in the question asked. Although identifying <200 individuals will greatly underestimate the true richness of an assemblage, our rarefaction results suggest that statistical tests for differences in richness based on as few as 100 individuals are nearly as sensitive as analyses based on a larger collection of individuals. Thus for questions that rely only on data about relative differences in biotic richness, these procedures appear robust. Furthermore, fixed counts negate the need to use rarefaction procedures that may be required if samples vary from low to high numbers of individuals. Conversely, these procedures are biased toward finding smaller, more ubiquitous taxa and missing larger, rarer ones. Missing rare taxa may be an acceptable tradeoff if only comparisons of richness indices are made. However, if other metrics are calculated, especially ones based on the presence and absence of specific taxa, e.g., indicator species or community similarity measures, then fixed-count data may entail high sampling error and thus have low power in discriminating real differences among invertebrate assemblages.

Though several reports in the general ecological literature show the need for rarefaction when comparing taxa richness between assemblages (e.g., Sanders 1968, Hurlbert 1971, James and Rathbun 1981), very few benthologists appear to use these procedures or even be aware of them. This apparent lack of familiarity is surprising considering the number of diversity-related studies published in the lotic literature and

the historically important use of diversity and richness as assessment indices. We suspect benthologists may have avoided using rarefaction techniques because the procedures for estimating expected richness values are based on somewhat complex algorithms that are computationally intensive (Colwell and Coddington 1995).

The need for fixed-count or rarefaction procedures will depend on the completeness of sampling and how many individuals are routinely sorted and identified. The procedures used by the BLM Aquatic Monitoring Center were intentionally designed to provide samples containing 350–450 individuals. Raw richness estimates in samples with >300 individuals are much less sensitive to differences in sample counts than are samples with <300 individuals (Figs. 2, 3), hence analyses of raw richness values from samples with variable counts >300 may often result in accurate inferences. However, if statistical tests are being conducted with samples that contain <300 individuals, estimation error associated with differences in counts could be large, thereby reducing statistical power and increasing the likelihood of committing Type II statistical errors (i.e., accepting the null hypothesis of no difference when a difference really exists). Because some ecoregions and habitats are more productive than others and hence will differ in the number of individuals collected and identified, it seems prudent to use rarefaction procedures whenever feasible.

Although no single sampling or subsampling procedure can meet all of the specific objectives of diverse projects, we argue that extensive sampling of habitats in the field coupled with 2-phase sorting of samples in the laboratory represents a nearly ideal compromise between information gained and cost expended. Once at the field site, it takes little additional time to collect samples from several quadrats, especially if these samples are then pooled before processing. Conducting a large–rare search before subsampling the remaining (often large) sample increases the number of taxa encountered. Adding these taxa to either the raw richness values from subsamples with >300 individuals or to rarefied values from small subsamples produces data that are defensible regardless of the metrics applied to these data in subsequent analyses and interpretation.

Broad-scale studies are considered by some to be ecology's next frontier (e.g., Brown 1995, Turner et al. 1995). Drawing accurate inferences from broad-scale temporal and spatial comparisons will require that we continue to increase standardization of both field and laboratory methods (Gurtz and Muir 1994). If ideas and data are shared among research laboratories and movement agencies at all levels, everyone will have a better understanding of freshwater benthic ecosystems.

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About the Authors

Mark Vinson has been a hydrologist for the BLM for 8 y and at the Aquatic Monitoring Center for 3 y. All of his time is spent worrying about the subject of this article and other water-resource issues. He received an MS from Idaho State University and a BS from the University of Wisconsin–Stevens Point.

Chuck Hawkins is a professor in the Department of Fisheries and Wildlife at Utah State University and is also affiliated with the Watershed Science Program, the Ecology Center, and the Aquatic Monitoring Center. He teaches courses in aquatic ecology, watershed science, and natural resources ecology and management. His research interests include the ecology of streams and lakes at broad spatial and temporal scales and the effects of landscape alteration on aquatic ecosystems. He received BA and MA degrees in Biology from California State University at Sacramento and a PhD in Entomology at Oregon State University.