A Database of Lotic Invertebrate Traits for North America

By Nicole K. M. Vieira, N. LeRoy Poff, Daren M. Carlisle, Stephen R. Moulton II, Marci L. Koski, and Boris C. Kondratieff

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Conversion Factors

SI to Inch/Pound

Multiply	By	To obtain
	Length	
millimeter (mm)	0.03937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
	Volume	
liter (L)	0.2642	gallon (gal)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:
°F=(1.8×°C)+32

Temperature in degrees Fahrenheit (°F) may be converted to degrees Celsius (°C) as follows:
°C=(°F-32)/1.8

Concentrations of chemical constituents in water are given either in milligrams per liter (mg/L) or micrograms per liter (µg/L).

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Abstract

The assessment and study of stream communities may be enhanced if functional characteristics such as life-history, habitat preference, and reproductive strategy were more widely available for specific taxa. Species traits can be used to develop these functional indicators because many traits directly link functional roles of organisms with controlling environmental factors (for example, flow, substratum, temperature). In addition, some functional traits may not be constrained by taxonomy and are thus applicable at multiple spatial scales. Unfortunately, a comprehensive summary of traits for North American invertebrate taxa does not exist. Consequently, the U.S. Geological Survey's National Water-Quality Assessment Program in cooperation with Colorado State University compiled a database of traits for North American invertebrates. A total of 14,127 records for over 2,200 species, 1,165 genera, and 249 families have been entered into the database from 967 publications, texts and reports. Quality-assurance procedures indicated error rates of less than 3 percent in the data entry process. Species trait information was most complete for insect taxa. Traits describing resource acquisition and habitat preferences were most frequently reported, whereas those describing physiological tolerances and reproductive biology were the least frequently reported in the literature. The database is not exhaustive of the literature for North American invertebrates and is biased towards aquatic insects, but it represents a first attempt to compile traits in a web-accessible database. This report describes the database and discusses important decisions necessary for identifying ecologically relevant, environmentally sensitive, non-redundant, and statistically tractable traits for use in bioassessment programs.

Introduction

Distributions of lotic species correspond with physical and chemical characteristics of their environment (Townsend and Hildrew, 1994; Statzner and others, 2001b). Unfortunately, the multi-scaled nature of lotic systems (Frissell and others, 1986) and broad-scale changes in taxonomic pools often hinder our ability to predict changes in community composition along environmental gradients. Historically, the ability to circumvent this limitation has led to leaps in our understanding of stream ecosystems. For example, the River Continuum Concept predicted community change along a longitudinal stream gradient in terms of functional feeding guilds rather than taxonomic composition

(Vannnote and others, 1980). Feeding guild is a functional attribute of an organism describing the primary method of food collection. The functional attributes that a species possesses are theoretically the product of natural selection by the environment in which the species evolved. Thus, functional attributes are intrinsically associated with local environmental drivers (for example, hydrologic regime, temperature). This is especially true for less mobile organisms like lotic invertebrates.

The functional attributes of species include morphological, physiological, behavioral, and ecological characteristics. The definition of functional attributes used in this report includes all of these characteristics, but hereafter they are referred to collectively as "traits" or "species traits" (*sensu lato*), even though functional attributes are often characterized at genus and higher taxonomic levels.

Predictable changes in assemblage-wide trait representation have been observed for lotic invertebrate communities along gradients of hydrologic disturbance (Richards and others, 1997; Townsend and others, 1997; Vieira and others, 2004) and anthropogenic pollution (Charvet and others, 1998). Commonalities among these studies, such as the presence of highly mobile, short-lived species under harsh conditions, demonstrate how the use of traits can facilitate identification of patterns in aquatic community responses to anthropogenic disturbance. As such, a trait-based approach has much potential as a tool for use in biomonitoring. Several invertebrate traits are already used widely as indicators for biological assessment (for example, functional feeding guild; Barbour and Yoder, 2000; Hering and others, 2004). A broader set of traits is being used to define assemblage types and determine expected biological conditions at reference sites for biomonitoring programs outside of the United States (Charvet and others, 1998, 2000; Dolédec and others, 1999, Usseglio-Polatera and others, 2000a, b; Statzner and others, 2001a; Gayraud and others, 2003; Chessman and Royal, 2004).

There are many theoretical and practical advantages in using species traits for biological monitoring and assessment. First, a species' attributes are shaped by the environment through natural selection over evolutionary time scales, but also influenced by how the species responds to more recent environmental change. When anthropogenic environmental changes are imposed on biological communities, only species possessing certain traits are likely to persist (Poff, 1997; Statzner and others, 2004; Lamouroux and others, 2004). As a consequence, patterns in the distribution of traits in disturbed environments could be diagnostic of the stressors (for example, sedimentation) that may have caused community alteration. In addition to providing a mechanistic framework for interpretation of patterns, trait-based metrics also provide a consistent method for assessing community responses to environmental gradients across local, regional and continental scales. This flexibility is due to the tendency for species traits to be less constrained by biogeography than species composition. Finally, traits such as feeding guild, mobility and habitat preference can be linked to food web dynamics, thus reflecting not only community structure but also ecosystem function (Heino, 2005).

In addition to theoretical advantages, there also are practical benefits of using traits in bioassessment programs. For instance, trait-based approaches may be more time-efficient than taxonomic-based approaches because higher levels of taxonomic identification (for example, genus and family) may adequately describe trait occurrence (Dolédec and others, 1998, 2000; Gayraud and others, 2003). Trait-based metrics also may be robust to taxonomic ambiguities (Moulton and others, 2000), which can influence how taxonomically based metrics respond to environmental gradients. Ambiguities can occur when taxa are not identifiable to lower taxonomic levels until they reach a certain developmental milestone, and individuals of the same species are inadvertently counted as two taxonomic groups (for example, at both the genus and family levels). Finally, traits describing environmental tolerance are often invoked to explain observed biological responses to environmental disturbance. The availability of tolerance-related traits relevant to specific environmental factors (for example, acid tolerance) improves the empirical basis for interpretations of tolerant taxa.

The limiting factor for application of trait-based metrics in North America is the lack of comprehensive summaries of traits for the continent's aquatic invertebrate taxa. Merritt and Cummins (1996) summarize a narrow range of traits for aquatic insects of North America, but analogous information for non-insects and a wider array of traits is generally not available. Further, existing compilations are not updated frequently, nor are they widely available to the public. This limitation inspired the development of a web-accessible compilation of species traits of North American invertebrate taxa. The National Water-Quality Assessment (NAWQA) Program of the U.S. Geological Survey (USGS), in cooperation with Colorado State University (CSU), compiled trait information from keys, texts, peer-reviewed publications, and reports for nearly 1,200 invertebrate genera. The purpose of this report, is to describe how the trait database was constructed, identify necessary considerations in summarizing trait data, and discuss analytical tools for developing trait-based metrics for use in biological assessment.

Acknowledgments

The genesis of this work occurred during the 2003 Annual Meeting of the North American Benthological Society in Athens, Georgia. Subsequently, Carol Couch (formerly USGS) recognized the importance of this work and facilitated the development of a Cooperative Ecosystems Studies Agreement between USGS and CSU. We thank Richard Thorp, Jeremy Monroe, and Cecily Mui (all CSU) for entering the majority of the trait information, and Jason Schmidt for his assistance in compiling Coleoptera literature. Bob Zuellig (USGS) and Julian Olden (CSU) provided comments regarding the use of trait-based analytical approaches in stream ecology. Ian Waite (USGS) and Bob Zuellig (USGS) greatly improved the manuscript through their technical reviews.

Methods

This section describes the traits presented in this database. Biological and ecological traits were grouped into one of four general categories: ecology, morphology, behavior, or physiology. Finally, descriptions of the compilation process and quality assurance procedures are given.

Selecting traits for the database

A given species trait can have several potential states or modalities (rarely continuous). The delineation of states for each trait often is arbitrarily defined based on the resolution of information available. For instance, the feeding guild trait can be defined based on a species' mouthpart morphology (for example, shredder or grazer). Alternatively, the states of the same trait may be defined to reflect the food consumed (for example, detritivore or herbivore). If the understanding of a trait is poor, then the states may simply be defined as binary (for example, detritivore or non-detritivore). The matrix of traits and trait states for an organism can be considered its "functional trait niche" (sensu Poff and others, 2006).

Two general types of traits are distinguished in bioassessment programs; biological (for example, voltinism) and ecological (for example, altitude preference) (see Charvet and others, 2000; Dolédec and others, 2000; Statzner and others, 2001a, Gayraud and others, 2003). Biological traits reflect physiological requirements, morphological adaptations, and life histories that are innate to an organism. These traits provide a mechanistic explanation for how a species responds to the environment, but may also be phylogenetically constrained. That is, species or genera that are phylogenetically related likely have similar states of these traits because they are evolutionarily conserved among taxa (for example, case construction by some Trichoptera taxa). In contrast, ecological traits are those that reflect an organism's environmental preferences and behaviors associated with these preferences. Ecological traits are phylogenetically more plastic, and thus, may be more responsive to current environmental conditions (Poff and others, 2006). Ecological traits, however, are often defined by correlations with environmental factors (for example, species presence and altitude), creating a tautological problem when they are applied to a gradient based on the same factors. Clearly, tradeoffs exist between these two types of traits.

Biological and ecological traits targeted for this database were differentiated into four general categories: ecology, morphology, behavior, and physiology (table 1). States of each trait were delineated to anticipate the types of information available in the literature and were expressed in categorical, binary and quantitative terms. Traits were allowed to be mutually exclusive (for example, body is either round or flattened in shape) or co-occurring (for example, a species may be a collector-gatherer and also a predator). In total, the database includes information for 62 traits.

Finally, as discussed above, traits are a product of the natural selection of species, but may also be useful when described at higher taxonomic levels. As a result, species-level resolution was maintained in the database, but traits for genus or higher-level taxa were recorded when species information was not available from a specific information source. Consequently, many genus- and family-level traits are present in the database.

Compiling Traits Information

More than 3,000 texts, keys, reports, and publications on North American aquatic invertebrates were reviewed from the entomological libraries of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University, and Dr. Boris C. Kondratieff. As each literature source was searched, a record in the database was created for each taxon for which any trait information was reported. The spelling and validity of taxonomic names were checked for families and genera; species-level nomenclature was not reviewed because of the potential need to resolve synonymy issues and because this study focused on family- and genus-level summaries of traits. Duplicate entries (by different observers) were made for 266 records in the database. These duplicates were compared to determine whether information from the same literature source was comparable between two observers.

Summary Statistics

About one third (967) of the citations contained relevant and useable information about functional traits. A total of 14,127 records of trait information was created for 2,255 species, 1,165 genera, and 249 families. The most trait information was collected for aquatic insect taxa. The richest species-level trait information (greatest number of records) was collected for families within the insect orders Ephemeroptera (Heptageniidae, Baetidae, Ephemerellidae, Leptophlebiidae), Trichoptera (Hydropsychidae, Rhyacophilidae, Hydroptilidae, Leptoceridae, Polycentropodidae, Lepidostomatidae, Limnephilidae, Philopotomatidae, Brachycentridae, Glossosomatidae), Plecoptera (Perlidae, Perlodidae, Capniidae, Nemouridae, Pteronarcyidae, Taeniopterygidae), and Coleoptera (Dytiscidae, Elmidae). Greater numbers of records for these taxa are probably a result of two factors. First, the literature search for the database was extensive but biased because searches of the primary literature were largely made in an entomological museum. A lack of species trait records for non-insect taxa, therefore, does not necessarily indicate a lack of information in the literature. Second, a lack of species-level records for non-insect taxa may also be due to less research in these groups relative to insects. This database clearly represents a first step toward compiling invertebrate traits for North America, but additional literature and expert opinion should be consulted periodically, especially for the non-insects. In the meantime, summarizing traits at higher taxonomic levels may be adequate to address community responses to environmental gradients when trait information cannot be generated for a genus or species (Dolédec and others, 1998, 2000; Gayraud and others, 2003).

The number of genera for which information on a specific trait was available is highly variable ranging from 5 to 1,127) (table 1). The traits most frequently available were water-body type (n=1,127), primary feeding guild (n=986), primary habit (n=976), and microhabitat preference (n=914). The traits least available were lethal temperature (n=5), measurements of body height (n=9), and lethal dissolved oxygen levels (n=12), which may indicate that little information exists for these traits for many aquatic invertebrate taxa. On average, resource acquisition and ecological traits were most frequently reported whereas physiological tolerance and reproductive traits were least frequently reported. Morphological and life-history traits were reported with intermediate frequency. The database, aside from being useful for development of trait-based biomonitoring metrics, also identifies potential gaps in knowledge regarding the biological and ecological characteristics for many invertebrate species. Clearly, more research is needed on physiological tolerance and reproductive biology of North American invertebrates.

The quality-assurance procedures built into the compilation process were effective. Of the 3,411 taxa for which trait data were entered, 101 (3 percent) were found to have errors in the taxonomic name, which represented an error rate of 0.7 percent of the 14,127 trait records (table 2). For the most part, duplicate entries were identical. Most notable differences occurred in the interpretations of “early and late season” for emergence, and some confusion existed as to whether *season collected in*, *mating season*, and *emergence season* could be considered synonymous. In addition, several data entry technicians included additional information on armoring and other morphological adaptations obtained from photographs and schematics in the reviewed document. The most complete of the duplicate records were retained in the database and all others were deleted.

Considerations in Using Trait Information from the Database

This database represents the most comprehensive matrix of traits available for North American invertebrates. The extensive volume of trait data available in the database and the variety of ways in which it may be summarized will require forethought by users regarding: (1) which traits are appropriate to the environmental gradient of interest; (2) whether the traits are intended to reflect changes in community structure or ecosystem function along the gradient; (3) the consequences of linked traits or “trait syndromes”; (4) the desired/necessary level of resolution for taxonomic identifications; (5) how trait states are assigned to a particular taxon; and (6) the analytical and statistical tools that will be used to analyze data. These necessary decisions are further discussed below to provide database users with a roadmap to selecting ecologically relevant, environmentally sensitive, non-redundant, and statistically tractable traits for use in biomonitoring and assessment programs.

Traits and Environmental Gradients

Different suites of traits are expected to correspond with specific hydrological, physical, and chemical gradients in the lotic environment (Poff and others, 2006; table 3). For instance, thermal change may be best indicated by changes in body size, voltinism, timing of emergence, and fecundity (see Hogg and Williams, 1996; Huryn and Wallace, 2000). Hydrologic disturbance may be indicated by voltinism, rheophily, habit, microhabitat preferences and body shape (see Richards and others, 1997, Vieira and others, 2004). Traits such as respiration mode, ability to exit the water, and mobility via drift or swimming may be sensitive to chemical contamination (for example, Charvet and others, 1998, 2000). The level of specificity of individual trait responsiveness to different environmental gradients must be considered when developing indices (for example, multi-metric) for general environmental alterations. *A priori* selection of relevant traits will result in refined indices that better characterize community responses to specific environmental gradients or general environmental degradation.

Traits and Ecosystem Function

Bioassessment metrics that relate aquatic community responses along environmental gradients to ecosystem function generally are lacking (Heino, 2005). Whereas all traits can be incorporated into metrics that indicate community structure, such as richness and diversity, some traits also can be linked to ecosystem function. For example, feeding guild information (Cummins and Klug, 1979) can represent nutrient cycling, resource processing (for example, shredder or grazer) and trophic position (for example, predator or omnivore) (Wallace and Webster, 1996). Some traits may reflect ecosystem function when considered in combination with other traits (Heino, 2005). For example, maximal body size in combination with emergence timing and voltinism indicate biomass turnover or changes in secondary productivity (Huryn and Wallace, 2000). Emergence and oviposition behaviors, when considered with the ability for immatures or aquatic adults to temporarily exit the stream, may indicate differences in subsidies to the terrestrial foodweb (Baxter and others, 2004). Traits that are structurally and functionally informative should be included in the set of traits identified as relevant to the environmental gradient of interest.

Linked Traits / Trait Syndromes

Traits that are plastic and phylogenetically decoupled from other traits probably are most robust for use in biological assessments. Plastic traits are anticipated to respond more quickly, and to a greater degree, to changes in environmental conditions than phylogenetically constrained traits (for example, those traits that vary little among related taxa). For example, traits reflecting ecological roles such as feeding guild, temperature preference, and mobility mechanisms such, as drift propensity and crawling rate, are more plastic among North American lotic insects than are most life-history traits (see Poff and others, 2006). This relative plasticity of ecological traits may make them superior to other traits in some applications (see Usseglio-Polatera and others, 2000a). Evolutionarily conserved traits pose an additional problem because they often co-occur in closely related taxa. As a result, groups of traits may respond to an environmental gradient similarly and in tandem (Poff and others, 2006), creating redundancies that complicate interpretation. For example, the trait states describing semi-voltinism, preference for depositional habitats, and long-lived and strong-flying adults cluster together phylogenetically (Poff and others, 2006). This "syndrome" is represented mostly by members of the Odonata. Vieira (2003) found that this odonate "syndrome" led to the counterintuitive positive correlation between semi-voltinism and flashfloods in a stream affected by wildfire. Specifically, semivoltine odonates were able to persist in the community because of the "strong adult dispersal" element of the adaptive suite of traits. Other semivoltine taxa that lacked such dispersal ability were notably absent (for example, elmid beetles).

Traits and Taxonomic Resolution

Once traits have been identified that are appropriate for a specific objective, the resolution of information for these traits must be determined. Specifically, decisions must be made regarding the appropriate and (or) minimally sufficient taxonomic resolution of data extraction, and the modes of characterization for the traits (for example, trait states). Options for statistical analyses must also be considered.

Although this database contains information at the species level, species information typically is not necessary for trait-based analytical approaches used in bioassessment programs. As previously mentioned, taxonomic resolution at the genus and family levels has resulted in successful application of traits to characterize aquatic communities for bioassessment purposes (Dolédec and others, 1998, 2000; Gayraud and others, 2003). Species-level identification typically is more costly and error prone, and may also result in taxonomic ambiguities because individuals are not identifiable to the same taxonomic level (Moulton and others, 2000). Ambiguities often are due to differences in the timing of specimen collection or damage caused by field or laboratory sampling processing. As a result, inconsistencies in taxonomic identifications across regions are likely to occur in a broad-scale bioassessment program. Since congeneric species typically have similar functional trait niches (Poff and others, 2006), developing functional trait niches for invertebrate genera are appropriate. Family-level trait information may also be adequate for evolutionarily conserved traits such as body shape. Species-level resolution may be desired if the goal of the study is to investigate adaptive radiation in highly heterogeneous habitats, or conversely, if the fauna is so depauperate that differences among the few species that do exist may be the only indication of environmental change.

Defining Trait States

Trait states often are defined arbitrarily based on the questions of interest, the available trait information, or the anticipated statistical analysis. Recent applications of trait-based analytical approaches to bioassessment have categorized traits into states, which are coded either in a binary or "fuzzy" manner for each species. Binary coding characterizes trait states as mutually excusive (for example, yes/no) categories. Alternatively, fuzzy coding characterizes the affinity of each state (Chevenet and others, 1994). An affinity score of zero indicates no affinity of a species to that state, whereas the highest affinity level indicates that a species has that particular state exclusively. To give the same weight to each species and each trait, affinity scores typically are standardized so that the sum for a given species and a given trait equals one (Chevenet and others, 1994). For example, the affinity of a taxon to three states of voltinism (semivoltine, univoltine, multivoltine) could be assigned in a binary way (for example, 0,1,0, respectively) or using fuzzy coding (for example, 0.3, 0.7, 0.0, respectively).

Fuzzy coding represents a more realistic characterization of trait states, especially for those organisms with ontogenetic shifts in trait states. Furthermore, fuzzy coding can be used to consolidate information on trait states at lower levels of taxonomic resolution. For example, if organisms are identified to the family level, trait affinity scores can be used to express the diversity of states occurring among the member genera. Trait-based studies in Europe have used the fuzzy-coding approach with much success, because the traits for the limited pool of European fauna are well known. The database presented here should provide important information to adopt this approach for North American aquatic invertebrates and also provide an opportunity to express traits such as maximal body size, thermal tolerance/preference, and elevational preference in a quantitative fashion. Lack of species trait information for North American taxa has, until now, limited this type of continuous, numeric characterization of traits.

Statistical Analysis of Traits

Appropriate statistical analyses in trait-based bioassessment programs will vary depending on study objectives. For example, if multiple, relevant and robust traits are incorporated into metrics, a host of univariate and multivariate tools (for example, linear modeling, ordination) are available to link changes in the metric with changes in environmental conditions. Statistical tools, however, do not exist for developing models that associate traits with environmental conditions to predict community composition. In general, linking traits, species presence or abundance, and environmental variables is difficult because few statistical approaches have been developed to deal with the simultaneous analysis of three matrices: (1) species composition (species by site matrix), (2) environmental gradients (habitat characteristics by site matrix), and (3) functional attributes (species by traits matrix). Approaches thus far have included the simultaneous ordination (see Dolédec and others, 1996) or constrained multiplication (the fourth-corner method by Legendre and others, 1997) of these matrices. These approaches consider only a single trait at a time, and thus, do not consider how a trait-environment relationship may be conditional upon another trait. As such, these approaches have limited predictive capacity.

Other approaches to trait-species-environment data include separate, multivariate ordinations (for example, Willby and others, 2000), and a number of complex analytical procedures, such as multivariate analysis in combination with matrix multiplication (Díaz and Cabido, 1997) and multiple regression tree analyses. Nygaard and Ejrnæs (2004) developed a method based on a novel application of the analysis of variance that represents a considerable simplification over a number of ordination approaches and facilitates the use of binary, categorical, and continuous data. More sophisticated mathematical approaches have been forwarded that use state-space models to define community composition in terms of a “centroid” in a three-demensional trait space (Billheimer and others, 2001). Recently, this approach was extended to handle multiple traits and examine main and interactive effects in a Bayesian framework (Johnson, 2003). Finally, Moss (2000) describes the integration of species traits (that is, pollution tolerance scores) and models that predict community composition using natural environmental gradients. This approach is promising because if species presence or abundance can be predicted, then it follows that the associated traits also can be predicted.

Currently, statistical methodologies relating species and their traits to environmental gradients do not consider multiple traits and environmental variables, which is ultimately necessary to provide a quantitative basis for prediction. Until such tools are available, the application of traits in bioassessment programs will be largely descriptive and limited to composite trait indices. As such, it is critical to refine the working trait matrix to include only traits that are relevant to the questions of interest, robust (responsive) enough to measure environmental change, and not phylogenetically correlated.

Using the Traits Tables from the Database

To facilitate the use of this database, this report includes electronic tables (in tab-delimited text format) of traits derived from a series of queries of the trait database. The traits tables represent summaries of information contained in the traits database, and were compiled at the genus and family levels of taxonomic resolution. Each table is a matrix of taxon (rows) and trait states (columns). The cells represent the *count* of records in the database that classified the taxon into each trait state. For continuous traits (for example, body length), average values and the number of observations are provided.

Additional data manipulation is required before the traits summary tables can be used. Traits summary tables are provided so that users can determine how trait states are represented (See "Defining Trait States"). If users wish to assign a single trait state to each taxon, they may do so by summing the record counts across states of each trait, then dividing each count by this total. The trait state with the highest proportion of records can then be flagged as the desired state designation for that taxon. Alternatively, users employing fuzzy coding may retain the proportions computed above for each trait. Raw counts also were retained in the traits tables so that users can use counts of records to guide their confidence in trait classifications. Traits with greater numbers of records may be more reliable than those with few records.

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Data Files

Data file	Brief Description
InvertTraitsFields_v1.txt	Descriptions of fields used in the invertebrate traits data table; tab-delimited text file (8 Kilobytes)
InvertTraitsTable_v1.txt	Complete invertebrate traits data table; tab-delimited text file (5,465 Kilobytes)
InvertTraitsCitations_v1.txt	Literature cited in invertebrate traits table; tab-delimited text file (225 Kilobytes)

Table 1. A list of traits included in the database for species traits of North American invertebrates.

[No., number; mm, millimeter]

Trait Category	Trait Type	Trait Description	State Type	No. Genera Classified
Ecology	Ecological	Type of water bodies found in	Binary for each category	1,127
		Primary water body found in	Categorical	163
		Upper elevation distribution	Numeric	222
		Lower elevation distribution	Numeric	253
Morphology	Morphological	Maximal body size of immatures	Ordinal category	704
		Length of immatures (mm)	Numeric	677
		Width of immatures (mm)	Numeric	97
		Height of immatures (mm)	Numeric	9
		Body shape	Categorical	580
		Body shape with case/retreat	Categorical	133
		Does the shape mediate drag?	Binary or unknown	49
		Adaptations to deal with flow or silt present?	Binary for each category	581
		Degree of body armoring	Ordinal category	707
		Respiration mode of early instars	Categorical	528
		Respiration mode of late instars	Categorical	591
		Respiration mode of aquatic adults	Categorical	293
Behavior	Reproduction/Life history	Emergence behavior/location	Binary for each category	185
		Can emergence occur year round?	Binary or unknown	94
		Emergence synchrony	Binary or unknown	131
		Season that emergence begins	Categorical	480
		Season that emergence ends	Categorical	463
		Primary oviposition behavior/location	Categorical	453
		Secondary oviposition behavior/location	Categorical	214
		Are the eggs cemented?	Binary or unknown	243
		Oviposition duration	Categorical	20
	Resource Acquisition/Preference	Primary feeding guild based on mouthparts	Categorical	986
		Secondary feeding guild based on mouthparts	Categorical	427
		Food materials consumed	Text comment	841
		Primary habit (how to deal with flow)	Categorical	976
		Secondary habit (how to deal with flow)	Categorical	510
		Current preference/rheophily	Ordinal category	515

Trait Category	Trait Type	Trait Description	State Type	No. Genera Classified
Behavior continued	Resource Acquisition/Preference continued	Microhabitat preference (subtrate)	Binary for each category	914
		Lateral habitat position in water column	Binary for each category	893
		Vertical habitat position in water column	Binary for each category	693
	Mobility	Drift propensity for early instars	Ordinal category	63
		Drift propensity for late instars and aquatic adults	Ordinal category	82
		Larval travel distance (crawling/swimming/drift)	Ordinal category	48
		Adult dispersal distance (crawling/swimming/flight)	Ordinal category	224
		Ability to exit aquatic environment	Binary or unknown	193
Physiology	Life history	Number of aquatic life stages	Ordinal category	231
		Voltinism	Ordinal category	459
		Overwintering of eggs or immatures?	Text comment	327
		Development speed/pattern of development	Categorical	218
		Adult lifespan	Ordinal category	279
		Fecundity (number of eggs laid)	Ordinal category	281
		Egg type (single, multiple batches, one batch)	Binary for each category	403
		Time it takes to hatch eggs	Ordinal category	298
		Egg diapause?	Binary or unknown	136
	Tolerance	Oxygen tolerance/requirements	Binary for each category	258
		Lethal dissolved oxygen levels	Numeric	12
		pH tolerance	Binary for each category	287
		Salinity tolerance	Binary for each category	220
		Thermal preference	Categorical	288
		Minimum temperature surviving in	Numeric	155
		Maximum temperature surviving in	Numeric	171
		Lethal temperature	Numeric	5
		Turbidity tolerance	Categorical	196
		Indicator value for ionic strength	Ordinal	102
		Indicator value for nutrients	Ordinal	102
		Indicator value for oxygen/temperature	Ordinal	102
		Indicator value for suspended sediments	Ordinal	98
		Indicator value for fine substrates	Ordinal	102

Table 2. Error rates for data entry in the traits database.

[No., number; NAWQA, National Water-Quality Assessment; n/a, not applicable; %, percent]

	No. records not matching NAWQA list	**No. entry errors**	**No. blank/incomplete records**	**No. taxonomic updates**	**Total errors**	**Error rate* (%)**
Species level	n/a	n/a	n/a	n/a	n/a	
Genus level	639	11	33	13	57	1.56
Family level or higher	40	8	28	8	44	1.27
				Total errors in taxonomic fields	101	2.93

* error rate per the total number of taxa in the taxonomic list

Table 3. Examples of species traits relevant for different environmental gradients.

Environmental Gradient	Examples of Appropriate Species Traits
Thermal	Maximal body size of immatures
	Voltinism
	Timing of emergence
	Fecundity
	Elevational distribution
Hydrological	Rheophily
	Habit
	Vertical/lateral habitat position in water column
	Body shape and mediation of drag forces
	Oviposition behavior/location
Physical (streambed)	Feeding guild or food materials consumed
	Microhabitat preference
	Adaptations to deal with silt
	Larval travel distance
	Drift Propensity
Chemical	Respiration mode
	Ability to exit the aquatic environment
	Egg diapause
	Drift propensity
	Feeding guild or food materials consumed