

Species versus generic identifications in water-quality monitoring and ecological studies of Trichoptera in North America: Is this question still unresolved after half a century?*

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Abstract

Species-level identifications of the larval stages of caddisflies are available for only a limited number of taxa that are used currently in water-quality monitoring programs. This has been a long-lamented condition, but the proportion of species identifications available for aquatic forms that are used in these efforts has increased little over the past half-century. This is despite repeated and documented advantages that species-level identifications add to monitoring studies. Approaches to examining this question have ranged from anecdotal accounts of pollution tolerance among species within a genus to detailed analyses comparing information available through different hierarchical levels of taxonomy, from species to family. Justifications for not using species-level taxonomic resolution have ranged from financial considerations to suggestions that higher levels are equally as valid in showing trends as are species-level identifications. However, the evidence justifying the use of higher levels of taxonomy is lacking and more evidence favors the value of species-level identifications. Genetic techniques offer the promise of more larval-adult associations, more useful identification keys, and improved biological monitoring.

Key Words

biomonitoring, history, pollution assessment, taxonomic sufficiency, water quality

Introduction

The First Trichoptera Symposium held in Lunz-am-See, Austria, 50 years ago brought together caddisfly researchers from around the world. Many collaborations and friendships were formed there that have lasted for decades.

At that first symposium, I presented a paper demonstrating that changes in caddisfly occurrence at an impacted site may be more evident when using species-level identifications compared to identifications made at generic levels. The examples presented also demonstrated that different water-quality tolerances are evident within the same genus (Resh 1974).

Over the past one-half century, many authors have discussed the significance of taxonomic levels used in water

quality studies in various forums in the United States and throughout the developed world (e.g., Resh 1974; Schmidt-Kloiber and Nijboer 2004; Robinson 2023). Currently, this issue is often discussed under the label of “taxonomic sufficiency,” which attempts to determine what level of identifications is necessary to answer the question or hypothesis under analysis (Jones 2008). Analysis of taxonomic sufficiency has been widely applied in marine (e.g., Dethier and Schoch 2006), freshwater (e.g., Mueller et al. 2013), and terrestrial systems (e.g., Pik et al. 1999).

Even after long debate, there is still no clear consensus as to what levels of taxonomy are necessary for biological monitoring of fresh waters. While many researchers have argued that when finer levels of taxonomy are used,

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better results are obtained (e.g., Lenat and Resh 2001). Others have argued that similar trends are evident even when higher taxonomic levels (genus or sometimes even family) are used (e.g., Bailey et al. 2001). Jones (2008) has reviewed this topic in detail.

In this article, I examine the question of how considerations of appropriate identification levels have evolved for Trichoptera and other benthic macroinvertebrates over the past 50 years and I attempt to provide some reasons as to why this issue is still unresolved. I present anecdotal and quantitative data along with speculation underlying reasons for this controversy and future advances that could provide resolution to this ongoing debate.

Anecdotal evidence of temporal species-shifts within a genus as the result of water quality changes

Resh (1974) presented the results of surveys of Trichoptera conducted over time in the Rock River, Illinois, and Lake Erie, Ohio, as specific examples of species changes within a genus that may have reflected temporal changes in water quality. Examination of faunal changes over time is now widely used for both invertebrate and vertebrate populations, along with plants, to indicate the effects of climate change, environmental alteration, conservation needs, and a variety of other topics.

Robert Richardson, a scientist at the Illinois Natural History Survey in Champaign, Illinois, made a detailed series of light-trap collections along the Rock River, Illinois, USA, from 1924–1927. Following these collections, the area surrounding this river underwent changes in land use and especially increases in urbanization and industrialization. In Richardson's collections, *Ceraclea menteius* (reported then as in the genus *Athripsodes*) was previously abundant but was absent in collections made in 1971. Then, the co-generic *Ceraclea transversa* was common (Resh 1974).

Likewise, collections made in Put-in-Bay, Ohio, which is located on Lake Erie, in the 1930s found nine species of *Ceraclea* (as *Athripsodes*) to be common (Marshall 1939). However, Horwath (1964) found only 4 of the original 9 species of *Ceraclea* reported earlier to be present. During this interval, Lake Erie underwent a period of severe environmental degradation (Beeton 1961).

The results of the above two faunal studies conducted over long periods, and with sampling efforts conducted over the same months as the original studies, suggest that faunal changes likely reflected the environmental changes that occurred in these two areas (Resh 1974). The studies demonstrated that there were replacements or declines in certain species within the caddisfly genus *Ceraclea*. Although there was no evidence for the underlying cause of the changes, major water-quality changes had occurred between the times of these collections.

Benthic macroinvertebrate genera can have species with different pollution tolerances

During the 1960s and 1970s a series of studies correlated water quality with the presence of different species of fish and benthic macroinvertebrates. These studies were used to assign tolerance values to organisms present under different environmental conditions (e.g., Tarzwell 1965; USEPA 1973). The U.S. Environmental Protection Agency compiled this information into a handbook for biological monitoring of water quality (Weber 1973). Resh and Unzicker (1975) examined water-quality tolerances reported in that handbook for genera of benthic macroinvertebrates where tolerances had been assigned to more than a single species within a genus. They found that the assignments often varied among species within a genus, and sometimes these tolerances varied greatly. For example, in macroinvertebrate genera where water-quality tolerance was reported for more than a single species, all the species in 6 genera were reported to be tolerant. Likewise, all species were reported as intolerant in 17 genera. However, 28 genera contained species within the same genus that were reported as being tolerant or intolerant to water pollution. Since then, similar results of varying water-quality tolerances within a genus of benthic macroinvertebrates have been reported for some North American genera of other caddisflies (e.g., *Hydropsyche*), mayflies (*Baetis* and *Stenonema*), black flies (*Simulium*) and many other groups of aquatic insects in different parts of the world (e.g., Moog 1995; Jones 2008).

Development of species-level larval identification-keys

Over the last 70 years, identification keys were published that enable generic- and species-level identifications of North American caddisfly larvae. The number of keys first increased until the 1990s but then remained steady through to the present (Table 1). Of the identification keys developed over time for North American Trichoptera, only 50% include larval information (Table 1, data from Morse et al. 2019b).

Table 1. North American generic and family level revisions, and regional keys and of Trichoptera including larval and adult keys, based on tables in Morse et al. (2019a: 724–725).

Years	Only Larval Keys	Both Larval and Adult Keys	Only Adult Keys
<1950	0	1	7
1951–1960	4	1	7
1961–1970	5	6	6
1971–1980	5	6	13
1981–1990	2	13	14
1991–2000	5	6	11
2001–2010	4	6	10
2011–2019	3	4	3
Total	28	43	71

Why didn't the development of larval-identification keys in North America continue to rise even though the number of research articles on Trichoptera rose steadily from the 1990s onward? Although several factors could have influenced this, I believe that at least part of this leveling off was the result of three significant articles that were published in the 1970s and 1980s that raised questions about the need for species-level identifications. These articles were by eminent researchers in aquatic entomology and ecology but statements made in these articles may have given the impression that generic- or even higher-level identifications were sufficient for Trichoptera and other macroinvertebrates. First, Noel Hynes (1984) suggested that ecological niches are usually defined at the family level. Hynes did mention that there were exceptions, but this part of his statement is often not included when cited (e.g., Jones 2008). Second, Glenn Wiggins and Rosemary Mackay (1978: 1211) opened the abstract of a provocative paper about ecological relations among Trichoptera with the statement "Based on the general premise that the genus represents an ecological, as well as a morphological type...". Third, a series of papers by Kenneth Cummins and Richard Merritt (Cummins 1973; Cummins et al. 2019) developed the functional-feeding group concept that was based on generic identifications.

The impact of the simple statements in the first two articles that de-emphasized the importance of species identifications is obvious, but I do not believe that similar implications drawn from the functional feeding group concept were intentional. As originally proposed and applied, this concept was based on the notion that the mouthparts of various aquatic insects could serve as the basis of classifying their feeding mechanism and preference. However, it soon developed into tables where feeding-group characterizations were published at the generic level (e.g., in the aquatic-insect taxonomic chapters in Merritt et al. 2019) that, I believe, eventually led to support of the idea that generic-level designations are sufficient in determining functional feeding groups. However, it has long been known that different species of Trichoptera in the same genus may fall into different functional group categories (e.g., Resh 1976) and that, moreover, many species occupy more than one functional feeding group (e.g., Ramírez and Gutiérrez-Fonseca 2014). Cummins et al. (2019: 105) recently stated in discussing the use of functional feeding groups that although "species identification is the appropriate level of taxonomy for many ecological questions" and that "species level resolution is not always required in ecological investigations, particularly in process oriented studies", such as with the use of functional-feeding groups. This statement does suggest that the authors accept functional feeding group-designations at the generic level as being sufficient for water quality monitoring programs that use this approach as a metric for assessing water quality.

Current state of identifications in water-quality monitoring

Trichoptera are a vital component in the assessment of water quality biomonitoring programs worldwide (Resh 2008; Chang et al. 2014). I have argued that identifications to species-level are necessary to achieve the full potential of using Trichoptera and other aquatic insects in water-quality assessments. The larval stages comprise the vast majority of specimens collected and analyzed in such studies. Therefore, larvae of more species than presently identifiable need to be associated with the taxonomically named adults (e.g., Resh and Unzicker 1975; Lenat and Resh 2001; Jones 2008; and Jackson et al. 2019).

California has one of the most successful biological monitoring programs in the United States (Mendez et al. 2019). In California, there are two basic identification levels that are used in biomonitoring studies. For volunteer monitoring that involves citizen scientists, identifications are made to a mix of family and generic levels (K. Lunde, personal communication and SAFIT website). For state-funded monitoring programs and those that are required to be conducted when mandated under state requirements, a mix of generic and species identifications is used.

The California biomonitoring program (CEDEN 2022) includes 80 of the 83 genera of Trichoptera that occur in California (Resh and Mendez 2022) that are identified to the genus level in monitoring programs. 49 of these genera include some species-level characterization of water quality tolerance, and 19 genera have some identifications to species groups within that genus. However, water quality tolerances at the species-level or species-group designations total only ~19% of the 358 species listed as occurring in California (Resh and Mendez 2022). Moreover, K. Lunde (personal communication) indicated that when final analyses are done in biomonitoring programs in California, larvae identified at the species level are typically elevated to the generic level for consistency. Therefore, potential species-level information, even when present, is lost by this elevation of identifications from the species or species-group to the genus level.

In contrast to the Trichoptera and other holometabolous orders of insects, some of the hemimetabolous orders of aquatic insects have higher levels of association between nymphs and adult stages. In California, for example, 100% of the larval stages of Odonata, 77% of Ephemeroptera, and 60% of Plecoptera can be identified to species. The morphological similarity of the hemimetabolous larval stages and adults, and perhaps the ease of rearing them to adults, may provide some reasons behind this disparity from the holometabolous Trichoptera.

Other parts of North America have higher rates of larval-adult associations, and these have resulted in more effective biomonitoring programs (Carter and Resh 2013). For example, in the Southeastern US, Morse et al. (2017a: 248) estimate that 47% of the Trichoptera larvae are "described sufficiently to provide

at least tentative diagnosis". Even considering larval associations of species that have broad western or transcontinental distributions, I would estimate that the proportion of larvae of California Trichoptera that could meet this criterion would only be about 20%. Other chapters in Morse et al. (2017b) reported higher rates for larval-adult associations for Ephemeroptera (96%) but similar levels for Plecoptera (55%) found in the California monitoring program.

The species versus generic identification question

Mazor et al. (2019) noted that the level of identifications done in biomonitoring programs differs depending on the purpose of the study. Jones (2008) suggested that the increased costs and time to do species identification, the lack of available expertise, and the lack of identification keys for larval stages are all factors that result in less-precise levels of identification being used and the consequent loss of information.

Part of the difficulty in producing species-level keys has been that the techniques used to make associations of larvae and adults are time consuming and often unsuccessful (Jackson et al. 2019). The use of metamorphotypes (Milne 1938), where larval sclerites that remain in the case of the developing pupa are used for associations, depends on both timing and chance.

Until recently, most larval identification-keys have been based on associations made using rearing immature stages to adults and metamorphotypes. However, advances in molecular approaches have demonstrated that associations can be made more efficiently and may require less time and cost (e.g., Morse et al. 2019a; Kuntke et al. 2020; Resh and Mendez 2022). For example, Zhou et al. (2007) developed protocols for larval-adult associations of Trichoptera using standardized segments of mitochondrial and nuclear DNA for this purpose. The Trichoptera Barcode Initiative documented molecular diversity and developed a species-level phylogeny for this order (Zhou et al. 2016). Some recent larval-adult associations of Trichoptera have resulted in the creation of identification tools (e.g., Ruiter et al. 2013) and a recent generic study did this for the caddisfly genus *Polycentropus* (Orfinger et al. 2022). Resh and Mendez (2022) recently proposed that museum records of California Trichoptera may lead to increased numbers of larval-adult associations by involving citizen scientists in these activities. Availability of localities and dates of collections of adults through digitization of museum records may enable volunteers to find larval specimens for traditional rearing, link larvae and adults through metamorphotypes, and/or be a source of fresh material for molecular analysis.

Molecular research is advancing so rapidly that innovative approaches are being developed that could greatly

enhance biomonitoring programs. For example, biomonitoring in many California programs now involves the routine collection of environmental DNA (eDNA samples) along with conventional benthic sampling. eDNA examines the genetic material of the fauna present at a site directly from collected water samples. Museums in California have begun the California Insect Barcoding Initiative that will sequence identified specimens from existing entomological collections along with collecting fresh material from the field using standardized sampling methods. There are many other DNA barcoding projects happening around the world at both smaller and larger scales, such as LIFEPLAN in Europe. When genomic libraries of Trichoptera and other species of aquatic organisms are available, I anticipate that there will be widespread improvement of species-level identification keys or even the potential development of new and innovative approaches to making identifications. This information coupled with more information on water-quality tolerances will certainly revolutionize biomonitoring programs worldwide.

In conclusion, I believe that the answer to the question raised in the title of this article is clear: species-level identifications of Trichoptera and other aquatic organisms can provide far more information for ecological studies and water quality monitoring than is available from generic or other less-precise levels of taxonomy. The reasons given in the past for not using species-level identification—cost, effort, lack of expertise—will likely cease to be an issue as new genetic advances will make larval-adult associations easier and less costly. Furthermore, these advances will result in better identification tools for immature stages. Consequently, species-level identification will eventually be the norm in freshwater biomonitoring-programs that use benthic macroinvertebrates. Of course, the development of these tools will also advance research in systematics, ecology, and other research fields for trichopterologists and benthic-macroinvertebrate specialists in water quality monitoring.

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