

Taxonomic sufficiency: The influence of taxonomic resolution on freshwater bioassessments using benthic macroinvertebrates

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Abstract: Changing the taxonomic scale of a biotic-assemblage dataset influences our ability to detect ecological patterns. In bioassessments, a test-site's biological community is compared against a benchmark to indicate ecosystem condition, but the taxonomic resolution needed to judge impairment reliably is the subject of much scientific debate. This paper reviews taxonomic sufficiency for freshwater benthic-macroinvertebrate bioassessments. Three main issues are discussed: (1) the ecological significance of different taxonomic aggregations; (2) trade-offs involving taxonomic detail and information content versus money, time, expertise, and data quality; and (3) sampling- and analytical-method-specific factors affecting taxonomic sufficiency. Although Species should be the default taxonomic level for bioassessments, taxonomic sufficiency is chiefly determined by a study's purpose, and pragmatism often dictates reduced detail. When a taxonomic-minimalism approach is necessary, a quantitative criterion for taxonomic sufficiency should be specified; this criterion should be based on an optimization of cost-benefit trade-offs associated with different taxonomic scales. Mixed-level aggregations, as well as morpho-species and ecological-trait classifications should be considered in this optimization process. Looking to the future, closer ties between taxonomists and bioassessment researchers would benefit both of their disciplines. Such coordination would provide the autoecological information and better diagnostic tools (such as keys and molecular methods) needed for biomonitoring, and better (and more widespread) biomonitoring would fuel taxonomy's resurgence.

Key words: taxonomic sufficiency, benthic macroinvertebrates, biomonitoring, review.

Résumé : Le changement d'échelle des données d'un assemblage biotique influence notre capacité à déceler des patrons écologiques. En bioévaluation, pour indiquer les conditions de l'écosystème, on compare la communauté biologique d'un site d'essais avec une référence, mais la résolution systématique nécessaire pour juger de l'inadéquation de façon fiable fait l'objet de beaucoup de débats scientifiques. L'auteur passe en revue la suffisance taxonomique en bioévaluation des macroinvertébrés benthiques d'eau douce. Il discute trois questions principales : (1) la signification écologique des différentes agrégations taxonomiques; (2) les compromis impliquant le détail taxonomique et le contenu informatif, vs les coûts, le temps, l'expertise et la qualité des données; et (3) les facteurs spécifiques aux méthodes analytiques affectant la suffisance taxonomique. Bien que l'espèce devrait être le degré taxonomique par défaut, pour les bioévaluations, la suffisance taxonomique se détermine surtout par l'objectif d'étude, et le pragmatisme impose souvent une réduction des détails. Lorsqu'une approche taxonomique minimaliste s'avère nécessaire, on devrait spécifier le critère de suffisance taxonomique, lequel devrait se définir sur la base d'une optimisation des compromis coûts bénéfiques associés à différentes échelles taxonomiques. Dans cette opération d'optimisation des processus, on devrait considérer les agrégations à degrés multiples aussi bien que les classifications basées sur les morphotypes et les caractères écologiques. Dans l'avenir, de meilleurs liens entre les chercheurs en taxonomie et en bioévaluation devraient profiter aux deux disciplines. Une telle coordination fournira l'information autécologique et de meilleurs outils diagnostiques (tel que des clés et des méthodes moléculaires) nécessaires pour le suivi biologique, et réciproquement un meilleur suivi biologique provoquera une résurgence de la taxonomie.

Mots-clés : suffisance taxonomique, macroinvertébrés benthiques, suivi biologique, revue.

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Introduction

Species tend to follow all sorts of gradients through time and space, and one could make the case that species are a consequence of the taxonomists [sic] desire to classify. At any rate, however, the practice of placing organisms

into categories called species, which are frequently not very discrete ... has proven to be of considerable operational value and utility. [John Cairns Jr. 1981]

Problem statement and purpose

Although hierarchical Linnean taxonomy is fundamental

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to biology (Cranston 1990; Mallet and Willmott 2003), it creates challenges for ecologists because species, and their biological attributes, are non-uniformly distributed among taxonomic groups.

Some researchers in ecology — for example those investigating physiological processes, toxicity, population dynamics, or biodiversity — need species-level data because they intend to make inferences *about species* (Rosenberg et al. 1986; Reynoldson and Wright 2000; Culp et al. 2003; Feio et al. 2006). By contrast, bioassessment studies exploit Cranston's (1990) observation that living things reflect environmental conditions: they use biotic composition as a measure of condition, and inferences are made about the *ecosystem* more than about its species. What is important to a bioassessment researcher, therefore, is that sufficient detail or information is provided in a dataset to allow a site's biological condition to be compared to a benchmark — and the taxonomic detail required for this comparison is not obvious.

Although there has been substantial debate among scientists regarding optimal design, sampling, sample-processing, and analytical approaches for ecological studies, one of the most contentious issues is *taxonomic sufficiency* (*sensu* Ellis 1985; referred to as *taxonomic penetration* by Morris and Brooker 1980), the level of taxonomic detail with which organisms must be identified, to assess biological condition with acceptable certainty, or to recognize ecological patterns having at least some specified signal strength (e.g., Bailey et al. 2001; Carter and Resh 2001; Orr et al. 2003; Waite et al. 2004; Feio et al. 2006).

Herein I review taxonomic sufficiency for community-level benthic-macroinvertebrate bioassessments of freshwater ecosystems. This paper has three purposes: (1) to provide a guide to the taxonomic-sufficiency literature; (2) to highlight the ways that taxonomic resolution affects bioassessment outcomes; and (3) to provide some recommendations to researchers facing decisions about taxonomic sufficiency.

Taxonomic resolution in bioassessments: the state-of-the-practice

Taxonomic sufficiency is a pragmatic concept in which the level of identification is balanced against the need for information. [Ferraro and Cole 1992]

Some researchers regard taxonomic sufficiency as a compromise between the scientific ideal and political, financial, and logistic realities (e.g., Warwick 1993; Bowman and Bailey 1997; Bauernfeind and Moog 2000; Moog and Chovanec 2000; Stubauer and Moog 2000; Carter and Resh 2001; King and Richardson 2002; Marshall et al. 2006). Most claim that the limits of compromise, either in favor of information content (i.e., detailed taxonomy or *high* taxonomic resolution) or reduced costs (i.e., coarse taxonomy or *low* taxonomic resolution), are determined primarily by study objectives: how well patterns in species composition are represented by more coarsely aggregated data, and how accept-

able any information loss is. Other important considerations are the effect-size that requires detection, and the length of the ecological gradient(s) being investigated (e.g., Resh and Unzicker 1975; Kaesler et al. 1978; Ferraro and Cole 1992; Beattie and Oliver 1994; Bowman and Bailey 1997; Taylor 1997; Moog and Chovanec 2000; Reynoldson and Wright 2000; Bailey et al. 2001; Carter and Resh 2001; Lenat and Resh 2001; King and Richardson 2002; Landis 2003; Schmidt-Kloiber and Nijboer 2004; and Marshall et al. 2006). Marshall et al. (2006) stressed the scientific ideal, suggesting that taxonomic resolution should be determined by three things: (1) the reliability of site classifications used for predictive modeling (i.e., for predicting biotic composition); (2) the precision and accuracy of measures of control and test-site similarity; and (3) the ability to detect species-at-risk (taxa facing extirpation or extinction), this last criterion leaving little room for aggregations above Species² (Schmidt-Kloiber and Nijboer 2004). Other considerations have also been stressed, for example, study-area size, the methods used to sample biota and summarize assemblage composition, study areas' taxonomic richness, and more subtle details about the distribution of taxa counts within assemblages (e.g., Corkum 1989; Ferraro and Cole 1992; Norris and Georges 1993; Bowman and Bailey 1997; Moog and Chovanec 2000; Bailey et al. 2001; Carter and Resh 2001; Lenat and Resh 2001; King and Richardson 2002; Schmidt-Kloiber and Nijboer 2004; and Marshall et al. 2006).

Although many authors have discussed the dramatic effects that taxonomic resolution can have on bioassessment outcomes, taxonomic detail is often set without explicit justification, and is often based on subjective criteria for what sample-processing costs or times are acceptable (Cranston 1990). At worst, researchers disregard the issue altogether, so that taxonomic detail defaults to convenience or tradition (Carter and Resh 2001).

Reviews by Resh and McElravy (1993) and Carter and Resh (2001) summarized the state-of-the-practice for taxonomic sufficiency. By examining methods described in 90 published aquatic biomonitoring studies, Resh and McElravy (1993) reported the following trends:

- In river studies, the relatively well-known non-odonate insects (e.g., Ephemeroptera, Plecoptera, Simuliidae), as well as Platyhelminthes and Crustacea, were commonly identified to genus or species; and lesser known, or otherwise more challenging to identify, taxa (e.g., Nematoda, Annelida, and Hydrachnidia) were most often assigned to their families or higher taxonomic groups.
- In lake studies, insects were most commonly identified to genus, but non-insects were often identified to species.
- Twenty-one percent of lake researchers, and 24% of river researchers, consulted taxonomists.
- Specimens collected in lake studies were never reported as archived, but specimens were archived in 4% of the river studies they consulted.

Resh and McElravy (1993), therefore, noted that taxonomic-detail norms were different for river and lake studies,

²To avoid ambiguity, taxonomic terms like *Genus* and *Family* are capitalized throughout this paper when they are used as proper nouns; that is, when they are used in reference to a specific level of taxonomic aggregation. These terms are not capitalized when used in their normal sense. Thus, "...*Family* Ordinations showed more distinct patterns...", but "... The study considered 16 *families* of insects and one mollusc genus...".

and they speculated three main reasons for this: (1) the proportional abundances of benthos groups are different in lakes and streams, (2) our taxonomic knowledge is more comprehensive for some groups than for others, and (3) there are differences in the investigative scale of lake and river bioassessment studies (lake researchers often focus on a specific taxonomic group, and river researchers more commonly undertake whole-community studies). Quantifying the lack of consensus around taxonomic sufficiency, they also reported that, of the 34 papers that discussed taxonomic detail, 18 (53%) emphasized the importance of species-level identification, 9 (26%) argued that less detailed taxonomic aggregation was sometimes acceptable, and 4 (12%) recommended mixed-level taxonomic aggregations.

In the second major review, Carter and Resh (2001) surveyed US-state-agency biologists involved in stream benthic macroinvertebrate biomonitoring programs. Based on information given by 90 respondents, they observed the following trends:

- There was a general lack of agreement about taxonomic sufficiency.
- Government programs favored genus- or species-level diagnoses.
- Crustaceans, mites, oligochaetes, and mollusks were generally identified more coarsely than the Ephemeroptera, Plecoptera, Trichoptera, and Chironomidae.
- Immature animals were usually identified only coarsely, and damaged organisms were generally identified with protocol-specified detail, as long as diagnostic characters could be seen.
- Reference or voucher collections were commonly maintained.

Many other authors have commented on the widespread (and growing) use of rapid bioassessment methods (e.g., Schmidt-Kloiber and Nijboer 2004; Melo 2005), which typically involve qualitative or semiquantitative sampling, subsampling to obtain fixed-count samples, and coarse taxonomy (e.g., Plafkin et al. 1989; Barbour et al. 1999; Metzeling and Miller 2001). The major driver behind this shift in practice is the problem of money and personnel being insufficient to allow detailed surveys of Earth's vast water resources. Despite resources being already too scarce for such surveys, Savan et al. (2004) blamed declining government funding for the increased involvement of nonspecialist researchers (i.e., citizen-scientist volunteers in government-run biomonitoring programs), who generally assign animals only to major taxonomic groups (Chessman 2003).

Summary of key arguments for more- and less-detailed taxonomic diagnoses

Many arguments related to taxonomic resolution have been presented in the scientific literature, some in favor of species-level diagnoses, and some in favor of less-detailed diagnoses. I have classified these arguments by issue into the following 4 classes: summarizing biological composition using an ecologically meaningful unit, dataset information content, technical and financial considerations, and mathematical considerations. These classes are not perfectly dis-

crete, but they allow the key arguments to be presented logically.

Summarizing biological composition using an ecologically meaningful unit

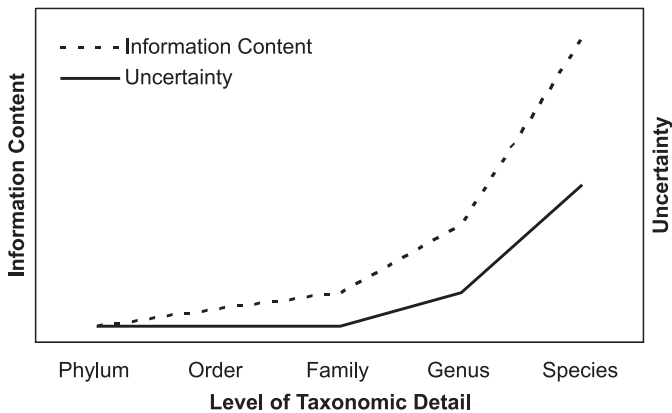
Because ecosystem changes necessarily affect an ecosystem's species, and because — notwithstanding considerable resilience (Taylor 1997) — changed species composition ultimately affects ecosystem processes (Millennium Ecosystem Assessment Board 2005), many authors consider *species* to be an ecologically meaningful unit that is appropriate for use in ecological investigations (e.g., Resh and Unzicker 1975; Rosenberg et al. 1979; Herricks 1984; Resh and McElravy 1993; Stubauer and Moog 2000; Schmidt-Kloiber and Nijboer 2004; Verdonschot 2006). Others dispute this logic, arguing that, although indicator taxa must typically be identified to species, information contained in bioassessment datasets can be effectively summarized in other ways, for example with compositional indices, which do not necessarily require species data and are often robust to taxonomic aggregation (Resh and McElravy 1993; Vlek et al. 2006). Other counter arguments include: that biologists do not agree on the definition or ecological significance of *species* (Kaesler and Herricks 1980; Hynes 1984; Ebach and Holdrege 2005a, 2005b; Fitzhugh 2005; Holdrege and Ebach 2006; Kunz 2006); that many species remain undescribed, so their identification is simply not possible; that the biology of most species is poorly known, so it is difficult to interpret species-level compositional changes; and that agreement on classification increases (Marshall et al. 2006), and the frequency of taxonomic revisions decreases (Ferraro and Cole 1992), as one moves up through the levels in the taxonomic hierarchy.

Dataset information content

... The debate is really about resolution of information and not taxonomy. [Landis 2003]

The resolution-of-information concept is important to discussions about taxonomic sufficiency because the ecological information conveyed by a biotic assemblage is founded on the niche-defining traits, preferences, and tolerances of its component taxa (Marshall et al. 2006), and because there is generally some within-taxon variability in niches. Species is the lowest group in the taxonomic hierarchy, so individuals of the same species exhibit lower variability in traits than occurs within any other taxonomic group. It is widely acknowledged, therefore, that species data provide the most information for discriminating between samples collected at different locations or times (Resh and Unzicker 1975; Learner et al. 1978; Resh and Grodhaus 1983; Slooff 1983; Krieger 1984; Waterhouse and Farrell 1985; Rosenberg et al. 1986; Hall and Ide 1987; Pinder 1989; Resh and McElravy 1993; Moog and Chovanec 2000; Lenat and Resh 2001; Landis 2003; Melo 2005; Verdonschot 2006). Many authors have argued that aggregating data at coarser levels than Species reduces the amount of potentially discriminatory information contained in a dataset (e.g., King and Richardson 2002; Schmidt-Kloiber and Nijboer 2004; Verdonschot 2006; also see Fig. 1), and reduces bioassess-

Fig. 1. Relationship between taxonomic resolution, a dataset's ecological information content, and uncertainty. Hypothetical data; Adapted from Landis (2003).



ment sensitivity (Howmiller and Scott 1977; Krieger 1984; Stubauer and Moog 2000; Marshall et al. 2006) such that rapid bioassessment methods have been criticized for detecting only gross impacts (e.g., Taylor 1997; Bauernfeind and Moog 2000; Metzeling et al. 2003).

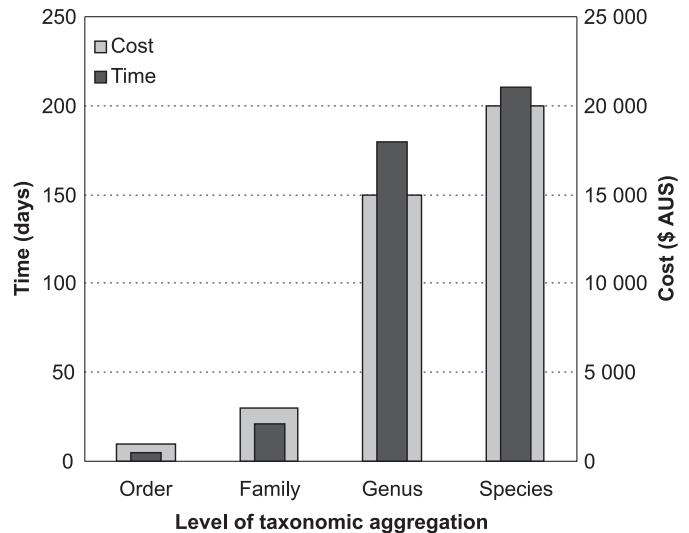
On the other hand, some authors have argued that unless a given study is concerned with making inferences about certain species, less-detailed identifications may be adequate. For example, many studies have shown that taxonomic detail has little influence on multivariate descriptions of benthic communities, suggesting that Genus, Family, or even coarser aggregations provide sufficient resolution for sensitive and accurate bioassessments (e.g., Warwick 1988; Bowman and Bailey 1997; Bailey et al. 2001). To these findings, the Species camp counters that although detailed identification may only slightly improve our ability to distinguish sites and recognize ecological patterns in some cases, species-level datasets always have more taxa, each representing a line of ecological evidence available to guide our interpretation (Guerold 2000; Waite et al. 2004).

Technical and financial issues

Analysis of all but the simplest ecosystems reveals a complexity of communities requiring taxonomic expertise across many orders and several phyla. The attempt to achieve species-level identification for all taxa is hindered by differences in taxonomic refinement, by problems in coordinating the input of different specialists, and by the frequent inability to identify the particular life-history stage revealed in the survey. [Cranston 1990]

Detailed benthos identifications are more costly and time consuming than coarse identifications are (Furse et al. 1984; Sheldon 1984; Kilgour and Barton 1999; Hawkins and Norris 2000; Hewlett 2000; Bailey et al. 2001; Metzeling and Miller 2001; Gayraud et al. 2003; Schmidt-Kloiber and Nijboer 2004; Marshall et al. 2006), and they require more specialized knowledge, techniques (Hilsenhoff 1977; Kaesler et al. 1978; Furse et al. 1984; Grown and Grown 1997; Moulton et al. 2000), and equipment (e.g., microscopes). Furthermore, accuracy and precision are better for coarse taxonomic diagnoses than they are for detailed diagnoses (Chessman 1995; Hewlett 2000; Derraik et al. 2002; Landis

Fig. 2. Benthos identification costs for 29 Australian lowland-river samples, from data reported by Marshall et al. (2006). The maximum is plotted for any time expenditures reported as a range by the original authors.



2003; Marshall et al. 2006), so identifying animals to genus or species requires a significant investment in quality assurance: a comprehensive library of keys and a reference collection must be assembled, and taxonomic specialists must frequently be consulted (Furse et al. 1984; Chessman 1995; Bowman and Bailey 1997; Bailey et al. 2001; Landis 2003; Stribling et al. 2003; Jones et al. 2005; and Marshall et al. 2006).

Several authors have quantified the taxonomic detail vs. effort relationship. For example, Furse et al. (1984) estimated two person-days per sample for United Kingdom benthos samples, and Lenat (1988) reported species determinations requiring four to ten person-hours (depending on the sampling method employed) for North American samples. Although reported costs vary from study to study, they generally follow the pattern reported by Marshall et al. (2006), in which there are large incremental costs to increase resolution from family to genus, but relatively modest increases in investment required to make order–family and genus–species transitions (Fig. 2).

Several studies have shown that it is the abundance of difficult-to-identify taxa that drives sample-processing costs. For example, Hawkins and Norris (2000) reported that identifying midges to species more than doubled the time required to assign them only to their family, Chironomidae; and Vlek et al. (2006) reported that, when species-level enumerations were performed on Dutch and Slovakian stream samples, omitting Oligochaeta and Diptera reduced sample-processing times by factors ranging from 1.2 (for macrophyte samples in which worms and true flies are not abundant) to 2.7 (for sand samples where they dominate).

Pragmatism is the main support for rapid bioassessment methods, which save time and money by using coarse taxonomy (e.g., Ferraro and Cole 1992; Metzeling et al. 2003) and free-up resources for improving sampling methods and increasing replication (e.g., Warwick 1993; Beattie and Oliver 1994; Vanderklift et al. 1996; Taylor 1997; Lenat

Table 1. Percent of specimens (%) and number of taxa (*N*) identified to family, genus, and species, by macroinvertebrate group in a Mid-Atlantic Highlands, USA, study on taxonomic sufficiency. Adapted from Waite et al. (2004).

Group	Total specimens	Family		Genus		Species	
		%	<i>N</i>	%	<i>N</i>	%	<i>N</i>
Ephemeroptera	33886	98	14	77	32	25	57
Plecoptera	19144	98	9	85	38	1	14
Trichoptera	9380	99	18	90	50	17	24
Diptera	48171	100	18	83	172	29	144
Other insects	11013	100	29	95	61	38	34
Non-insects	8874	97	30	76	60	43	65
Total	130468	99 ^a	118	83 ^a	413	25 ^a	338

^aWeighted average.

and Resh 2001; Bradley and Ormerod 2002; Anderson et al. 2005; Melo 2005). In defense of detailed identification, however, some authors have claimed that the incremental costs of genus and species diagnoses are small considering the investments in field sampling, maintaining a reference collection, data quality assurance, and sample archiving that are (or should be) part of biomonitoring programs (e.g., Lenat and Penrose 1980; Bailey et al. 2001).

Morphology-based taxonomy itself poses several challenges to genus- or species-level identification: our taxonomic knowledge is patchy, ranging from rudimentary to imperfect, so that keys and descriptions — for at least some of the life stages or genders of many species — either do not exist, or are not readily available (e.g., Hynes 1984; Cranston 1990); using the keys that do exist requires years of experience; and dichotomous keys are of limited value because some species exhibit considerable variation in their diagnostic characters, and others have few morphological differences that keys can exploit (Evans 1988; Resh and McElravy 1993; Bauernfeind and Moog 2000; Moulton et al. 2000; Ball et al. 2005). Benthic macroinvertebrates are particularly difficult to key-out because they are relatively small, there are many closely-related, morphologically similar taxa, and because some immature forms must be reared to adulthood before accurate diagnoses can be made (Merritt et al. 1984; Waterhouse and Farrell 1985).

Different authors have different perspectives on the implications of these taxonomic difficulties. Pinder (1986), for example, observed that most index-based bioassessment approaches for rivers include Chironomidae as a single taxon or use only selected indicator species, and he questioned the value of species-level taxonomy as a general practice considering our lack of knowledge about species' biology. Lenat and Resh (2001) held a different perspective, cautioning that the combination of more species-level diagnoses and more comprehensive autoecological information (i.e., information about species) might expose a more pronounced taxonomic influence on bioassessments than we now acknowledge.

Detailed keys are available for some regions and benthic groups. For example the texts by Pennak (1978), Peckarsky et al. (1990), Merritt and Cummins (1996), and Thorp and Covich (2001) allow non-specialists working in North America to reliably diagnose specimens at least to family or genus. Furthermore, benthos native to the United Kingdom,

and other well-studied parts of western Europe, are well described to species. Our taxonomic understanding of these North American and European benthos, however, contrasts with our relatively poor understanding of benthos native to other areas of the Developed World (e.g., Hynes 1984; Cranston 1990; Bournaud et al. 1996; Waite et al. 2004; Melo 2005), and contrasts very sharply with our understanding of benthos from the least-studied parts of the world, for which most of the benthos are undescribed (Bauernfeind and Moog 2000; Schmidt-Kloiber and Nijboer 2004). To illustrate, Bauernfeind and Moog (2000), discussed the status of mayfly taxonomy, reporting that references for southern Europe, Central and South America, most of Asia, and Africa are insufficient to support detailed identification. The importance of this matter is highlighted by the many biomonitoring studies in which taxonomic difficulties were reported. For example, Marshall et al. (2006), discussed difficulties associated with assigning immatures to species, and Verdonshot (2006) reported that, despite standard bioassessment methods used in the European Union, substantial variability exists in the taxonomic detail of benthos identifications, at least partially due to regional differences in taxonomic knowledge.

To evaluate taxonomic sufficiency, researchers often compare the information content of species-level datasets with that of datasets expressed at different taxonomic scales (e.g., genus, family, and order). Our ability to make generalizations from these studies, however, is hampered by issues of comparability and data quality. Regarding comparability, different labs have different areas of expertise, different lumping-and-splitting rules, and hence different notions of what species, genus, or family taxonomic scale means. In Hewlett's (2000) "species" treatment, for example, Chironomidae were identified to genus, and Oligochaeta, Acarina, and Hirudinea were identified only to order.

Regarding data quality, fewer specimens can be identified to the required taxonomic level (i.e., precision decreases) and fewer specimens are correctly diagnosed (i.e., accuracy decreases) as taxonomic detail increases: the critical implication is that the quality of our gold standard (Species) is often surprisingly low. Marshall et al. (2006), for example, reported that only 54% of their specimens could be identified to species. Similarly, the gold standard used by Waite et al. (2004) was "lowest practical taxonomic level", a mixed-level aggregation in which 99% of specimens were

Table 2. Taxonomic accuracy and discrimination estimates from an Australian study of the influence of taxonomic resolution on stream classification and ordination. Accuracy is the proportion of taxa that were correctly identified (i.e., matched professional taxonomist's diagnosis); discrimination is the proportion of taxa in the dataset that were identified to the taxonomic level specified by a given taxonomic treatment. The acronym EPT represents Ephemeroptera, Plecoptera, and Trichoptera taxa. Adapted from Hewlett (2000).

Level of taxonomic aggregation	Accuracy (%)	Discrimination (%)
Species	91	50
Genus	95	86
Family	99	98
EPT species	96	62

identified at least to family and 83% of specimens were identified at least to genus, but only 25% were identified to species (Table 1). Furthermore, in a study of longitudinal ecological patterns occurring in the Rhone River, France, 14% of the specimens collected by Bournaud et al. (1996) could not even be identified to family (most of these were worms), and only 29% could be identified to species. Hewlett's (2000) study provides a useful case study: For species-level identifications, she reported achieving only 50% precision, despite having access to good keys and professionally maintained voucher collections. Sequentially coarser taxonomic treatments had better discrimination, such that 98% of specimens were identified to the required level in her family treatment (Table 2). Hewlett's (2000) reported accuracies showed similar trends: family-level taxonomy was 99% accurate, but species-level taxonomy was only 91% accurate (this translates to 46% accuracy overall because species diagnoses were only attempted for 50% of specimens).

Despite taxonomic difficulties, the reliability of detailed benthos identifications can be improved by: consulting expert taxonomists; curating reference- and voucher-specimen collections; and assembling databases of taxa-specific ranges and habitat preferences, so that regional keys can be developed, and the likelihood of a given taxa being collected at a site can be estimated (e.g., Resh and McElravy 1993; Carter and Resh 2001). Also encouraging are the prospects of molecular techniques like DNA barcoding, the use of short nucleotide sequences (e.g., sub-unit I of the mitochondrial DNA gene, cytochrome *c* oxidase) as molecular markers for identifying species (Ball et al. 2005; Kunz 2006). Some authors have speculated that DNA barcoding could be used to identify most species, because, for most of the genera studied so far, significant genetic differences have been observed between member species (Hebert et al. 2003; Ball et al. 2005; Hebert and Gregory 2005). The eventual widespread use of DNA-based identification in biomonitoring studies seems feasible: DNA extraction, polymerase chain reaction, and sequencing is routinely done at specialized labs, and costs will probably fall as the technology becomes more mainstream (Ball et al. 2005; Hebert and Gregory 2005). Presently, these techniques are mostly used to identify species that cannot, or are not easily, separated using

morphological features, but some authors (e.g., Ball et al. 2005) have speculated that automated identification of entire samples may one day be possible using DNA-microarray techniques now being developed.

A debate over the pros and cons of molecular identification methods is playing-out presently in the scientific literature. Some elements of that debate are relevant here because if taxonomists and geneticists work together, tremendous gains in taxonomic knowledge could result. There are two primary implications for bioassessment researchers. First, DNA-based methods may improve both the accuracy and precision of specimen identifications: they could help to identify animals that are difficult to diagnose morphologically (including early instars and damaged specimens), they could help associate different life stages, and they could enable non-taxonomists to identify species rapidly and reliably (e.g., Stribling et al. 2003; Janzen 2004; Moritz and Cicero 2004; Ball et al. 2005; Dayrat 2005; Ebach and Holdrege 2005a, 2005b; Gregory 2005; Hebert and Gregory 2005; Schindel and Miller 2005; Smith 2005). Second, taxonomic knowledge gained while processing many benthos samples would probably lead to many genera and species being re-named, but would have less of an affect on the organization of higher taxa (Hewlett 2000).

The availability of taxonomists has been another point of contention in the taxonomic-sufficiency debate. Researchers favoring detailed identifications claim that competent taxonomists are available, that the consulting sector grows in response to demand (Orr et al. 2003), and that published autoecological data argue for species-level determinations (Bauernfeind and Moog 2000). To the contrary, researchers favoring coarse taxonomic resolution point-out that the number of taxonomists is declining despite increasing demand for their services (e.g., Beattie and Oliver 1994; New 1996; Disney 1998; Godfray 2002; Stribling et al. 2003; Godfray and Knapp 2004; Ball et al. 2005; Ebach and Holdrege 2005a; Smith 2005; Marshall et al. 2006), and that "taxonomic minimalism" reduces bioassessment practitioners' dependence on taxonomists, whose time can be spent on primary taxonomic research and improving keys and other diagnostic tools (Beattie and Oliver 1994).

Mathematical considerations

... The great majority of taxa, often 80% or more, are usually too rare to provide enough information about their individual abundances for formal analyses. [Downes et al. 2000]

There are three main mathematical considerations related to taxonomic sufficiency: (1) bioassessment datasets generated using coarse taxonomy have fewer variables (i.e., fewer taxa) and fewer zero-values than are contained in species-level datasets (Norris and Georges 1993; Vanderklift et al. 1996; Cao et al. 2001; Anderson et al. 2005); (2) taxonomic detail constrains the analytical options available to a researcher; and (3) the effects of taxonomic resolution may depend on the type of data transformation used.

Taxonomic resolution affects multivariate and univariate statistical methods differently. Multivariate techniques are sensitive to both the number of variables and the number of

zero-values (e.g., Bowman and Bailey 1997): At worst, they are ill-suited to handling datasets in which zero-values are prevalent (Downes et al. 2000; Landis 2003), and at best, “methods for managing large numbers of rare species ... are confusing” (Cao et al. 2001). For these reasons, rare taxa are often eliminated from assessments (Norris and Georges 1993, Cao et al. 2001) despite many arguing that they convey important ecological information (e.g., Nijboer and Schmidt-Kloiber 2004; Nijboer and Verdonschot 2004). Univariate methods, by contrast, use *indices* to summarize ecological patterns, an approach that reduces variance and information content (Landis 2003), but provides some robustness to taxonomic detail.

Although reducing taxonomic detail may have some mathematical benefits, it also limits analytical options, particularly for univariate methods (e.g., Resh and Unzicker 1975; Lenat and Penrose 1980; and Brinkhurst 1985). For example, Schmidt-Kloiber and Nijboer (2004) described that, although indices of abundance or proportional abundance, richness, and diversity can always be re-calculated once a dataset’s taxonomic scale is changed, indices based on taxa-specific ecological information are more difficult to re-calculate because our generalizations about the ecological preferences of higher or lower taxa are often unreliable.

In addition, several authors have described interactions between taxonomic sufficiency and data transformation (e.g., Bowman and Bailey 1997; Anderson et al. 2005; and Melo 2005). For example, Melo (2005) reported that species- and family-level data revealed similar ecological patterns in Brazilian streams when composition was expressed using $\log(x+1)$ -transformed abundance; however species data better differentiated sites when composition was expressed as presence-absence.

Effects of taxonomic detail on compositional indices used in bioassessment studies

Bioassessment studies typically generate large datasets, often comprising multiple samples (each with multiple taxa) collected at different sites or times. Summary indices are used to simplify analyses (Hellowell and Holloway 1977; Davis 1995; Anderson et al. 2005); they are selected based on their agreement with accepted ecological theories and their known responses to ecosystem stressors (Norris and Georges 1993; Barbour et al. 1995; Gerritsen 1995; Resh 1995). According to Gray (1989), the three best-documented community-structure responses to environmental stress are: (1) the loss of taxa; (2) opportunistic (tolerant) species becoming more numerically dominant; and (3) a reduction in the body size of the numerically dominant taxa. Different indices, however, emphasize and summarize different patterns in assemblages, and respond differently to different stressors (e.g., Reynoldson and Metcalfe-Smith 1992; Barbour et al. 1995; Kilgour et al. 2004; Bowman and Somers 2005; but see also Taylor 1997); thus a variety of indices (both singly and in combination) have been used (Lenat 1993).

Several studies have shown that the way taxonomic detail affects summary indices, and the importance of these influences, is index specific. For example, in a study investigating the effects of marine-sediment hydrocarbon pollution, Ferraro and Cole (1992), demonstrated that taxonomic suffi-

Table 3. Taxonomic-scale effects on metric-specific discrimination-efficiencies (i.e., the proportion of sites for which a given combination of metric and taxonomic level distinguished impacted and unimpacted sites). Data were gathered in a study investigating the influence of taxonomic resolution on Australian- and Dutch-stream assessments using the AQEM multi-metric assessment system. The best-performing levels of taxonomic detail are shaded grey. Adapted from Schmidt-Kloiber and Nijboer (2004).

Metric	Discrimination efficiency		
	Species	Genus	Family
Richness	83	100	100
EPT richness	92	92	100
% Oligochaeta and Diptera	92	92	42
% Gathering collectors	100	92	92
EPT and Oligochaeta Richness	58	58	42
Shannon diversity	83	67	83
Margalef diversity	75	75	92
% Rheophilic ^a	83	67	92
% Hypocrenal ^b	92	83	92

^aCurrent-loving.

^bPreferring spring-brook habitats.

ciency depends on the size-range of animals collected (hence on the sampling-gear type) and on the response measure used to distinguish impacted from unimpacted sites. When they used richness as the response variable, the required taxonomic resolution depended on the sieve mesh size (family diagnoses were sufficient for 1 mm mesh samples, but species identifications were required for 0.5 mm mesh samples). When they used taxa-dominance, or any one of three diversity indices, as the response variable, species-level information was generally required. In another study, Schmidt-Kloiber and Nijboer (2004) calculated discrimination efficiencies for different metrics using near-species-, genus-, and family-level taxonomy (all of their metrics are used in the AQEM [Integrated Assessment System for the Ecological Quality of Streams and Rivers throughout Europe using Benthic Macroinvertebrates] Assessment Software). For metrics that increase in value with biological impairment, they calculated discrimination efficiencies as the percent of samples from stressor-exposed sites having metric values higher than the reference sites’ 75th percentile; for metrics that decrease with impairment, they calculated discrimination efficiencies as the percent of exposed-site samples having a value lower than the reference sites’ 25th percentile. Their results showed that species-level identification was not always best at differentiating impacted from unimpacted sites (Table 3): total richness and EPT richness (the number of Ephemeroptera, Plecoptera, and Trichoptera taxa combined), performed better at family than at species, and family-level diversity measures also performed well.

Richness (number of taxa)

Richness, or the number of taxa occupying a site or a time, is a meaningful and commonly used measure of ecological condition (e.g., Lenat 1993; Hawkins et al. 2000; Metzeling et al. 2006). Its use as a bioassessment index is widespread for two main reasons:

- (1) Some ecological theories propose that stressors shape biotic assemblages by acting as templates (Townsend and Hildrew 1994) or filters (Poff 1997): that is, by not allowing animals having unsuitable traits to colonize, or persist in, an area. The most obvious and convincing impairment anticipated along a stressor gradient, therefore, is successive deletions of taxa (e.g., Waterhouse and Farrell 1985). Richness indicators' prominence in bioassessments arises from the substantial empirical support (e.g., Lepori and Hjerdt 2006) for such theories. This prominence has not been compromised by the small number of benthic-macroinvertebrate studies that support competing theories — like the Intermediate Disturbance Hypothesis (e.g., Connell 1978), the Dynamic Equilibrium Model (e.g., Huston 1979), and patch-dynamics frameworks (e.g., Pickett and White 1985) — which predict maximal richness at intermediate levels of disturbance.
- (2) Richness is a surrogate for biodiversity (Growth and Grows 1997; Bailey et al. 2001; Marshall et al. 2006), which is important for resource management considering that the population sizes and distributional ranges of most of Earth's species are declining (Millennium Ecosystem Assessment Board 2005).

Taxonomic detail is known to influence measures of richness through several mechanisms. Lenat and Resh (2001), for example, argued that the ratio of the number of taxa per group influences the correlation between richness values calculated at different taxonomic scales. This is because different taxonomic groups have different numbers of members occupying their lower taxonomic ranks. The mean numbers of North American genera per family of Ephemeroptera (4), Plecoptera (11), and Trichoptera (7), and in the Dipteran families, Chironomidae (207) and Simuliidae (11) illustrate this phenomenon (Lenat and Resh 2001). These differences in species-to-family ratios demonstrate that aggregation at any level above Species distorts richness, the importance of these distortions being dataset specific.

Richness is systematically underestimated when it is calculated using data aggregated at a coarser resolution than Species (Hughes 1978; Resh 1979; Waterhouse and Farrell 1985; Resh and McElravy 1993; Marshall et al. 2006). Estimates using less detailed data, however, are often highly correlated with species-level counts (Growth and Grows 1997; Marshall et al. 2006), and, in bioassessments, richness is used to summarize biological condition, not to generate exhaustive species checklists, so coarse taxonomic resolution is often sufficient. For example, Marshall et al. (2006) reported only a 6% information loss when benthos data from dryland river sites in south-western Queensland, Australia, were rolled-up to family from species. They also revisited a previous study — in which Guerold (2000) concluded that the *absolute* differences in the number of Plecoptera, Ephemeroptera, and Trichoptera taxa between polluted and non-polluted streams in France was smaller when richness was calculated using genus and family data than when it was calculated with species-level data — noting that the *relative* differences were concordant. Showing that taxonomic effects are dataset specific, Waite et al. (2004) reported that the discriminatory abilities of family and genus richness measures were different for different regions in the Mid Atlantic Highlands. They found that when

total- and EPT-richness were used as response measures in their Plateau Ecoregion, there were slight differences in discriminatory power associated with the two taxonomic scales: family and genus total-richness and EPT-richness measures permitted sites affected by acid deposition or mine drainage to be distinguished from minimally-impacted controls; but EPT richness measures were only able to detect the effects of acid mine drainage. In their Ridge and Valley Ecoregion, both family and genus EPT-richness measures were able to distinguish enriched from minimally impacted sites, but when total richness was used as a response variable only the less detailed family data permitted these sites to be distinguished (using EPT richness, a sub-set of total richness, intuitively suggests a loss of information, but this loss may be counteracted by focusing on a sub-set of taxa known to be sensitive to human impacts — e.g., Hannaford and Resh 1995; Hewlett 2000; Melo 2005).

Diversity indices

Diversity indices combine information about the number of taxa present in a collection with information about the evenness of their counts (e.g., Shannon 1948; Kaesler et al. 1978; Washington 1984). They are based on the theory that unstressed communities should have many species, representing a variety of taxonomic groups, with no species being numerically dominant. This expected distribution theoretically arises because unstressed conditions provide suitable habitats for many species, but interspecific competition keeps the population of each species in check. Introducing stress (e.g., pollution) reduces the abundance of (or eliminates) sensitive taxa, permits tolerant taxa to expand their niches and increase in number, and results in a net loss of taxa but greater numerical dominance of those able to persist (Kaesler et al. 1978).

Diversity indices are widely used (especially in the United States, where some are required by law) despite substantial criticism — their underlying theories are not always supported empirically, they often convey minimal information related to ecological gradients, they depend on sample size, and their values are not comparable from region to region (Hurlbert 1971). At least partly because they respond to both richness and abundance, diversity indices respond strongly and unpredictably when taxonomic detail changes (Lenat and Penrose 1980; Lenat and Resh 2001).

In early papers on the subject, Kaesler et al. (1978) and Kaesler and Herricks (1979) proposed that diversity could be calculated for each taxonomic rank, yielding measures of *hierarchical diversity*. They showed that diversity components associated with orders and their component families, genera, and species are additive, and sum to the species diversity. Based on their examination of hierarchical partitioning of fish and stream insect diversities in US streams, the authors concluded that genus diversities provide almost as much information about community composition and response to stress as species diversities do (especially for datasets having a low ratio of species to genera). This conclusion followed from two main lines of evidence (Table 4, Fig. 3): (1) for many of their collections there was either no difference or a minor difference between diversity scores calculated using species- and genus-level data (the case of no difference occurs when collected genera were

Table 4. Hierarchical diversities of aquatic insect collections from Jeffreys Creek, South Carolina. (data from Kaesler et al. 1978 and Kaesler and Herricks 1979)

Sample	# of taxa				# of individuals	Diversity				Diversity component			
	O ^a	F ^b	G ^c	S ^d		H _O ^e	H _F	H _G	H _S	O	F	G	S
1	8	17	28	29	179	1.51	2.03	2.48	2.54	1.51	0.52	0.45	0.06
2	7	15	21	22	67	1.15	1.60	2.24	2.27	1.15	0.45	0.64	0.03
3	7	14	32	32	124	1.23	1.50	2.66	2.66	1.23	0.27	1.16	0.00
4	7	20	37	37	259	1.04	1.38	2.28	2.28	1.04	0.34	0.90	0.00
5	8	17	29	29	238	1.12	1.88	2.15	2.15	1.12	0.66	0.27	0.00
6	8	14	22	22	79	1.39	1.77	1.91	1.91	1.39	0.37	0.14	0.00
7	3	4	7	7	11	0.72	0.87	1.24	1.24	0.72	0.15	0.37	0.00

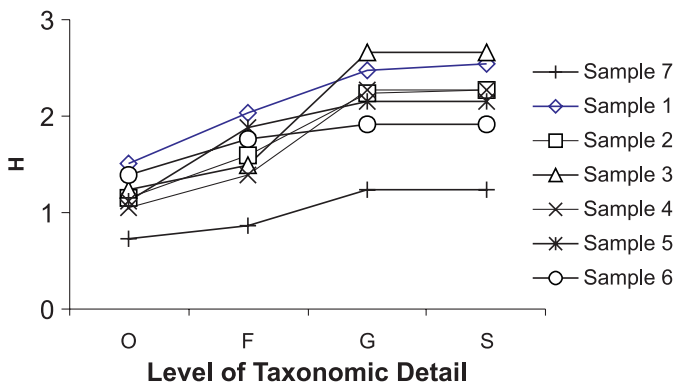
^aO denotes order.

^bF denotes family.

^cG denotes genus.

^dS denotes species.

^eH denotes diversity score.

Fig. 3. Hierarchical diversities of aquatic insect collections from Jeffreys Creek, South Carolina; *H* denotes diversity score; O = order, F = family, G = genus, and S = species (data from Kaesler et al. 1978 and Kaesler and Herricks 1979).

each represented by a single species); and (2) for all streams sampled, rank correlations between genus and species diversities were highly significant.

Lenat and Penrose (1980) pointed-out that the generality of conclusions made by Kaesler et al. (1978) and Kaesler and Herricks (1979) depends on the assumption of little difference between genus and species richness, which numerous datasets show to be untrue. The “Wu Effect” is one of the most well known arguments against relying on coarse taxonomy when calculating diversity indices. Wu (1982) observed that site ranks based on several diversity indices (e.g., Shannon-Wiener, maximum information index, evenness, Margalef’s species richness index, and Hurlbert’s probability of interspecific encounter) calculated using species-level marine macroinvertebrate data changed when taxa were aggregated at levels above Species. Similar to the taxonomic-detail effects on richness measures, Wu (1982) found that, in general, the less precise the identification, the lower the diversity index values and the larger the error (measured as % deviation from species-level scores). The Shannon-Wiener (H') and Margalef’s index were most sensitive to the effects of taxonomic resolution, and evenness was the most robust. Wu also found that the error depended on the distribution (or evenness) of individuals among species that

were aggregated, the largest errors occurring where evenness was high. Wu concluded that diversity indices calculated with genus or less-detailed data are inaccurate, and he cautioned that errors will be made unless both the number and distribution of individuals and species within coarse taxonomic groups are the same at sites being compared — obviously an unlikely situation. Based on these findings, Wu (1982) listed three rules for taxonomic sufficiency: (1) if animals can be distinguished by body form, but cannot be named, indices should be calculated with precise but inaccurate (i.e., morpho-species) information; (2) if a coarse taxon contains only a small number of individuals, error rates are likely negligible; and (3) if a higher taxonomic group contains many individuals, a large error is likely to occur and comparing index values across time or space may be meaningless.

Species-tolerance indices

Indicator taxa are organisms that have particular physical or chemical requirements, so that changes in their presence, abundance, morphology, physiology or behavior indicate that environmental conditions are outside their optimal ranges (Cairns and Pratt 1993). Hellawell and Holloway (1977) described two opposing views of indicator taxa by writing, in one instance, that, “in reality, few species are understood well enough to permit their use as ecological ‘litmus-paper’ and the complexities of biological systems probably precludes such a simple approach”; and, in another instance, that, “there appears to be no reason why, ultimately, all species should not be indicators, given sufficient knowledge of their ecology”.

Biotic indices are a family of weighted summaries that combine taxa-specific pollution tolerances with richness or abundance information (Hilsenhoff 1977; Washington 1984; Resh and Jackson 1993; Chessman et al. 1997; Jones et al. 2002; Chessman 2003); they permit water quality assessment by exploiting the empirical relationship between increasing disturbance and progressive loss of indicator taxa (e.g., Hilsenhoff 1977; Rossaro and Pietrangelo 1993; Poff 1997; Stubauer and Moog 2000; Marshall et al. 2006).

Despite some theoretical drawbacks, many different biotic indices are used, each developed and favored in a different part of the world. Examples include: the Trent biotic index

(Woodiwiss 1964), the Chandler biotic score (Chandler 1970), Hilsenhoff's biotic indices (Hilsenhoff 1977, 1988), and the Biological Monitoring Working Party (BMWP) score system (Armitage et al. 1983; Alba-Tercedor and Sanchez-Ortega 1988; Camargo 1993; Hawkes 1998), as well as many variants. The most substantial and obvious theoretical criticism of biotic indices is that assigning a single-number sensitivity score to a taxon disregards our understanding that an organism's niche is defined along multiple limiting environmental gradients (Hutchinson 1957; Hilsenhoff 1977; Poff 1997; Bonada et al. 2004; Metzeling et al. 2006; Vieira et al. 2006). Thus assigned tolerance scores reflect blended responses to multiple stressors (Wildhaber and Schmitt 1998; Chessman 2003; Bonada et al. 2004). The other main argument against tolerance indices is that, although assemblages are structured by human influences (Ricklefs 1987, 2004; Johnson et al. 2004), a site's biota is also determined by historical events, by random colonization processes, and by "the interplay between biotic and abiotic processes that drive evolutionary change" (Johnson et al. 2004); thus biotic indices may be misleading unless their scores are interpreted within the context of these potentially confounding factors.

The key taxonomic-sufficiency issue for bioassessments using biotic indices is within-taxon variability: the degree to which sensitivity scores assigned to a taxonomic group represent the responses of that group's species (Hilsenhoff 1988; Lenat 1993; Moog and Chovanec 2000). Chiefly because the tolerances of species may vary widely, even within genera, many authors have argued that species-level identification is optimal, if not necessary (e.g., Resh and Unzicker 1975; Hilsenhoff 1977; Saether 1980; Herricks and Cairns 1982; De Pauw and Vanhooren 1983; Slooff 1983; Furse et al. 1984; Rosenberg et al. 1986; Hilsenhoff 1988; Cranston 1990; Resh and McElravy 1993; Bauernfeind and Moog 2000; Moog and Chovanec 2000; Schmidt-Kloiber and Nijboer 2004); however, the lack of information about species' environmental requirements, and the difficulty of diagnosing species, mean that tolerance scores are more commonly assigned to genera (e.g., Hilsenhoff 1977), families (e.g., Chessman 2003), or mixed aggregations (e.g., Chutter 1972) than they are to species (Lenat and Resh 2001; Vieira et al. 2006).

Substantial within-group variability in tolerance values has been demonstrated for a variety of taxa, for example among the North American caddisflies, *Ceraclea* and *Hydropsyche*, and the mayflies, *Baetis* and *Stenonema* (Resh and Unzicker 1975; Lenat and Resh 2001). To give one quantitative example, Schmidt-Kloiber and Nijboer (Schmidt-Kloiber and Nijboer 2004; citing Graf et al. 1995) reported that saprobic scores for Austrian *Hydropsyche* species range from 0.6 to 2.8. Similar examples have been provided for the European blackfly genus, *Simulium* and the riffle beetle family, Elmidae (Stubauer and Moog 2000), as well as for Austrian mayflies (Moog et al. 1997). Moog and Chovanec (2000) studied the saprobities assigned to nearly 1600 Austrian aquatic species and found very few instances of congeners having the same saprobic score.

Bailey et al. (2001) hypothesized that the amount of information lost due to coarse taxonomy is area specific, being determined by speciation mechanisms, which govern be-

tween-species variability in sensitivities. They tested this hypothesis by comparing within-taxon variances in tolerance values and average tolerance scores at genus-, family-, and order-level. Their results showed that, in 4 of 5 US ecoregions, as much or more variation exists among families and among orders (in the class Insecta), as exists among genera. They concluded that much of the information available at genus-level would be retained by a family biotic index, calculated using average within-family sensitivities.

In his classic North American paper, Hilsenhoff (1988) reported strong correlations between Species and Family versions of his biotic index, but the Family version tended to overestimate perturbation in relatively good Wisconsin streams, and tended to underestimate it in polluted streams. Blaming within-family sensitivity-score averaging for these distortions, he cautioned that his Family index may distinguish reference sites from very-polluted sites, but is unlikely to detect more subtle disturbances, and is open to erroneous conclusions about water quality.

More recently, several authors have shown that stream classifications using the European saprobic system change erratically when data are aggregated at taxonomic resolutions coarser than Species. Stubauer and Moog (2000), for example, compared species-level saprobic analysis with family-level BMWP-ASPT analysis at 588 Austrian stream sites — BMWP being the Biological Monitoring Working Party Score system, and ASPT being the average BMWP score per taxon, calculated as the sum of BMWP scores for all taxa divided by the number of all occurring taxa (e.g., Hawkes 1998; Wright 2000). Although their results were correlated ($r^2 = 0.52$), there were "large method-related variances within water-quality classes". Of course the appropriateness of their conclusion, that family biotic indices can systematically misinterpret stream conditions, depends on the appropriateness of species-level saprobity as a gold standard (e.g., Bonada et al. 2006).

Chessman et al. (2002) evaluated taxonomic-scale effects on the Australian SWAMPS index (the Swan Wetlands Aquatic Macroinvertebrate Pollution Sensitivity index), a biotic index developed to reflect macroinvertebrate sensitivities to nutrient enrichment and related human impacts on wetlands. They calculated index values at two taxonomic scales: "family", in which all taxa were assigned to their families, except Chironomidae, which were aggregated at sub-family; and "species", a mix of species, morpho-species, and, in the case of groups with difficult taxonomy (e.g., Turbellaria), higher taxonomic units. The authors found index values calculated at the two taxonomic scales to be strongly correlated with measures of nutrient status, but correlations were higher when the index was calculated using species-level data. In addition, species data better discriminated individual wetlands, and the standard errors of families' sensitivity scores were higher and more variable than those of species' scores (except in the case of single-species families, for which errors were similar for the two taxonomic scales).

Although the above findings favored detailed taxonomy, family biotic indices have been used extensively for water quality assessments in Australia (e.g., Ladson et al. 1999), Europe (e.g., Camargo 1993; Hawkes 1998), and the US (e.g., Hilsenhoff 1988); and acceptable correlations between

index values and stressor impacts have been observed (e.g., Camargo 1993; Wright et al. 1993). Great Britain's BMWP considers family to be the minimum taxonomic detail required to discriminate "between different degrees of biological quality" (Hawkes 1998); but, because of within-taxon variance, BMWP families are assigned the sensitivity of their most sensitive species, thus the index systematically overestimates effect-sizes. Numerous other indices are based on the BMWP index. Spanish researchers, for example, considered a version adapted for the Iberian Peninsula to be cost effective, simple to calculate and interpret, widely applicable and responsive to changes in rivers' habitat and chemistry (Camargo 1993). Chessman (1995) proposed another variant, the Australian SIGNAL index, for assessing salinization and organic enrichment in preliminary screening studies; and later proposed the coarser-still SIGNAL2 index, for which sensitivity scores were assigned to 171 families and sub-families (Chironomidae only) as in the original index, but also to 33 higher taxa (Chessman 2003). Correlations between SIGNAL2 scores and environmental variables were weaker for the coarse index than for the family index, but the differences were small enough that Chessman considered SIGNAL2 suitable for community groups (Table 5). Support for coarse taxonomic detail was also provided by Waite et al. (2004) who reported that acidification and eutrophication effects were detected just as well using the family version of Hilsenhoff's biotic index as with his genus version.

Within-taxon variance in sensitivity to perturbation is not the only taxonomic issue relevant to biotic indices, and several authors have commented on the implications of taxonomic completeness (i.e., the portion of the benthic assemblage whose composition is used to indicate ecological condition). Waterhouse and Farrell (1985), for example, argued that analyses based on only a few indicator taxa are more sensitive to taxonomic resolution than those based on more complete assemblages.

Biological- or ecological-trait indices

... The primary aquatic (insect) groups have become highly adapted to life in water. Within these groups there has developed a wide diversity of niche, and most of the groups are represented in almost every type of aquatic habitat. Among the Ephemeroptera and Trichoptera in particular, diversity of form and way of life are very wide ... Among other groups there has been some conservatism (e.g., carnivory in some families ... and the necessity for cool well-oxygenated water among Plecoptera), but even in these groups there is great diversity in habitat and life-style. [Hynes 1984]

Arguing that taxonomic composition provides little information about ecosystem function, many researchers have turned their attention to alternate approaches in which sites-by-taxa datasets are re-cast, using functional- or biological-trait information (such as foraging behaviours, habitat preferences, or life-history strategies), into sites-by-trait datasets (e.g., Statzner et al. 1994; Townsend and Hildrew 1994; Usseglio-Polatera et al. 2000; Dolédec et al. 2006). This shift in focus disregards Taylor's (Taylor 1997) argument that functional assessments ignore resiliency, which maintains

Table 5. The influence of taxonomic resolution on SIGNAL biotic-index correlations with environmental variables. Shown are Pearson rank correlations between environmental variables and SIGNAL biotic index scores calculated at two levels of taxonomic resolution (all significant, $p < 0.001$). Modified from Chessman (2003).

Variable	SIGNAL _{family}	SIGNAL2 _{coarse}
Altitude	0.28	0.27
Distance from source	-0.36	-0.25
Water temperature	-0.42	-0.34
Turbidity	-0.36	-0.30
Conductivity	-0.55	-0.46
Alkalinity	-0.50	-0.44
pH	-0.32	-0.25
Dissolved oxygen	0.37	0.33
Nitrogen _{total}	-0.50	-0.45
Phosphorus _{total}	-0.49	-0.46

ecosystem function (despite species substitutions) until the point of collapse. Nonetheless, recent studies cite several advantages of trait-based approaches: (1) biological traits that are sensitive to animals' use of specific resources, and are sensitive to habitat or chemical deterioration, can be selected (Dolédec et al. 2006); (2) functional composition is more consistent over large geographic areas than taxonomic composition is (Dolédec et al. 2006); (3) trait-based indices reflect life-history, physiological, and behavioral patterns, and may help to identify the mechanisms of stressor responses better than taxonomic indices can (Dolédec et al. 2006); and (4) some ecological traits can be assigned to higher taxa so that taxonomic problems may be circumvented (e.g., Cranston 1990; Dolédec et al. 2000, Moulton et al. 2000; Beche et al. 2006; Poff et al. 2006; Vieira et al. 2006).

Despite these ostensible benefits, the requirement for autoecological information constrains the use of ecological trait-based approaches because large data repositories do not exist for many parts of the world. Progress is, however, being made in certain areas. Examples include: the European AQEM/STAR Taxalist, which contains ecological information for nearly 10 000 macroinvertebrate taxa (Schmidt-Kloiber et al. 2006); a database of biological and ecological information for over 2 200 species of North American macroinvertebrates, assembled by the US Geological Survey and Colorado State University (i.e., Vieira et al. 2006); and several internet databases (see Statzner et al. 2007 for a partial review).

Because systematics is based mostly on morphology and phylogeny rather than on ecological traits, the problem of closely related species having different ecological requirements also arises (Cranston 1990). This issue has been best explored for trophic designations. Hildrew et al. (1985), for example, showed that, even with species-level data, it is difficult to assign members of the Chironomid sub-family, Tanyptodinae to a single trophic guild because they have detritus and prey in their diets, the proportions depending on the season and the age of the larvae. Similarly, Lenat and Resh (2001) described trophic-status variability in the caddisfly genus, *Rhyacophila*, which is widely regarded as a predator even though some species are obligate detritivores. Substantial within-taxon variability has also been reported

Table 6. Functional-feeding-group assignments for selected freshwater benthic macroinvertebrate groups, based on ecological data provided in Merritt and Cummins (1996).

Group	Number of families	Number of families assigned to >1 trophic guild	Number of genera	Number of genera assigned to >1 trophic guild
Ephemeroptera	21	10	81	28
Trichoptera	22	13	149	47
Diptera (not including Tipulidae, Culicidae, Simuliidae, and Chironomidae)	25	11	232	23
Chironomidae	1	1	208	35

Table 7. Number of citations listed as ecological references for selected genera in Merritt and Cummins (1996). Genera are designated as either multi-guild (congeners belonging to at least two functional feeding groups) or single-guild (congeners restricted to one functional feeding group).

	Number of genera	Mean number of ecological citations		Median number of ecological citations	
		Multi-guild genera	Single-guild genera	Multi-guild genera	Single-guild genera
Ephemeroptera	81	9.8	3.8	7.5	2.0
Diptera	231	6.5	2.7	5.0	2.0
Chironomidae	209	10.1	1.3	7.5	0.0
Trichoptera	149	7.4	4.3	6.0	2.0

for saprobities, for example among the Austrian species of *Hydropsyche* caddisflies (Graf et al. 1995). Examining tables in Merritt and Cummins (1996) gives a more complete picture of the proportions of families and genera of major insect groups that include more than one trophic group (e.g., collector-gatherer, shredder, or predator): 48% of families and 35% of genera in Ephemeroptera; 59% of families and 32% of genera in Trichoptera; 44% of families and 10% of genera in Diptera; and 17% of Chironomidae genera (Table 6). In addition, better-known insect groups (i.e., those having a larger number of ecological citations in Merritt and Cummins 1996) have a higher occurrence of multi-guild genera than lesser-known taxa do (Table 7), which lends some support to Lenat and Resh's (2001) caution that better taxonomic knowledge might uncover more substantial taxonomic-scale effects than we now acknowledge. This problem of within-taxon variability, has led some researchers to deem it difficult or impossible to generalize the responses of higher taxa (e.g., Schmidt-Kloiber and Nijboer 2004); however, fuzzy coding may be a partial solution because it allows one to express the diversity of states occurring either among related species or among members of the same species, as may occur between different life stages, or between individuals living in different locales (Vieira et al. 2006).

Notwithstanding the considerable within-taxon variability observed in environmental preferences and behaviors, certain biological or functional traits reflect species' physiological requirements, morphological adaptations, or life histories, and are therefore phylogenetically constrained, meaning that related species have similar designations (Vieira et al. 2006). Such traits have been exploited by several authors, demonstrating that family or less-detailed taxonomy can be sufficient for bioassessments (Dolédéc et al. 2000; Gayraud et al. 2003; Vieira et al. 2006). The

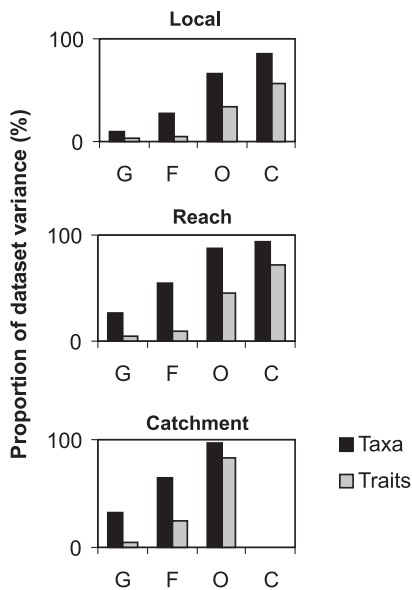
downside to this argument is that if multiple trait-based indices are used to summarize composition, and traits are evolutionarily conserved, problems of redundancies among indices are likely to arise, just as often occurs when a suite of taxonomic-composition indices are used in assessments (Vieira et al. 2006).

Some of the most compelling evidence favoring the use of ecological-trait-based bioassessments was published by Dolédéc et al. (2000), who showed trait abundances to be more robust to taxonomic resolution than taxonomic abundances are. In their study, variance estimates for within-taxon species abundances ranged from 9% to 85% at the local scale, 26% to 94% at the reach scale, and 33% to 97% at the catchment scale. Within-group variance of ecological traits showed a similar pattern, but variances were lower, especially with genus and family aggregations: within-group variances ranged from 3% to 56% at the local scale, 4%–72% at the reach scale, and 4%–83% at the catchment scale (Fig. 4). Ordinations provided corroborating evidence, showing trait-based measures to be more robust to taxonomic scale than taxonomy-based measures were. In a more recent paper, Gayraud et al. (2003) reported obtaining the same river-bioassessment results, regardless of whether biological traits (e.g., body morphology, life history, reproductive method, dispersal potential, and feeding habits) were assigned to families, genera, or species.

Effects of taxonomic detail on multivariate approaches

Views about the best ways to summarize biotic composition and investigate ecological patterns are diverse, and cases for and against multivariate approaches, index-based approaches, and hybrid approaches have been presented

Fig. 4. Effects of taxonomic resolution and spatial scale on the stability of selected taxa-based and ecological-trait-based measures of benthic community structure. Stability is measured as within-group variability, expressed as the portion of dataset variance. Maximum and minimum values for each of the six data series were specified by the original authors, but intermediate values were visually interpolated from the chart in the published manuscript. G denotes genus taxonomy, F denotes family taxonomy, O denotes order taxonomy, and C denotes class taxonomy. Adapted from Dolédec et al. (2000).



(Gerritsen 1995; Reynoldson et al. 1995; Cao et al. 1996; Norris and Hawkins 2000; Bowman and Somers 2005; Bonada et al. 2006). In multivariate approaches, sites are typically considered replicates, and taxa are considered variables (Norris and Georges 1993; Linke et al. 2005); composition is often summarized with a set of orthogonal ordination axis-scores (Anderson and Willis 2003) or pair-wise similarity or distance measures (such as Jaccard's Coefficient and Bray-Curtis Distance), and a variety of statistical methods are used to investigate ecological patterns (e.g., Norris and Georges 1993; Wright et al. 2000; Bailey et al. 2004).

The need for detailed taxonomy in multivariate assessments has been stressed in Australian (e.g., Marchant 1990; Metzeling et al. 2002), US (e.g., Hawkins et al. 2000; King and Richardson 2002), and European papers (e.g., Verdonshot 2006). Marchant 1990 reported that reducing taxonomic detail from Species to Family obscured seasonal patterns in benthic community composition and distorted watershed-scale spatial patterns revealed by ordination and classification. In his Lower Latrobe River (Australia) dataset, using family-level rather than "species"-level taxonomy (i.e., highest resolution achievable): (1) caused the magnitude and direction of vectors separating sites in ordination space to change; (2) lowered correspondence-analysis eigenvalues (which correspond with variance explained by the axes); and (3) narrowed the range of axes' site-scores. Coarser taxonomy also reduced the number of groups produced by TWINSpan clustering from 6 to 4. In his Upper Latrobe dataset, Marchant (1990) reported similar effects of using coarse taxonomy: ordinations less clearly distin-

guished sites according to their bottom materials, and seasonal variation in benthic assemblages was obscured. Reducing taxonomic resolution from Species to Family also obscured temporal trends in a larger-scale study of the Latrobe and Yarra river systems in south-eastern Australia (Metzeling et al. 2002).

In a study of California streams, Hawkins et al. (2000) reported three mechanisms behind their observation that genus-species data performed better than family data in bioassessments (i.e., better distinguished minimally-impacted reference sites from sites impacted by land-use alterations): (1) taxonomic detail affected classification, with a greater number of reference-site groups formed with genus-species data than with family data; (2) the classification success of discriminant models used to predict test sites to their expected reference-site group was better with the more-detailed data; and (3) measures of statistical differences between impacted sites and reference sites were greater when genus-species data were used than when family data were used. In another US study, King and Richardson (2002) reported similar findings from a study of 126 wetland sites spanning a eutrophication gradient in the Florida Everglades: genus-species data better discriminated sites, and produced stronger assemblage-environment relationships, than family data did. Suspecting the difference in performance to be attributed to the information content of the Chironomidae, which dominated their samples, the authors re-ran their analyses using a mixed-level aggregation, in which Chironomidae were identified to species and all other taxa were identified to family. This method's results matched those generated when all organisms were identified to genus or species. Based on data from several European countries, Verdonshot (2006) reported that "stream typology depends on taxonomic resolution, the finer the resolution the more distinctive the types become."

Contrary to the above findings, several studies have concluded that genus- or species-level taxonomy contributes little or no additional signal than what coarser resolution provides. In a marine study of the Upper Spencer Gulf, in South Australia, Vanderklift et al. (1996) found that — although changing taxonomic detail, the variables/sites ratio, and the number of rare taxa all affected association matrices and hence ordination results — patterns associated with habitat changes and lead pollution were evident even with coarse order- and class-level taxonomy. They documented a sequential loss of information as taxonomic detail was reduced: (1) correlations between association matrices decreased in strength; (2) stress values increased (roughly indicating that plots' representation of statistical distances between samples became sequentially distorted); and (3) compositional patterns, assessed using Procrustes analysis, changed (their Procrustes analysis used root-mean-square residuals, calculated between corresponding points of the two ordinations being compared: the smaller the residual, the better the match — as per Gower 1971 and Belbin 1993).

In another marine study, De Biasi et al. (2003) found that reducing taxonomic detail from species- to family-level did not reduce the ability of correspondence analysis (CA) ordinations to convey spatial and temporal patterns in benthos data collected at four sites occupying different positions along an estuarine-marine gradient on the Italian coast.

Table 8. The proportion of families and genera, by insect order, for which significant differences were observed between low- and high-impact classes in the Plateau, and Ridge and Valley ecoregions of the US Mid Atlantic Highlands. # Sig. denotes the number of taxa for which differences between impact classes were observed (based on values of the chi-square statistic); *N* denotes the number of taxa collected; and % denotes the percent of collected taxa exhibiting significant differences. Adapted from Waite et al. (2004).

Order	Plateau						Ridge and Valley					
	Family			Genus			Family			Genus		
	# Sig.	<i>N</i>	%	# Sig.	<i>N</i>	%	# Sig.	<i>N</i>	%	# Sig.	<i>N</i>	%
Ephemeroptera	5	10	50.0	13	26	50.0	5	12	41.7	10	31	32.3
Plecoptera	7	8	87.5	10	30	33.3	4	9	44.4	8	28	28.6
Trichoptera	5	15	33.3	5	34	14.7	3	17	17.6	7	38	18.4
Diptera	2	14	14.3	15	134	11.2	1	13	7.7	32	136	23.5
Other	4	17	23.5	4	34	11.8	2	21	9.5	6	45	13.3
Non-insects	0	11	0.0	0	21	0.0	6	20	30.0	7	42	16.7
Total	23	75	30.7	47	279	16.8	21	92	22.8	70	320	21.9

When taxonomic detail was further reduced, however, information was lost: at Order, sites were no longer distinct in ordinations, and they were not ordered logically along the marine–estuary gradient; at Class and Phylum, no patterns were evident.

Corroborating results have been obtained with freshwater data. For example, in a review of 10 bioassessment studies, Bowman and Bailey (1997) found that genus data performed better than family or order data when composition was expressed as presence-absence. When abundances were used, genus data gave the same description of community patterns as were evident at Family and Order. Whereas Bowman and Bailey (1997) concentrated on ordination effects, Furse et al. (1984) and Reece et al. (2001) investigated taxonomic effects on predictive models used in reference-condition-approach bioassessments. Although species-level taxonomy resulted in better predictions of stream-site assemblages, Furse et al. (1984) concluded that family data were sufficient for detecting environmental gradients. Similarly, Reece et al. (2001) found family- and genus-level models predicting Fraser River (British Columbia, Canada) benthic assemblage types to be equally sensitive to seasonal variation; and Reynoldson et al. (2001) reported that family data yielded better-performing predictive models, and more sensitive ordination-based assessments, than were obtained with species data.

In a recent study from the US Mid Atlantic Highlands, Waite et al. (2004) showed that ordinations using family and genus data were equally able to distinguish large and small streams, and to distinguish coarse impacts of acid deposition, mine drainage, and nutrient enrichment. In addition, their chi-square analysis of individual taxa illustrated that a larger portion of families than genera discriminated sites impacted by mine drainage (Table 8).

Using benthos data from Victoria, Australia, Metzeling et al. (2006) reported that Species detail did not appreciably improve their ability to detect a stream salinity gradient using ordinations and principal axis correlations, although some summary indices' information content was improved with more detailed taxonomy. Feio et al. (2006) evaluated 20 test sites in the high-biodiversity Mondego River, Portugal, using predictive modeling and Benthic Assessment of Sediment (BEAST) ordination-based methods (e.g., Rey-

noldson et al. 1995). Predictive models were built using order-, family-, and genus–species-level data. Prediction success (the probability of correctly predicting reference-site group membership, as estimated by jackknife procedures) was marginally better for family and order models (81% success) than for the genus–species model (78% success). Variables predicting assemblage structure were common to the genus and family models, but substrate quality was the only order-model predictor. The authors concluded that the three models were highly sensitive to water quality, yet sensitivity decreased as taxonomic detail decreased: results using the order model matched the family and genus–species models in 55% of the 20 test sites evaluated.

The case for coarse taxonomy is further strengthened by several authors' reports that correlations between ordination site-scores and environmental variables are little affected by taxonomic detail (e.g., Hewlett 2000; Waite et al. 2004; Metzeling et al. 2006). For example, Waite et al. 2004 demonstrated that, for a number of water-chemistry and habitat variables, significant correlations with at least one axis existed regardless of whether genus- or species-level data were ordinated. Similarly, Metzeling et al. (2006) reported that reducing taxonomic detail from Species to Family had little effect on ordination plots, and gave similar principal-axis correlations with environmental variables. Stronger evidence still was provided by Hewlett's (2000) classification- and ordination-based study of Australian stream sites: she showed that the rank order of ordinations' principal-axis correlations with environmental variables (e.g., alkalinity, conductivity, water temperature, catchment area, and dissolved oxygen) was unaffected by taxonomic scale.

Interactions between taxonomic sufficiency and other factors

In examining the importance of species identifications in biomonitoring, the question of the required level of taxonomy still can be asked. The answer, it seems, is 'It depends' — it depends on the purpose of the study, the level of sensitivity required, the type of index or analysis being used, and the particular group of organisms of primary interest. [Resh and McElravy 1993]

Taxonomic sufficiency is hypothesized to depend on many interrelated factors, including: the number of species

Table 9. Hypothesized influence of the species-to-group ratio on taxonomic sufficiency for studies investigating benthic-macroinvertebrate responses to pollution (S/G denotes the number of species per taxonomic group; H_0 denotes null hypothesis; H_a denotes alternate hypothesis). Adapted from Waterhouse and Farrell (1985).

Hypothesis	Ecological inference if true	Effect of coarse taxonomic resolution on bioassessment
H_{a1} : S/G at polluted sites is greater than expected by chance	Congeners have very similar pollution sensitivities (the many tolerant species belong to few groups).	Minimal information loss because much information about species composition is redundant
H_{a2} : S/G at polluted sites is less than expected by chance	Species within groups have widely different sensitivities (the many tolerant species are members of many different groups).	Coarse taxonomy obscures ecological patterns (changed species composition within groups conveys important information).
H_0 : S/G is not significantly different from that expected by chance (i.e., no interaction between the pattern of information loss and S/G)	Speciation and competition processes do not affect taxonomic sufficiency (possibly a mix of opposing H_{a1} and H_{a2} effects in which neither predominates).	No richness effect; negligible information loss if S/G is low

a given study area supports; the distribution of those species among higher taxonomic groups; the similarity of closely related species' ecological requirements; the study area's size; the sampling methods used; and the type and size of ecological effects to be detected.

Evolutionary history: speciation and biodiversity

Several authors have argued that the degree to which species-assemblage patterns are conserved when taxonomic detail is reduced depends on overall richness, high diversity requiring detailed species- or genus-level information, but less detailed data sufficing where diversity is low (Waterhouse and Farrell 1985; Ferraro and Cole 1992; Bowman and Bailey 1997; Hawkins et al. 2000; Hawkins and Norris 2000; Bailey et al. 2001; Landis 2003; Marshall et al. 2006). As discussed in previous sections, the key theoretical basis for this argument is within-taxonomic-group variability in responses to environmental stressors.

The number of species per taxonomic group is one measure of within-group variability. Where there are few species per taxonomic group, coarse diagnoses should convey most of the ecological information provided by species diagnoses, but where there are many species per taxonomic group, using coarse taxonomy would result in substantial information loss (Hawkins and Norris 2000; Marshall et al. 2006; also see Table 9).

Biogeographic and evolutionary processes not only determine an area's ratio of species per group, but they also determine how similar the niches of closely-related species are (Ricklefs 1987 and 2004). Hynes (1984) wrote that ecological niches are usually defined at the taxonomic level of family, but he also noted that there are many exceptions. For example, in the less-strictly-aquatic insect taxa, which more recently invaded fresh water (e.g., water striders, several families of beetles, aquatic moths, and some of the true flies), there is much less ecological diversity than there is among the more-strictly-aquatic and earlier-invading taxa (e.g., mayflies, stoneflies, and caddisflies), and there are fewer families (hence species) per order (Hynes 1984).

More generally, where allopatry (speciation through reproductive isolation imposed by some geologic or climatic barrier) was a major speciation process, present-day species would exhibit less than average ecological differentiation, hence relatively coarse taxonomy may be sufficient to de-

scribe ecological patterns with acceptable certainty. Then again, if an area's species chiefly arose sympatrically, for example through adaptive radiation, more than average ecological divergence of species would be expected, and greater taxonomic detail would theoretically be required (Cranston 1990; Dolédec et al. 2000).

Some evidence of taxonomic-sufficiency interactions with richness and the related factors described above is available. Because exposing the benthic community to environmental stress tends to reduce richness by removing sensitive or specialist taxa (e.g., Lenat 1993; Chessman et al. 1997; Chessman 2003), Marshall et al. (2006) provided indirect evidence of a richness – taxonomic-sufficiency interaction by reporting that faunal patterns observed at different taxonomic scales became more similar as the degree of disturbance increased (a phenomenon that had been previously described in marine studies by Vanderklift et al. 1996 and Olsford et al. 1998). More direct support was provided by Bowman and Bailey (1997), who reported that richness influenced the correlation of between-sample distance matrices calculated using published datasets expressed at different taxonomic scales (the higher the richness, the lower the correlation). Similarly, Hawkins and Norris (2000) investigated the relationship between the error rates of models predicting species richness, and the number of mayfly, stonefly, and caddisfly genera per family in British, Australian, and Californian streams. As a measure of adaptive radiation, genera-to-family ratios were used in this study instead of species-to-family ratios because: (1) the “consistency” of species identifications was different for the three geographic areas, but genera were consistently identified, and (2) the authors assumed (as per Wiggins and Mackay 1978) that differences in ecological specialization would be most evident between genera, with only minor differences observed among congeners. The authors found family models had 50% higher error rates than species models did. In addition, error rates for models built for species-rich areas were higher than those of models built for relatively species-poor areas (These results support the adaptive radiation hypothesis, but part of the observed relationship between increasing model error and decreasing taxonomic resolution may be attributed to assemblage classifications done at the different taxonomic levels having different numbers of sites and groups (Hawkins and Norris 2000)). Stubbauer and Moog

(2000) also showed that family-level BMWP scores did not provide acceptable characterization of Austrian rivers (where there was an average of 23 species per BMWP family) although family detail was sufficient in Great Britain, where there was an average of only 5 or 6 species per BMWP family.

Influence of study-area size and sampling methods

Because the factors structuring freshwater communities are spatial-scale dependent (Frissell et al. 1986; Anderson et al. 2005), taxonomic sufficiency may also depend on study-area size. Many authors have speculated that biotic-assembly patterns occurring in large geographic areas (e.g., across several large river basins) can be adequately represented with coarse taxonomy, whereas studies conducted in smaller areas (e.g., within a single river reach) require more detailed taxonomy (Marchant et al. 1995; Waite et al. 2004; Marshall et al. 2006; Verdonschot 2006). As articulated by Anderson et al. (2005) this is principally because species should be affected by large-scale processes (e.g., climate, historical colonization, and speciation processes) and small-scale processes (e.g., competition), but higher taxa should be affected only by large-scale processes. Supporting evidence includes results from a study of spatial variation in the composition of kelp-holdfast communities (i.e., Anderson et al. 2005). The authors observed that species composition was highly variable at both small and large spatial scales, and that the relative importance of small-scale variability (between neighboring plants) decreased upon reducing resolution from Species to Phylum. When animals were identified only to Phylum, little small-scale variation was detected but larger-scale spatial variation was still significant. A three-way interaction between taxonomic resolution, spatial scale, and data transformation was also apparent: when the authors summarized composition using presence-absence, decreasing taxonomic resolution resulted in large-scale patterns (i.e., between sites and between regions) accounting for greater variance than small-scale patterns accounted for; but when they summarized composition using abundance, the opposite pattern emerged.

Further evidence of spatial-scale dependence comes from synthesizing results of several similar studies. For example, Corkum (1989), successfully classified northwestern North American benthic invertebrate assemblages, and associated them with biogeographical and hydrological factors, using a mix of family and coarser taxonomy. Studies in the UK (e.g., Furse et al. 1984; Wright et al. 1989; Rutt et al. 1990) also demonstrated that regional-scale patterns in benthic-species' assemblages were adequately represented with family detail. Similar results were reported for the Australian state of Victoria by Marchant et al. (1995), even though previous work (i.e., Marchant 1990) showed that coarse taxonomy did not sufficiently represent species-assemblage patterns in a sub-area, the Latrobe River.

Melo's (Melo 2005) results, from a study of streams in a Brazilian catchment, contradicted the taxonomic sufficiency-spatial scale hypothesis by showing that (even in a relatively small study area) compositional differences between sites and between seasons were equally evident with family taxonomy as with species taxonomy. By contrast, Dolédec et al. (2000) showed that taxonomic scale influenced data-

sets' information content more so than spatial scale, and that these taxonomic effects were more pronounced when composition was summarized taxonomically than when it was summarized functionally. Nonetheless, their abundance-based analyses also contradicted the hypothesized relationship between study area size and taxonomic sufficiency because genus or family data sufficed for site-scale ordination-based assessments, but species data were required for catchment-scale studies. Furthermore, Bauernfeind and Moog (2000) described a dichotomy related to the potential dependence of taxonomic sufficiency and river catchment area: they reasoned that because richness tends to increase with river size, so should taxonomic resolution; but they also acknowledged that the many stressors affecting most large rivers result in depauperate communities that may be described adequately with coarse taxonomy.

Warwick's (Warwick 1988) explanation for the sufficiency of coarse taxonomy in pollution studies was that changes in habitat (i.e., water depth, bottom materials) tend to affect communities at a lower level of taxonomic organization than pollution does, perhaps because species have adapted to habitat fluctuations but they are less able to tolerate pollutant exposure. This hypothesis, combined with our understanding of interactions with richness and study-area size, led to several other predictions about the dependence of taxonomic sufficiency on sampling methods. For example, Vanderklift et al. (1996) showed that reducing taxonomic resolution *can* improve our ability to detect pollutant signals in studies having confounding habitat gradients; they then extended this argument to suggest that detailed taxonomy is more suitable for studies in which a single habitat is sampled than it is for studies generating multi-habitat composite samples. In another Australian paper, Metzeling and Miller (2001) showed that the correlation between sample size and richness varied in response to taxonomic resolution. For riffle samples they observed a consistent increase in the number of "species" — more correctly, recognized taxonomic units, because most specimens were identified to species, but Oligochaeta, Nematoda, Nemertea, Turbellaria, and Acarina were not identified further, and Chironomidae were identified to genus — collected as the size of their sampling unit increased; however they found no consistent trend using family taxonomy, or using data from samples collected in different habitats (i.e., pool rocks, edges, or macrophyte beds).

Using marine benthos data from Puget Sound, Washington, Ferraro and Cole (1992) demonstrated a variety of taxonomic-sufficiency interactions, including dependence on the type of sampling gear (particularly on the size-range of animals collected), and on the analytical method used. They sampled a reference site and an impacted site near a fuel depot using two different types of sampling gear (i.e., a box corer and a van Veen grab) and two different mesh sizes for sieving samples (i.e., 1 mm and 0.5 mm). They identified benthos to "lowest possible taxa, usually species" (estimates of accuracy and precision were not given) and then re-cast their data at genus-, family-, order-, and phylum-level. Sampling area had little effect on taxonomic sufficiency, but other interactions were apparent: when richness was used as the response variable, Family was required for the 1-mm-mesh samples, but Species sufficed for the 0.5-

mm-mesh samples. Species data were usually required when dominance or diversity indices were used as the response variable (perhaps because these indices automatically have lower information content than richness does). The authors also noted that, because certain stressors can affect one size class of fauna more than another, the relative strength of the interaction between mesh size and taxonomic sufficiency may also depend on the stressor of interest (e.g., Ferraro and Cole 1992).

Influence of the type and size of effects

Another often-cited factor influencing taxonomic sufficiency is the type and clarity of the ecological pattern to be detected; the prevailing hypothesis is that species data are required to detect subtle patterns, but genus, family, or even more coarsely aggregated data permit obvious patterns to be detected (Waterhouse and Farrell 1985; Lenat and Resh 2001; Melo 2005). Notwithstanding Guerold's (Guerold 2000) results — which showed that family-level bioassessments using EPT diversity and abundance underestimated effect sizes associated with a relatively strong acidification gradient (i.e., test-streams' pH 4.7–6.0, reference-streams' pH 6.7–7.0) — earlier studies by Ferraro and Cole (1992) and Wright et al. (1995) showed that family (or coarser) data were able to distinguish what Waite et al. (2004) viewed as relatively dramatic sewage impacts. Other supporting evidence was provided by Hawkins et al. (2000), who reported that family data underestimated relatively subtle logging effects that were evident at species-level. Waite et al. (2004) illustrated that the influence of effect size on taxonomic sufficiency is dataset specific. They showed that family and genus data were similarly able to distinguish sites, based on subtle acid-exposure and stream-size classifications, in one ecoregion; but in another ecoregion, genus data performed better than family data. Evidence contradicting the effect-size hypothesis was provided by Melo (2005), who studied taxonomic-detail effects on the detection of small spatial (i.e., within-catchment) and temporal (i.e., between seasons) changes in benthic community composition. In this case, family taxonomy revealed the same groups as species taxonomy did, demonstrating that, at least in some situations, taxonomic resolution can be reduced even when the effect sizes requiring detection are small.

Summary

The key issues discussed in this paper are: within-taxon variability in ecological attributes (hence the ecological relevance of different taxonomic units); taxonomic-scale effects on dataset information content, data-quality assurance, and mathematical assessment methods; and the many possible interactions — with factors like richness, study-area size, and the effect-size of interest — that makes taxonomic sufficiency dataset specific.

Despite the relatively large number of published papers evaluating taxonomic effects on bioassessments, it is still difficult to make generalizations about taxonomic sufficiency and the implications of taxonomic minimalism. The most obvious reason for this is that study results conflict, as

demonstrated, for example, by the contradictions among studies investigating taxonomic sufficiency for multivariate bioassessments: Marchant (1990), Hawkins et al. (2000), King and Richardson (2002), Metzeling et al. (2002), Verdonshot (2006) all showed a benefit of detailed benthos identification; but Furse et al. (1984), Vanderklift et al. (1996), Bowman and Bailey (1997), Hewlett (2000), Reece et al. (2001), Reynoldson et al. (2001), De Biasi et al. (2003), Waite et al. (2004), Feio et al. (2006), and Metzeling et al. (2006) showed either that coarse identification is sufficient in certain situations, or that coarse identifications give as much sensitivity as detailed identifications give. Another complication is that taxonomic detail is only *sometimes* qualitatively described. For example, Hilsenhoff (1977) indicated that, to calibrate his biotic index, all collected arthropods "... were identified to species if possible, but species could not be identified in many genera". Similarly, Hawkins et al. (2000) reported using "near-species-level" data: aquatic insects were identified to species, but the detail of identifications for non-insect fauna ranged from "species to class, depending on the group". If we are to fully understand taxonomic effects on bioassessments, surely taxonomic precision must be described fully.

Several other factors make study results difficult to compare: Different authors practicing taxonomic minimalism weight differently the factors traded-off (some highly value the information content of detailed taxonomy, but others favor the cost-savings of coarse taxonomy); different authors use different response variables and analytical methods; different authors are interested in different stressors and different habitats; and, different authors use different lumping-and-splitting rules when they process samples, such that "species" identification in one study is not equivalent to "species" identification in another study. Furthermore, conclusions are often subjective, because few researchers specify objective, quantitative criteria for taxonomic sufficiency. Low taxonomic precision is another problem: If, in our gold standard, only 25%–50% of specimens can actually be identified with the required species-level detail, are we underestimating the value of species taxonomy? Is the notion of identifying species, using conventional morphology-based techniques, pure fantasy?

So how can we summarize our scientific understanding of taxonomic sufficiency for freshwater benthic-macroinvertebrate bioassessments? The only assertion for which there is true consensus is also the premise upon which the debate is founded: that different taxa within a given level of the taxonomic hierarchy often have different biological attributes. Although few question the value of species-level data, there is also near consensus that species taxonomy is not always required for bioassessments. That is, bioassessments are special studies in applied ecology that require only sufficient information to distinguish sites impaired by human activities from those in their natural or near-natural state. Where we disagree, is on the *optimal* amount of detail.

Recommendations

Below are 7 recommendations regarding taxonomic sufficiency for bioassessments, each with a brief rationale and discussion.

1. The default taxonomic level should be Species

... For greatest sensitivity, everything should be identified to species. [Hilsenhoff 1977]

Species detail ensures that summaries of biotic composition are not distorted and that maximal information content is available for, and no limits are imposed on (Yoder and Rankin 1995), statistical analyses. Species datasets maximize the lines of evidence (i.e., the number of taxa) available for interpreting bioassessment results (Zamora-Muñoz and Alba-Tercedor 1996; Hawkins and Vinson 2000; Moulton et al. 2000; Waite et al. 2000); and they are most easily mined for other scientific uses, such as testing ecological theories (Hart 1994) and evaluating threats of extirpation or extinction to aquatic taxa (DeWalt et al. 2005).

2. Classify by morpho-species when unique taxa cannot be assigned names

Morpho-species (i.e., recognizable taxonomic units) schemes allow detailed identifications to be made even if keys and expert taxonomists are not available (Cranston 1990; Resh 2007). Relative to taxonomic approaches, their major disadvantage is loss of comparability, because morpho-species can only be described by reference to voucher specimens, and because the subtlety of morphological distinctions that can be made depends on practitioners' training and experience (Cranston 1990).

3. When taxonomic minimalism is warranted, specify a quantitative criterion for taxonomic sufficiency. This criterion should represent an optimization of cost-benefit trade-offs

We do not suggest that good taxonomy is unimportant. Instead, we urge ecologists to consider the purposes of their studies, to apply methods that will yield the best results, and to recognize that time-honoured methods may not provide the best answers to questions in applied ecology. [Kaesler et al. 1978]

When researchers and bioassessment practitioners lack the money, time, equipment, or expertise needed to identify species, taxonomic minimalism is the only alternative to doing nothing. Taxonomic minimalism, however, should be a more formal and scientific process than is often practised. Ideally, the information content of bioassessment datasets expressed at different taxonomic scales should be estimated quantitatively a priori using data from exploratory surveys. Thus cost-benefit relationships can be modeled, and an optimal criterion for taxonomic sufficiency can be set, within the boundaries specified by study objectives. Evidence shows that family taxonomy is often a reasonable compromise (e.g., Furse et al. 1984; Plafkin et al. 1989; Marchant 1990; Ferraro and Cole 1992; Wright et al. 1993, 1995; Chessman 1995; Marchant et al. 1995; Bournaud et al. 1996; Vanderkluft et al. 1996; Zamora-Muñoz and Alba Tercedor 1996; Bowman and Bailey 1997; Marchant et al. 1997; Olsgard et al. 1998; Kilgour and Barton 1999; Urkiaga-Alberdi et al. 1999; Hewlett 2000; Bailey et al. 2001; Metzeling and Miller 2001; Reece et al. 2001; King and Richardson 2002; Thompson et al. 2003; Culp et al. 2003; Gayraud et al. 2003; Schmidt-Kloiber and Nijboer 2004; Marshall et al.

2006); hence it is a useful starting point for such cost-benefit studies.

4. Use mixed-level aggregations to fine-tune taxonomic minimalism

Numerically dominant, sensitive, or well-known taxa (particularly those having many species or much variability in ecological traits among member species) are likely to provide greater discriminatory information than other taxa do. Providing detailed identifications for high-information taxa, but only coarse identifications for low-information taxa, is a way of optimizing taxonomic-sufficiency trade-offs (e.g., Hawkins et al. 2000; Hewlett 2000; Bailey et al. 2001; King and Richardson 2002; Waite et al. 2004).

5. Match data-quality-assurance plans with the potential for, and consequences of, mis-identification errors

There are well-known inverse relationships between taxonomic detail and accuracy, and between taxonomic detail and precision (e.g., Chessman 1995; Hewlett 2000; Derraik et al. 2002; Landis 2003; Schmidt-Kloiber and Nijboer 2004; Marshall et al. 2006); thus, studies using species taxonomy need more rigorous quality-control procedures than are needed for studies using coarse taxonomy. The value of specific quality-control procedures — including training and certifying bioassessment practitioners, consulting expert taxonomists, conducting data-quality audits, and curating voucher specimens — are well known (e.g., Resh and McElravy 1993; Bauernfeind and Moog 2000; Carter and Resh 2001; Cao et al. 2003; Metzeling et al. 2003; Ransinghe et al. 2003; Haase et al. 2006).

6. Continue taxonomic (and related) research

... Continuing studies on fundamental life history traits and the ecological requirements of species to improve our knowledge on such biological and ecological information is one of our most important future tasks. [Schmidt-Kloiber and Nijboer 2004]

Taxonomic research directly benefits bioassessment: the knowledge it provides changes taxonomic-minimalism trade-offs, usually in favour of detailed identifications. By improving keys and advancing molecular methods, further research will improve the accuracy and precision of benthic-macroinvertebrate identifications, at the same time making species diagnoses less expensive. Taxonomy also provides autoecological information, which makes species-level datasets more valuable and facilitates alternate approaches (Alternatives include classification by ecological trait, which warrants further investigation — Hawkins and Sedell 1981; Reynoldson and Metcalfe-Smith 1992; Dolédec et al. 2000; Gayraud et al. 2003; Dolédec et al. 2006; Vieira et al. 2006).

In addition to primary taxonomy, two areas of applied research — both opportunities for bioassessment researcher-taxonomist collaboration — are of immediate importance: First, additional scrutiny of the multiple interactions between taxonomic sufficiency and factors like richness, biogeography and speciation history, sampling methods, and the effect-size of interest, would move us toward consensus

on this highly controversial topic. Such studies could pave the way for a more detailed set of guidelines than I provide here, and ultimately for a comprehensive taxonomic-sufficiency theory. Second, developing numerical methods for optimizing cost-benefit trade-offs would allow taxonomic-sufficiency criteria to be developed quantitatively and transparently.

If any significant gains in taxonomic knowledge are to be made, however, taxonomy's currently declining funding trend must be reversed. Taxonomists could catalyze such a reversal by uniting around goals for their discipline that are clear, realistic, and relevant to society; and by integrating all available phylogenetic, descriptive, and diagnostic technologies to advance our knowledge about taxa (Dharmapalan 2001; Godfray and Knapp 2004). Nevertheless, responsibility lies with funding agencies, which need to recognize taxonomy's value to science and society by spending more on it.

7. Better coordinate *delivery* (sensu Doyle and Lynch 2005) of keys, autoecological information, and other taxonomic research products to bioassessment practitioners

As Doyle and Lynch (2005) wrote, "information delivery involves a two-way dialogue between consumer and producer, and creates improved knowledge on both sides, as well as mutual understanding". *Delivery*, therefore, would be a useful model for future collaborations between taxonomists and bioassessment researchers (Godfray and Knapp 2004).

Carter and Resh (2001) called for internet-delivery of locally produced keys; I agree in principle, but care must be taken to avoid the norm: oversimplified (i.e., ambiguous) language that encourages picture-matching and does a disservice to both the fields of taxonomy and bioassessment. Good examples of delivery include family-level keys and other internet resources produced by The University of Minnesota's Chironomidae Research Group (<http://www.entomology.umn.edu/midge/GuidePage.htm> and <http://www.entomology.umn.edu/midge/VSMIVP.htm>). Their keys have found the right balance between ease-of-use and precise terminology, and on-line forms allow practitioners to contact university researchers when ambiguities arise. The North American Benthological Society's Taxonomic Certification Program is another promising example, because it sets professional standards for taxonomic practice, adds structure to our current bioassessment-taxonomy community-of-practice, and may ultimately result in more jobs for taxonomists (information about this program is available on the North American Benthological Society's Web site, at <http://nabstep.atlanticwebfitters.ca/>).

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