Recent trends in life-history research on benthic macroinvertebrates

Authors: Resh, Vincent H., and Rosenberg, David M.

Source: Journal of the North American Benthological Society, 29(1) : 207-219

Published By: Society for Freshwater Science

URL: https://doi.org/10.1899/08-082.1

J. N. Am. Benthol. Soc., 2010, 29(1):207–219

DOI: 10.1899/08-082.1
Published online: 5 February 2010

Recent trends in life-history research on benthic macroinvertebrates

Vincent H. Resh[1]
Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720-3114 USA

David M. Rosenberg[2]
Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6 Canada

Abstract. Life-history research has a long tradition in benthic biology because of its value in explaining patterns observed in nature, quantifying trophic relationships and energetics, and interpreting experimental results. We examined articles published in the *Journal of the North American Benthological Society (J-NABS)* during a 23-y period (volumes 5–27) to determine trends in life-history research and to assess future needs in these types of studies. Of the 9 life-history elements we examined, growth and mortality of benthic macroinvertebrates were most commonly reported in the 412 *J-NABS* studies containing ≥1 of these elements. Recruitment and dormancy were the least-studied elements, and development, reproduction, dispersal, voltinism, and phenology were intermediate. Most of these studies were based on aquatic insects, especially Ephemeroptera and Trichoptera, and mollusks (particularly bivalves). Detailed life histories of single species published in *J-NABS* have averaged ~1/volume, with most studies being on Ephemeroptera, Plecoptera, Trichoptera, and Odonata. Both detailed life-history studies and studies containing life-history elements have declined over time, especially when considered as a percentage of articles published in *J-NABS*. In a timeline of important developments in life-history studies, 4 time periods or themes were evident: 1) an emphasis on descriptive natural history, which was the earliest type of ecological research conducted and which extended into the 1970s; 2) synthesis of life-history information in books and review articles, which was most prevalent in the 1970s and 1980s; 3) adoption of functional-feeding groups as a measure of trophic status of benthic organisms, which began in the 1970s and continues through today; and 4) the use of a species-trait approach to examine both basic and applied aspects of benthic biology, which began in the 1990s, is an expanding research area, and is a valuable application of life-history information. Life-history research has been published more often in specialized proceedings and regional journals than in *J-NABS*. Clearly more life-history research is needed, but time, logistical considerations, and funding constraints restrict professional benthologists from conducting this kind of research. Perhaps anglers and those participating in volunteer monitoring groups can be encouraged to conduct studies to provide this needed information.

Key words: functional-feeding groups, life-history studies, species traits, Ephemeroptera, Plecoptera, Trichoptera.

Because of their importance as human food sources, the gathering and transmission of information about the biology of benthic macroinvertebrates, fish, and other aquatic organisms predates recorded history. Undoubtedly, this knowledge was the product of the first research done on freshwater animals. An understanding of the behavior, habitat preferences, and spatial and temporal availability of these organisms enabled hunters to find and consume these animals, and enhanced human survival.

Life-history research also has the longest tradition as a topic of interest in the modern study of ecology. Even today, textbooks and journal articles contain detailed, descriptive accounts of life-history characteristics, often to explain population dynamics or describe specific environmental adaptations. Moreover, these features, especially the near science-fiction nature of certain examples (Berenbaum and Leskoskey 1992), have long been a way of interesting students in ecology. Even when ecology texts focus

[1] E-mail addresses: vresh@nature.berkeley.edu
[2] dave.rosenberg@dfo-mpo.gc.ca

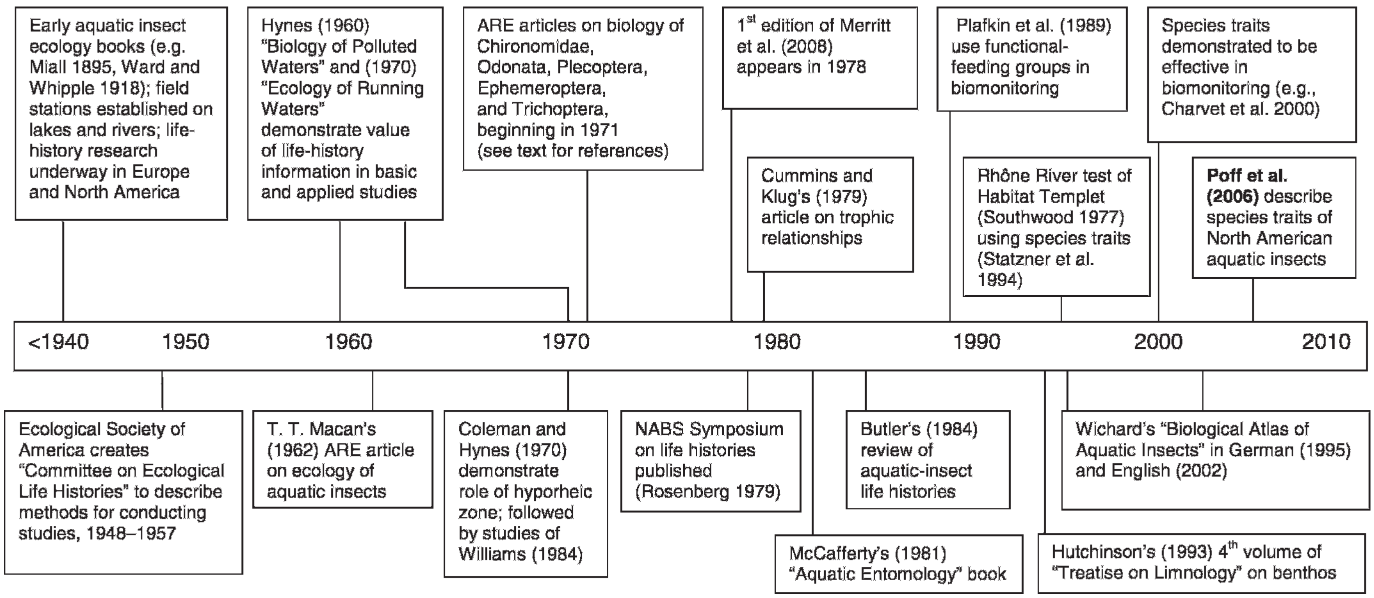

FIG. 1. Timeline of important developments in life-history studies of benthic macroinvertebrates. ARE = Annual Review of Entomology. Boldface indicates article was published in *J-NABS*.

on communities or ecosystem-level processes, guilds (which essentially are groups of species with a similar life-history phenomenon, e.g., mechanisms for food-gathering or types of food consumed) and secondary productivity (which reflects growth and survivorship) are commonly discussed topics. In fact, life-history research was such a common component of ecology that the Ecological Society of America created a committee in the 1950s specifically to design protocols about how detailed life-history studies should be conducted (Resh 1979). Several protocols were published for different types of taxa (e.g., Linsley et al. 1952).

The North American Benthological Society (NABS), through special symposia that it has sponsored at annual meetings and from publications resulting from these symposia (e.g., Rosenberg 1979; Fig. 1), has shown strong interest in life-history research. Likewise, the *Journal of the North American Benthological Society* (*J-NABS*) and other freshwater-ecology journals publish studies reporting research on life-history topics.

In our paper, we will examine the frequency and types of life-history studies published since the first issue of *J-NABS* appeared in 1986. We will then attempt to evaluate *J-NABS*'s role in the publication of life-history research. Last, and perhaps most importantly, we will assess what we think are the key milestones in the publication of life-history information and evaluate the current state of life-history research in the benthic-biology literature.

Methods

The components of life history described by Butler (1984; see especially his fig. 3.1) were used to determine which elements would indicate whether or not an article published in volumes 5 to 27 of *J-NABS* constituted a life-history study, and therefore, should be included in our analysis. Nine elements were identified: recruitment, mortality (or some aspect, such as survival), growth, development, dormancy, reproduction, dispersal, voltinism, and phenology. Choices involved some selectivity and judgment, i.e., each of these elements also has factors that could affect life-history features but, in themselves, are not direct life-history features, and articles that addressed such factors were not selected for inclusion. For example, nutrition affects growth, voltinism, and phenology, but nutrition studies were not included because nutrition is not a direct element of life-history studies.

The titles and abstracts of all papers in volumes 5 to 27 of *J-NABS* were read for evidence of $\geq$1 of the 9 elements. The tables and figures in each article also were examined, and sometimes the entire article was perused when none of the 9 elements appeared in the above checks but the article potentially could have contained life-history information. Articles that presented superficial coverage of a life-history element were not included. All taxa were included in the search (e.g., bacteria, algae, invertebrates, fish, frogs).

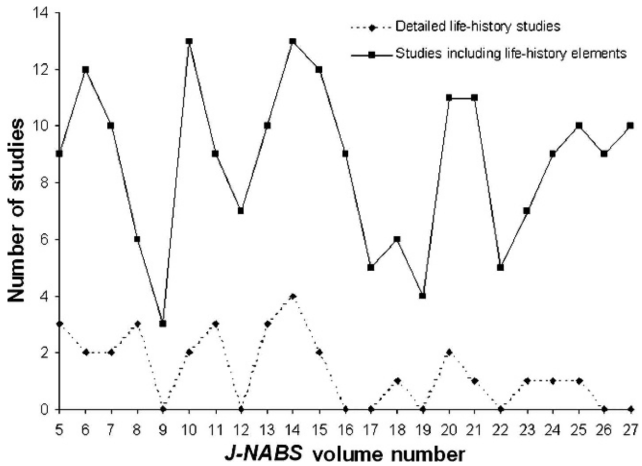

FIG. 2. Number of articles in *J-NABS* by volume that contain detailed life-history studies (lower dashed line) or life-history elements (upper solid line).

Following the analysis of life-history elements, those articles in *J-NABS* that contained a detailed description of the life history of a freshwater organism were retained for further study. These studies typically contained the words "life history" or "biology of" at the beginning of the title, or the abstract made it clear that several elements (including voltinism and phenology) were studied and were the main objective of the research.

An inventory of articles having $\geq$1 of the 9 life-history elements or containing a detailed life-history study was compiled and analyzed according to 3 objectives: 1) identification of the most frequently used elements, 2) changes over time in the frequency of appearance in *J-NABS* of articles reporting either detailed life-history studies or containing some element of life histories, and 3) identification of the most frequently used taxa in life-history studies in *J-NABS*.

Results

Elements of life histories

The distribution of the 412 articles examined in volumes 5 to 27 of *J-NABS* that contained various elements of life-history studies varied from 3 to 13 per volume (Fig. 2). Numbers fluctuated greatly over time, and no clear temporal pattern of change in number of articles was detected. However, because the number of articles in each volume of *J-NABS* has tended to increase over time, the percentage of articles containing life-history elements generally decreased over time (Table 1). The earlier volumes (e.g., 5–15) contain a higher percentage of articles published in a volume (11.4–48.2%) than do later volumes (7.1–22.0% in volumes 16–27).

Of the 9 life-history elements examined, the topics studied most were growth (97 articles), followed by development (69) and mortality (67) (Table 1). In contrast, recruitment (12) and dormancy (20) were studied least. The only clear temporal difference was that voltinism, phenology, and dormancy were elements that were reported more often in earlier volumes, although more studies on recruitment have been published recently. Most studies (101) focused on a single life-history topic, with a range of 0 to 6 topics/study.

Life-history elements were studied for a variety of benthic organisms (Table 2). Most articles were about aquatic insects (158) and mollusks (60), especially bivalves (43), followed by Ephemeroptera (31), Diptera (27), and Trichoptera (24). Many studies dealt with multiple taxa, and 15 of the studies reported life-history information as a function of secondary-production studies (data not shown).

Detailed life-history studies

The 31 articles that reported detailed life-history studies varied from 0 to 4/volume (Fig. 2). A clear temporal trend was observed; more studies were published in the earlier volumes of *J-NABS* than in the later ones. This decrease is even more pronounced when the percentages of articles reporting detailed life histories in volumes 5 to 15 and 16 to 27 are compared: 6.2% in the earlier volumes (range 0–10.3% per volume) to <1% (range 0–4.0%) in the later ones.

The detailed life-history studies examined 84 species. This number exceeded the total number of studies conducted (31) because, as with life-history elements, several studies involved multiple species. Most of the species studied were in the order Ephemeroptera (23 studies), followed by Plecoptera and Trichoptera (13 each), and Odonata (11). Of the 35 different families examined, the Capniidae (Plecoptera) had the most species studied (10). Leptocerid caddisflies (7 species), libellulid dragonflies (6 species), and ephemerellid mayflies (5 species) also were studied commonly. Perhaps not surprisingly, no species was studied in $\geq$1 detailed life-history study published in *J-NABS*.

Discussion

Our analysis clearly demonstrates that the number of studies of life-history elements and detailed life-histories of benthic macroinvertebrates published in *J-NABS* has declined over time. We think that this trend

TABLE 1. Number of articles covering specific life-history topics by volume in *J-NABS*. % total articles refers to the percentage of articles containing ≥1 life-history elements in that volume.

Volume	Recruitment	Mortality	Growth	Development	Dormancy	Reproduction	Dispersal	Voltinism	Phenology	% total articles
5	0	2	3	4	2	2	1	2	3	31.0%
6	0	1	7	4	1	1	1	4	3	48.2%
7	0	1	7	5	1	3	1	2	2	25.6%
8	0	1	2	3	0	2	0	2	3	11.4%
9	0	2	2	2	0	1	0	2	1	13.8%
10	0	4	6	4	4	3	0	5	5	37.1%
11	2	2	6	7	1	2	0	3	2	30.3%
12	0	2	4	2	1	1	1	1	1	14.0%
13	2	5	5	5	2	0	1	2	3	20.4%
14	0	8	4	3	2	2	2	3	2	24.5%
15	0	5	5	7	4	3	3	2	4	23.6%
16	2	3	3	2	0	2	4	0	1	12.7%
17	0	3	2	2	0	1	1	0	3	15.0%
18	0	4	0	2	0	0	1	1	2	15.4%
19	0	1	2	0	0	0	1	0	0	7.1%
20	0	6	8	1	0	3	2	1	1	22.0%
21	0	5	6	2	0	1	4	2	0	20.0%
22	0	2	4	1	0	0	0	1	0	10.9%
23	0	3	2	5	0	3	4	1	2	13.8%
24	1	5	4	1	0	2	3	0	1	13.9%
25	2	1	5	3	0	0	3	1	0	13.5%
26	2	1	7	2	1	1	1	0	1	14.5%
27	1	0	3	2	1	4	4	0	1	13.2%
Total	12	67	97	69	20	33	38	35	41	412
% total topics	2.9%	16.3%	23.5%	16.7%	4.9%	8.0%	9.2%	8.5%	10.0%	100.0%

TABLE 2. Summary of taxa in articles dealing with elements of life history published in *J-NABS*, Volumes 5 to 27. Specific taxonomic group refers to percentages within large taxonomic groups (e.g., Insecta, Crustacea, Mollusca).

Taxon/special topics	Number of articles	% of total: Specific taxonomic group	% of total: All taxa
Insecta			
Odonata	11	7.0	4.1
Ephemeroptera	31	19.6	11.5
Megaloptera	2	1.3	0.7
Plecoptera	16	10.1	5.9
Trichoptera	24	15.2	8.9
Diptera	27	17.1	10.0
Chironomidae	16	10.1	5.9
Simuliidae	5	3.2	1.9
Other	6	3.8	2.2
Coleoptera	3	1.9	1.1
Other (multiple taxa)	17	10.8	6.3
Total	158	100.0	58.5
Crustacea			
Zooplankton	4	17.4	1.5
Amphipoda	6	26.1	2.2
Shrimp	5	21.7	1.9
Crayfish	8	34.7	3.0
Total	23	100.0	8.5
Mollusca			
Bivalvia	43	71.7	15.9
Snails	17	28.3	6.3
Total	60	100.0	22.2
Other invertebrates	9		3.3
Bacteria	1		0.4
Algae/macrophyton	8		3.0
Vertebrates			
Fish	5		1.9
Frogs	1		0.4
Miscellaneous	5		1.9
Overall total	270		100.0

is occurring in other journals as well. For example, Resh (1985) reported that 48% of articles on aquatic entomology and benthic biology dealt with descriptive studies of life-history characteristics. Even a casual perusal of the current contents of the journals used in that study indicate that the proportion of articles dealing with this topic is much lower in recent years. Moreover, certain life-history elements (e.g., growth, mortality, and development) have received far more attention than others. Perhaps this pattern reflects the ease of studying these elements or their perceived importance.

Is the decline of published life-history studies a problem? All of us have sat in research presentations and heard speakers end their talks with a call for more data on the biology of the organism they studied. As Dayton and Sala (2001) and Greene (2005) articulately emphasized, descriptive ecology and life-history information are essential in conducting modern evolutionary and ecological research. A recent example of the importance of life-history research is the increasing interest in the use of species traits (also called biological traits, functional traits, or ecological traits) of benthic organisms in both basic and applied aspects of benthic biology. The use of information about species traits to explain ecological phenomena dates back to the origins of benthic ecology (early 20th-century works of Wesenburg-Lund and Thienemann) and even earlier for ecology in general (Statzner et al. 2001).

Not surprisingly, the life-history characteristics of some groups have been studied more than others. Specific life-history elements of Mollusca have received much attention, but detailed life histories of these organisms are less frequently published. The same pattern is evident for Diptera; they are the focus of many studies of life-history elements but few detailed life histories. Moreover, most of the life-history studies on taxa in this order that are published in *J-NABS* have been done on species of Deuterophlebiidae, which while fascinating in terms of their biology, are not the most widely encountered dipterans by benthic biologists. In contrast to Mollusca and Diptera, both life-history elements and detailed life histories of species of Ephemeroptera, Plecoptera, and Trichoptera are well studied.

In the timeline of what we consider to be the significant milestones of benthic research (Fig. 1), 4 time periods or themes can be discerned: 1) an early emphasis on descriptive natural history, which was the earliest type of ecological research, and which was popular into the 1970s; 2) the synthesis of life-history information in books and review articles, predominantly in the 1970s and 1980s; 3) adoption of functional-feeding groups as a measure of trophic status of benthic organisms, starting in the 1970s and continuing through today; and 4) more recently, the adoption of a species-trait approach to examine basic and applied aspects of benthic biology.

Natural history of benthic macroinvertebrates

The 1st period was characterized by detailed descriptions of life cycles of benthic organisms, their adaptations to different aquatic habitats, and their life-history factors that might affect the abundance and distribution of their fish predators. Life cycle and life history refer to different phenomena (Butler 1984; Fig. 1). Life cycle refers to the sequence of morphological stages and physiological processes from one generation to the next. In contrast, life history denotes the qualitative and quantitative details of the variable events that are associated with that life cycle.

An important early development in life-history research was the establishment of permanent biological research stations along lakes and rivers. These centers (such as at Plön in Germany, Douglas Lake in Michigan, Sagehen Creek in California, and many other sites) provided logistical ease of observation and the opportunity to conduct extra research on topics that might have been tangential to the main programs of the research stations. In addition, these field stations were often in isolated locations, and life-history research often was viewed as a welcome diversion and became a hobby for both resident and visiting scientists. Likewise, the concurrent establishment of organizations emphasizing natural history and field research (e.g., the Illinois Natural History Survey) codified some of these activities as organizational goals.

Collections made at biological stations and field-research institutions have served as an important basis for examining faunal changes over time (Shaffer et al. 1998), and many examples are known for benthic macroinvertebrates (e.g., Resh and Unzicker 1975, Hall and Ide 1987, DeWalt et al. 2005). These studies have provided much useful information about life-history characteristics and the effects of anthropogenic activities. For example, such temporal surveys have demonstrated that long-lived taxa, such as predators, are most susceptible to extirpation, particularly in large rivers. Perhaps this sensitivity results from a life cycle that is too long to escape pollution episodes or anthropogenic activities that modify some requisite of their life history.

The importance of life-history research during this natural-history era was evidenced by the Ecological Society of America's establishment of the "Committee on Ecological Life Histories" (Fig. 1). Today, the term ecological life-history might seem redundant, but 40 y ago, this adjective was commonly used to emphasize the relationship of the life cycle to the environment.

Synthesis of information on life histories

The 2nd period was characterized by the compilation of general information on the life histories of benthic organisms (most often insects) and syntheses of life-history information based on taxonomic groupings (e.g., aquatic insect orders) or specific habitat types. We see 4 sources of important information, and examples of each are presented in our timeline of key milestones in life-history research (Fig. 1). The 1st of these sources is books published that included some information on the ecology of benthic macroinvertebrates. Early works, such as Isaac Walton's (1653) *The Compleat Angler* were written primarily for anglers. Over 300 editions of this book have appeared, and *The Compleat Angler*, along with the King James version of the Bible and the complete works of William Shakespeare are the 3 most published books in English literature!

Scholarly treatments started to appear at the end of the 19th century (e.g., Miall 1895; Fig. 1) and continue into the 20th century. They include Ward and Whipple (1918; Fig. 1), Hynes (1960, 1970; Fig. 1), McCafferty (1981; Fig. 1), Resh and Rosenberg (1984), Williams and Feltmate (1992), Ward (1992), Hutchinson (1993; Fig. 1), and Wichard et al. (1995, 2002; Fig. 1), and they continue to this day. For example, a variety of excellent textbooks, many intended for specialized university classes, and reference works are available (e.g., Hutchinson 1993, Thorp and Covich 2001, Merritt et al. 2008 [Fig. 1]), as are some for the general public (e.g., Voshell 2002). However, these academic books are a small portion of the market relative to the hundreds of books on this topic written for anglers engaged in the sport of fly fishing (e.g., Swisher and Richards 1991, Hafele and Roederer 1995).

The use of aquatic insects and other benthic macroinvertebrates in water pollution monitoring, which began in Germany over a century ago (Bonada et al. 2006), also resulted in the compilation of information on aquatic insect life histories and in particular their response to various types of pollution. Hynes' (1960) book on the *Biology of Polluted Waters* was instrumental in laying the foundations for this approach in North America. Plafkin et al. 's (1989; Fig. 1) manual on biological monitoring not only proposed guidelines for biologically based water-quality monitoring but also provided the first wide-scale use of a life-history characteristic, the use of functional feeding groups, in North American assessments. This manual was also the 2nd-most cited article in the articles appearing in *J-NABS* between 1995 and 2000 (**Resh and Kobzina 2003**[1]). Like biological monitoring, the discovery of the importance of the hyporheic zone in the life histories of insects (Coleman and Hynes 1970, Williams 1984; Fig. 1) sparked a great deal of study on this habitat and its faunal components.

The 2nd source of life-history information is synthetic review articles. Numerous reviews on the life histories of aquatic insects (Macan 1962; Fig. 1) and most importantly specific insect orders or families, such as Trichoptera (Mackay and Wiggins 1979, Wiggins and Mackay 1979), Ephemeroptera (Brittain 1982), Plecoptera (Hynes 1976), Odonata (Corbet 1980), Chironomidae (Oliver 1971, Pinder 1986), and Tipulidae (Pritchard 1983), or groups, such as riffle beetles (Brown 1987), have been essential references that are widely used and cited by benthic biologists worldwide. These articles typically have appeared in the *Annual Review of Entomology* but one detailed review of species traits has appeared in *J-NABS* (**Poff et al. 2006**; Fig. 1). Furthermore, Hutchinson (1981) provided excellent "thoughts" on this topic that are still applicable, and Huryn et al. (2008) recently provided an excellent overview of life-history details of aquatic insects. Reviews also are available about the life histories of benthic organisms occurring in habitats other than streams and lakes. Adaptations to temporary ponds (Wiggins et al. 1980) and streams (Williams 2005), springs (Williams and Danks 1991), and the hyporheic zone (Boulton et al. 1998) illustrate the importance of habitat as a filter for life-history characteristics.

The 3rd source is the special symposia or collections of articles that have been published on life-history topics. These collections include an older compilation (Rosenberg 1979) and more recent symposia published in *J-NABS* on benthic macroinvertebrates in temporary streams (**Mackay 1996**) and tropical streams (**Wantzen et al. 2006**).

The 4th major source of information on life histories of benthic macroinvertebrates is the primary literature published in journals. Some of these articles have appeared in *J-NABS* (Fig. 2), but a very large number of studies (e.g., reviewed in the tables of Huryn et al. 2008) appear in other journals. Mendez and Resh (2007) provided data indicating that specialized publications might be more important outlets than general freshwater journals, such as *J-NABS,* in publishing this type of research. Mendez and Resh (2007) examined 100 of what they considered to be the most complete life-history studies published, in English, on Trichoptera to determine which aspects of the life history of the aquatic insects in this order have been studied most. These 100 studies were drawn from 32 different journals. Most articles (23) appeared in the 12 *Proceedings of the Trichoptera Symposia*, which are published every 3 y, followed by the *Canadian Journal of Zoology* (10), *Archiv für Hydrobiologie* (now called *Fundamental and Applied Limnology*) (8), *Hydrobiologia* (8), *Aquatic Insects* (6), *American Midland Naturalist* (4), *Freshwater Biology* (4), and *Annals of the Entomological Society of America* (4). In their list of 100 detailed life-history studies of Trichoptera, only 1 article had been published in *J-NABS*.

There are several explanations why other journals publish more life-history studies on Trichoptera (and probably other groups of benthic macroinvertebrates) than *J-NABS*. These include the number of articles that appear in a volume of a given journal and the length of time a journal has been publishing research. However, we think that a point not generally acknowledged is that editors of many scientific journals like *J-NABS* want to publish articles from which generalities can be developed or that present clearly unique examples of certain phenomena. In terms of life-history studies, meeting these criteria can be difficult. Some studies might appear to be incomplete because of logistical complications, such as a lack of multiple years or sites that limit comparative analysis, or insufficient physical-habitat (e.g., detailed and regular hydrologic measurements) information. In contrast, the editors of proceedings of special symposia (e.g., on Trichoptera, Ephemerop-

[1] Boldface indicates paper was published in *J-NABS*

tera, Chironomidae, Oligochaeta, and other taxonomic groups) might be more interested in publishing the most information possible on individual taxa in those groups. Thus, these periodical compendia might be more important than broader-coverage journals as publication outlets for life-history research. Moreover, regional journals (e.g., *Journal of the Kansas Entomological Society*, *Proceedings of the Entomological Society of Washington*) and journals in which nonprofessional researchers publish (e.g., *Entomologist Gazette*, *Entomologist's Monthly Magazine*) also are important outlets for life-history research.

J-NABS might fill a special niche in terms of the large number of studies containing molluscan, especially freshwater mussel, life-history elements. Perhaps fewer outlets comparable to those listed above for aquatic insects exist for publication of research on freshwater mussels than for aquatic insects. Also, mollusks might appear more in these types of journals because they are often the topic of conservation issues.

Literature availability is a major problem in accessing life-history research. In a detailed literature review of reproductive traits of aquatic insects, Statzner et al. (1997) warned that many journals containing relevant and potentially valuable life-history information could not be found, despite extensive searching in libraries. This warning suggests that authors should chose to publish life-history information in journals that are well archived. Conversely, perhaps well-archived journals also have an obligation to publish research that has a "longer research life" rather than just this year's "hot topic" (Ioannidis 2005).

Functional-feeding groups

The 3rd period was characterized by the use of the functional-feeding approach in North America. This approach was popularized by early review articles by Cummins (1973) and Cummins and Klug (1979; Fig. 1) and is based on morphological and behavioral mechanisms of food acquisition. Cummins et al. (2008) present the best overview of this approach as currently used, and Merritt and Cummins (2006) provide examples of how this life-history trait can be used as an ecosystem descriptor (e.g., Vannote et al. 1980) and in producing qualitative evaluations of stream-ecosystem health.

A perennial problem encountered by researchers using this trait is the way in which functional-feeding group categories are assigned. For example, Cummins (1988) stated that the original intent was to base functional distinctions on mouthpart morphology and means of food acquisition (as described in Cummins and Wilzbach 1985). However, researchers typically have assigned taxa to functional-feeding groups based on the ecological data tables in Merritt et al. (2008 and earlier editions) or derivative lists, which actually are based on digestive-tract analysis. Although widely used, we think it was unfortunate that the functional-feeding group was the first life-history trait to be applied quantitatively in North American studies because its use deviated from the authors' intentions from the start. Moreover, it is probably the most difficult of the life-history traits to quantify because the categories used are discrete (e.g., shredders, collectors, scrapers), whereas many benthic macroinvertebrates are omnivores or might belong to >1 functional-feeding group over the course their life cycle.

Species traits

The 4th period is still underway and is characterized by the increased use of a species traits-based approach for water-quality assessments and for broad spatial and temporal studies of stream and river systems. Life-history information is essential to the description and quantification of species traits of benthic macroinvertebrates. The use of species traits has a long tradition in biology (Statzner et al. 2001), but the recent interest in these characteristics, which include potential size reached, voltinism, body form, and respiration technique, was initiated with the project of Statzner et al. (1994; Fig. 1) that synthesized 20 y of ecological research on the Upper Rhône River in France. There, >30 researchers designed and applied a strategy to test concurrently developed theories focused on the Habitat Templet Concept of Southwood (1977; Fig. 1). At the beginning of that study, Townsend and Hildrew (1994) predicted which species traits were likely to occur in a particular spatial-temporal templet, which assumed some positive relationship between temporal variability and frequency of disturbance, and between spatial variability and refugia from disturbance. Based on the results obtained from a variety of benthic macroinvertebrates (along with fish, macrophytes, and other organisms), Resh et al. (1994) emphasized the need for future studies to identify new traits for analysis, examine the tradeoffs between various combinations of traits, and focus on systematic groups that developed a consistent evolutionary solution to particular challenges of coping with environmental features of habitats. Following that call, Townsend et al. (1997) did a further test on species traits and habitat templet theory.

Until recently (e.g., **Resh et al. 2005**, Bêche et al. 2006, **Poff et al. 2006**, Bêche and Resh 2007), North American studies based on species traits focused predominantly on functional-feeding groups. Most of the research on the use of species traits has been published by Europeans and in non-North American journals, but the project on the Rhône River (Statzner et al. 1994) had a strong connection to NABS and *J-NABS*. The original idea for doing this type of analysis on a large, well-studied river came from a presentation by Colin Townsend at the Tuscaloosa NABS annual meeting (17–20 May 1998) that was later published in *J-NABS* (**Townsend 1989**). Furthermore, the first presentation of the Rhône results was at a special symposium at the Calgary NABS annual meeting (25–28 May 1993).

Theoretical and applied studies of species traits began to appear in the literature soon after the Rhône study was published. For example, Statzner et al. (1997) used information available worldwide to examine species traits related to reproductive biology of 131 species in 8 orders of aquatic insects. Numerous articles demonstrating how species traits can be used in biomonitoring of streams and rivers have been published (e.g., Charvet et al. 2000 [Fig. 1], Usseglio-Polatera et al. 2000, Gayraud et al. 2003, Bonada et al. 2006, **Dolédec and Statzner 2010**). More recently, Bêche et al. (2006) and Bêche and Resh (2007) used species traits to relate long-term community trends in benthic macroinvertebrates to annual flow variability, Resh et al. (**2005**) used species traits to explain why some taxa are temporally rare, and Bonada et al. (2007) compared traits of macroinvertebrate populations in Mediterranean and temperate regions to examine implications of climate change to benthic fauna.

Poff et al. (**2006**) recently made a major contribution to the study of species traits by providing a trait matrix in terms of life history, mobility, and morphological and ecological characteristics for genera of North American aquatic insects. They used this information to demonstrate how these traits can be used to predict responses of taxa to specific environmental gradients.

Information on species traits has come from several sources. The first source is the published literature (as in the study of Statzner et al. 1997). However, other studies have drawn on the individual expertise of specialists in a particular region (e.g., Statzner et al. 1994, **Poff et al. 2006**). In either case, this information is needed to conduct either applied or basic research using species traits.

Why are more life-history studies not done?

In the above discussion, we have pointed out why life-history studies are important and how information from them can be used. However, life-history studies clearly are not as widely done as in previous times. Why is this the case?

First, benthic biology, like other fields of ecological research, has entered a phase in which experimental research is viewed as worthwhile modern research, and unfortunately, descriptive studies often are viewed as the opposite (e.g., Greene 2005). However, life-history studies can be experimental, hypothesis-based, and predictive; furthermore, they can reset research cycles. Such studies can test whether aspects of a life history of related species are similar as would be predicted by phylogeny, whether local environmental features result in plasticity, or whether phylogenic factors override environmental response. Greene (2005) used the discovery of the marine benthic organisms of deep-sea thermal vents as an example of the types of life-history-related questions now being asked routinely and of new paradigms being developed. In 2009, the Ecological Society of America sponsored a symposium, with well known speakers, entitled "Natural History: The Basis for Ecological Understanding and a Global Sustainable Society" and a new electronic journal, *Journal of Natural History Education* has been started.

Second, life-history studies are time consuming. Multiple seasons and sometimes multiple years are needed to complete a detailed life history. Mendez and Resh (2007) examined 100 studies in terms of the length of field work done in completing life-history studies of Trichoptera and noted that study duration ranged from 1 to 11 y, with ~80% of the studies lasting 1 to 2 y but many lasting 3 to 7 y.

Third, with few exceptions, funding for conducting life-history research is not available. Species of special concern (such as endangered or introduced and potentially pestiferous taxa) might qualify for direct life-history research funding, but the vast majority do not. Savvy benthic biologists interested in life-history research might refer to what they are doing as evolutionary biology or behavioral ecology, and some researchers have successfully packaged proposals in certain ways to emphasize broader concepts. In fact, life-history studies are an example of research that can be done without external funding and, for most of its history (and actually for most of scientific history), this has been the case. The early naturalists (and scientists in general up until the 1950s) supported their research themselves.

How we can increase attention to life-history studies?

In this special issue, Holzenthal et al. (**2010**) have decried the lack of taxonomic expertise among researchers for most of the groups of benthic macroinvertebrates. In taxonomy, new techniques (e.g., genetic barcoding), although controversial (Will and Resh 2008), might offer a shortcut to traditional approaches. However, we have difficulty imagining how new techniques could shorten the time needed to obtain the life-history information required for determining species traits. Ironically, we do see that, in terms of securing extramural funding, a proposal to use stable isotopes to determine feeding relationships might sound more sophisticated (and be more expensive and time consuming) than just examining gut contents!

If life-history information is needed, but the motivation to collect it is missing, how can we encourage more life-history research? To us, the answer is to involve the nonprofessional who is interested in aquatic ecology and entomology in this type of research. For example, in North America, tens of thousands of people are involved in volunteer monitoring groups that assess the environmental quality of streams (e.g., USEPA 1994). Japan has >800,000 people who participate in annual monitoring surveys using benthic macroinvertebrates (Morse et al. 2007). Moreover, throughout the world, hundreds of thousands of anglers are tying flies to imitate aquatic insects to "match the hatch" in their fly-casting efforts. We avoid using the possibly pejorative term, amateurs, to describe these people because their skills and abilities (and time commitments) often match those of professional aquatic ecologists and entomologists.

We have excellent examples of these self-trained aquatic entomologists who have made outstanding contributions to the study of life histories of aquatic insects. Clarence Day, a Vice President of Levi–Strauss (the famous jeans maker), published many articles on the biology and taxonomy of mayflies. Perhaps even more remarkable, Raymond Hays, a custodian at Montana State University, read literature about stonefly biology while being responsible for cleaning the zoology library at that university. His collections and studies made Montana's Hyalitte Creek (where he found 55 species in this insect order) one of the best-studied stonefly streams in North America. His contributions were noted by including him as a co-author of the faunal study of the stoneflies of Montana (Gaufin et al. 1972). Furthermore, scores of fisherman and hikers collected information on winter stoneflies as part of the "Winter Stonefly Club", which was the basis for Ross and Ricker's (1971) seminal monograph on this group. Fly-fishing magazines and newsletters every month contain scores of columns describing intimate details of aquatic insect emergence, immature and adult behavior, and other life-history features that are written by self-trained entomologists. Certainly, the earliest people describing life histories of benthic macroinvertebrates (e.g., Isaac Walton) were entirely self trained!

The courses we teach to students also should emphasize what needs to be done in life-history research. Starting even earlier, suggestions for projects on aspects of life history make marvelous student science-fair projects for primary and secondary school students. In eastern Europe and Russia, teenage "eco-club" members often do life-history studies on stream invertebrates as part of their competitions; some of these studies are published in local natural-history journals.

When choosing which organism to use for a life-history study, we think potential researchers should keep certain characteristics in mind. First, the taxon selected should be readily distinguishable from other benthic macroinvertebrates in the field. For example, the presence of congeneric (or in some cases confamilial) taxa that cannot be easily separated from the study taxon could create difficulties. Early instars might not be distinguishable among these taxa, and the related taxa might have different phenologies that result in confounded patterns. Second, they should be easy to sample and be relatively abundant (or at least not rare). Third, and perhaps most important, the organism itself should be appealing to the researcher's interests.

Different groups also offer different study advantages. Holometabolous species are easier to use in phenology studies (and in descriptions of number of instars) than hemimetabolous species. Chironomids might be the group for which least is known in terms of life histories, but identification problems (particularly in the field) could make such studies difficult.

Although all of us conducting life-history research would like the species that we have selected to have some interesting, previously undescribed life-history characteristic, this feature unfortunately is rarely known in advance. However, even the most straightforward life-history patterns and characteristics are worth describing given the lack of this kind of information in the literature. In the end, the species chosen might have some unique features.

J-NABS can play an important role in advancing life-history and species-trait research by publishing review articles on the life-histories of different groups. Perhaps reviews that attempt to cover the biology of whole orders of aquatic insects have become too difficult a task, and competition for space in the few journals that publish reviews is too great to include them. Syntheses of life-history information on well-studied families, such as hydropsychid caddisflies or perlid stoneflies, or even genera, such as *Baetis*, might provide much needed information. Arguably, more synthesis of existing research is needed in all aspects of benthic science, and the popularity of the recent review of species traits by Poff et al. (**2006**) supports this view.

Last, both the value and the personal aspects of life-history studies should be stressed. A descriptive life history makes an excellent undergraduate or graduate degree thesis. Environmental influences and sources of ecological variation in populations can often best be described by taking a life-history approach. The point that we wish to make to both formally taught and self-trained students of benthic biology is that conducting and reporting life-history research is an important contribution and very enjoyable. In fact, a good life-history study provides a researcher a unique opportunity offered to few individual researchers: the chance to see life through another species' eyes.

Literature Cited

BÊCHE, L. A., E. P. MCELRAVY, AND V. H. RESH. 2006. Long-term seasonal variation of benthic-macroinvertebrate biological traits in two Mediterranean-climate streams in California, USA. Freshwater Biology 51:56–75.

BÊCHE, L. A., AND V. H. RESH. 2007. Biological traits of benthic macroinvertebrates in California Mediterranean-climate streams: long-term annual variability and trait diversity patterns. Fundamental and Applied Limnology 169:1–23.

BERENBAUM, M. R., AND R. J. LESKOSKEY. 1992. Life history strategies and population biology in science fiction films. Bulletin of the Ecological Society of America 73:236–240.

BONADA, N., S. DOLÉDEC, AND B. STATZNER. 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between Mediterranean and temperate regions: implications for future climatic scenarios. Global Change Biology 13:1658–1671.

BONADA, N., N. PRAT, V. H. RESH, AND B. STATZNER. 2006. Developments in aquatic insect biomonitoring: comparative analysis of recent approaches. Annual Review of Entomology 51:495–523.

BOULTON, A. J., S. FINDLAY, P. MARMONIER, E. H. STANLEY, AND H. M. VALETT. 1998. The functional significance of the hyporheic zone in streams and rivers. Annual Review of Ecology and Systematics 29:59–81.

BRITTAIN, J. E. 1982. Biology of mayflies. Annual Review of Entomology 27:119–147.

BROWN, H. P. 1987. Biology of riffle beetles. Annual Review of Entomology 38:253–274.

BUTLER, M. G. 1984. Life histories of aquatic insects. Pages 24–55 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger Scientific, New York.

CHARVET, S., B. STATZNER, P. USSIGLIO-POLATERRA, AND B. DUMONT. 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. Freshwater Biology 31:277–296.

COLEMAN, M. J., AND H. B. N. HYNES. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnology and Oceanography 15:31–40.

CORBET, P. S. 1980. Biology of Odonata. Annual Review of Entomology 25:189–217.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18:183–206.

CUMMINS, K. W. 1988. Rapid bioassessment using functional analysis of running water invertebrates. Pages 49–54 *in* T. P. Simon, L. L. Holst, and L. J. Shepard (editors). Proceedings of the First National Workshop on Biocriteria. EPA-905/9-89/003. US Environmental Protection Agency, Chicago, Illinois.

CUMMINS, K. W., AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10: 147–172.

CUMMINS, K. W., R. W. MERRITT, AND M. A. BERG. 2008. Ecology and distribution of aquatic insects. Pages 105–122 *in* R. W. Merritt, K. W. Cummins, and M. A. Berg (editors). An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing, Dubuque, Iowa.

CUMMINS, K. W., AND M. A. WILZBACH. 1985. Field procedures for analysis of functional feeding groups of stream macroinvertebrates. Contribution 1611. Appalachian Environmental Laboratory, University of Maryland, Frostburg, Maryland (now the University of Maryland Center for Environmental Science).

DAYTON, P., AND E. SALA. 2001. Natural history: the sense of wonder, creativity and progress in ecology. Scientia Marina 65 (Supplement 2):199–206.

DEWALT, R. E., C. FAVRET, AND D. W. WEBB. 2005. Just how imperiled are aquatic insects? A case study of stoneflies (Plecoptera) in Illinois. Annals of the Entomological Society of America 98: 941–950.

DOLÉDEC, S., AND B. STATZNER. 2010. Responses of freshwater biota to human disturbances: contribution of *J-NABS* to developments in ecological integrity assessments. Journal of the North American Benthological Society 29:286–311.

GAUFIN, A. R., W. E. RICKER, M. MINER, P. MILAM, AND R. A. HAYS. 1972. The stoneflies (Plecoptera) of Montana. Transaction of the American Entomological Society 98:1–161.

GAYRAUD, S., B. STATZNER, P. BADY, A. HAYBACH, F. SCHOLL, P. USSEGLIO-POLATERA, AND M. BACCHI. 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. Freshwater Biology 48:2045–2064.

GREENE, H. W. 2005. Organisms in nature as a central focus for biology. Trends in Ecology and Evolution 20:23–27.

HAFELE, R., AND S. ROEDERER. 1995. An angler's guide to aquatic insects and their imitations for all North America. Johnson Printing, Boulder, Colorado.

HALL, R. J., AND F. P. IDE. 1987. Evidence of acidification effects on stream insect communities in central Ontario between 1937 and 1985. Canadian Journal of Fisheries and Aquatic Sciences 44: 1652–1657.

HOLZENTHAL, R. W., D. R. ROBERTSON, S. U. PAULS, AND P. K. MENDEZ. 2010. Taxonomy and systematics: contributions to benthology and *J-NABS*. Journal of the North American Benthological Society 29:147–169.

HURYN, A. D., J. B. WALLACE, AND N. H. ANDERSON. 2008. Habitat, life history, secondary production, and behavioural adaptations of aquatic insects. Pages 55–103 *in* R. W. Merritt, K. W. Cummins, and M. A. Berg (editors). 2008. An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing, Dubuque, Iowa.

HUTCHINSON, G. E. 1981. Thoughts on aquatic insects. BioScience 31: 495–500.

HUTCHINSON, G. E. 1993. A treatise on limnology. Volume 4. John Wiley and Sons, New York.

HYNES, H. B. N. 1960. The biology of polluted waters. Liverpool University Press, Liverpool, UK.

HYNES, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool, UK.

HYNES, H. B. N. 1976. The biology of Plecoptera. Annual Review of Entomology 21:135–153.

IOANNIDIS, J. P. A. 2005. Why most published research findings are false. PLoS Medicine 2:696–701.

LINSLEY, E. G., J. W. MACSWAIN, AND R. F. SMITH. 1952. Outline for ecological life histories of solitary and semi-social bees. Ecology 33:558–567.

MACAN, T. T. 1962. The ecology of aquatic insects. Annual Review of Entomology 7:261–288.

MACKAY, R. J. 1996. Temporary aquatic habitats. Journal of the North American Benthological Society 15:407.

MACKAY, R. J., AND G. B. WIGGINS. 1979. Ecological diversity in Trichoptera. Annual Review of Entomology 24:185–208.

MCCAFFERTY, W. P. 1981. Aquatic entomology. Science Books International, Boston, Massachusetts.

MENDEZ, P. K., AND V. H. RESH. 2007. What aspects of the life history of Trichoptera have been studied. Pages 191–195 *in* J. Bueno-Soria, J. R. Barba-Alvarez, and B. Armitage (editors). Proceedings of the XIIth International Symposium on Trichoptera. The Caddis Press, Columbus, Ohio.

MERRITT, R. W., AND K. W. CUMMINS. 2006. Trophic relationships of aquatic insects. Pages 585–609 *in* F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. 2nd edition. Academic Press, San Diego, California.

MERRITT, R. W., K. W. CUMMINS, AND M. A. BERG (EDITORS). 2008. An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing, Dubuque, Iowa.

MIALL, L. C. 1895. The natural history of aquatic insects. MacMillan, London, UK.

MORSE, J. C., Y. J. BAE, G. MUNKHJARGAL, N. SANGPRADUB, K. TANIDA, T. S. VSHIVKOVA, B. WANG, L. YANG, AND C. M. YULE. 2007. Freshwater biomonitoring with macroinvertebrates in East Asia. Frontiers in Ecology and the Environment 5:33–42.

OLIVER, D. R. 1971. Life history of the Chironomidae. Annual Review of Entomology 16:211–230.

PINDER, L. C. V. 1986. Biology of freshwater Chironomidae. Annual Review of Entomology 31:1–23.

PLAFKIN, J. L., T. BARBOUR, K. D. PORTER, S. K. GROSS, AND R. M. HUGHES. 1989. Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. EPA/440/489/001. Office of Water, US Environmental Protection Agency, Washington, DC.

POFF, N. L., J. D. OLDEN, N. K. M. VIEIRA, D. S. FINN, M. P. SIMMONS, AND B. C. KONDRATIEFF. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. Journal of the North American Benthological Society 25:730–755.

PRITCHARD, G. 1983. Biology of Tipulidae. Annual Review of Entomology 22:1–22.

RESH, V. H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. Journal of the Fisheries Research Board of Canada 36:290–311.

RESH, V. H. 1985. Periodical citations in aquatic entomology and freshwater benthic biology. Freshwater Biology 15:757–766.

RESH, V. H., L. BÊCHE, AND E. P. MCELRAVY. 2005. How common are rare species in long-term benthic macroinvertebrate studies? Journal of the North American Benthological Society 24: 976–989.

RESH, V. H., A. G. HILDREW, B. STATZNER, AND C. R. TOWNSEND. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. Freshwater Biology 31:539–554.

RESH, V. H., AND N. G. KOBZINA. 2003. A perspective on the key citations in freshwater benthic science, and the studies that influenced them. Journal of the North American Benthological Society 22:341–351.

RESH, V. H., AND D. M. ROSENBERG (EDITORS). 1984. The ecology of aquatic insects. Praeger Scientific, New York.

RESH, V. H., AND J. D. UNZICKER. 1975. Water quality monitoring and aquatic organisms: the importance of species identification. Journal of the Water Pollution Control Federation 47:9–19.

ROSENBERG, D. M. (EDITOR). 1979. Freshwater benthic invertebrate life histories: current research and future needs. Journal of the Fisheries Research Board of Canada 36:289–345.

ROSS, H. H., AND W. E. RICKER. 1971. The classification, evolution, and dispersal of the winter stone fly genus *Allocapnia*. University of Illinois Biological Monographs 45:1–166.

SHAFFER, H. B., R. N. FISHER, AND C. DAVIDSON. 1998. The role of natural history collections in documenting species declines. Trends in Research in Ecology and Evolution 13:27–30.

SOUTHWOOD, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337–365.

STATZNER, B., A. G. HILDREW, AND V. H. RESH. 2001. Species traits and environmental constraints: entomological research and the history of ecological theory. Annual Review of Entomology 46:291–316.

STATZNER, B., K. HOPPENHAUS, M.-F. AHRENS, AND P. RICHOUX. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. Freshwater Biology 38: 109–135.

STATZNER, B., V. H. RESH, AND S. DOLÉDEC (EDITORS). 1994. Ecology of the Upper Rhône: a test of habitat templet theories. Freshwater Biology 31:253–554.

SWISHER, D., AND C. RICHARDS. 1991. Emergers. Lyons and Burford, New York.

THORP, J. H., AND A. P. COVICH (EDITORS). 2001. Ecology and classification of North American freshwater invertebrates. 2nd edition. Academic Press, San Diego, California.

TOWNSEND, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36–50.

TOWNSEND, C. R., S. DOLÉDEC, AND M. R. SCARSBROOK. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. Freshwater Biology 37: 367–387.

TOWNSEND, C. R., AND A. G. HILDREW. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265–275.

USEPA (US ENVIRONMENTAL PROTECTION AGENCY). 1994. National directory of volunteer environmental monitoring programs. 4th edition. EPA 841-B-94-001. Rhode Island Sea Grant, University of Rhode Island, Narragansett, Rhode Island, and Office of Water, US Environmental Protection Agency, Washington, DC.

USSEGLIO-POLATERA, P., M. BOURNAUD, P. RICHOUX, AND H. TACHET. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshwater Biology 43:175–205.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

VOSHELL, J. R. 2002. A guide to common freshwater invertebrates of North America. McDonald and Woodward Publishing Company, Blacksburg, Virginia.

WALTON, I. 1653. The compleat angler. Or, the contemplative man's recreation: being a discourse of fish and fishing for the perusal of anglers. Printed by T. Maxey for R. Marriot, London, UK.

WANTZEN, K. M., A. RAMIREZ, AND K. O. WINEMILLER. 2006. New vistas in Neotropical stream ecology—Preface. Journal of the North American Benthological Society 25:61–65.

WARD, J. V. 1992. Aquatic insect ecology. 1. Biology and habitat. John Wiley and Sons, New York.

WARD, H. B., AND G. C. WHIPPLE (EDITORS). 1918. Fresh-water biology. John Wiley and Sons, New York.

WICHARD, W., W. ARENS, AND C. EISENBEIS. 1995. Atlas zur biologie der wasserinsekten. Gustav Fisher, Stuttgart, Germany.

WICHARD, W., W. ARENS, AND C. EISENBEIS. 2002. Biological atlas of aquatic insects. Apollo Books, Stenstrup, Denmark.

WIGGINS, G. B., AND R. J. MACKAY. 1979. Some relationships between systematics and trophic ecology in nearctic aquatic insects, with special reference to Trichoptera. Ecology 59: 1211–1220.

WIGGINS, G. B., R. J. MACKAY, AND I. M. SMITH. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie Supplement 58:97–208.

WILL, K. W., AND V. H. RESH. 2008. Phylogenetic relationships and evolutionary adaptations of aquatic insects. Pages 139–156 *in* R. W. Merritt, K. W. Cummins, and M. A. Berg (editors). 2008. An introduction to the aquatic insects of North America. 4th edition. Kendall/Hunt Publishing, Dubuque, Iowa.

WILLIAMS, D. D. 1984. The hyporheic zone as a habitat for aquatic insects and associated arthropods. Pages 430–455 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger Scientific, New York.

WILLIAMS, D. D. 2005. The biology of temporary waters. Oxford University Press, New York.

WILLIAMS, D. D., AND H. V. DANKS (EDITORS). 1991. Arthropods of springs, with particular reference to Canada. Memoirs of the Entomological Society of Canada 155:1–217.

WILLIAMS, D. D., AND B. W. FELTMATE. 1992. Aquatic insects. CAB International, Wallingford, UK.

Received: 21 May 2008
Accepted: 1 September 2009