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Dry mass–length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada

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SUMMARY

1. We summarized previously published mass–length relationships for aquatic insects, and determined the relationship between dry body mass and body length for eight genera and seven families of benthic insects from Catamaran Brook, New Brunswick, Canada.
2. A power function was the most commonly used model in the earlier studies and best described the observed mass–length relationship for taxa from Catamaran Brook.
3. Predicted mass at length was highly variable (coefficient of variation ≥ 25%) among models developed in different studies for the same family group. This variability presumably resulted from both variation in the methods used to construct the models, and in the natural spatio-temporal and taxonomic variation in mass at length, although the relative contributions of these two sources cannot be determined from existing data.
4. Several recommendations are made for the development and application of mass–length equations in future studies.

Keywords: benthos, biomass, invertebrates, weight

Introduction

Estimates of the fresh (wet or dry) mass of freshwater benthic organisms are often required for studies of invertebrate growth and production, and of the feeding ecology of fish. However, determination of fresh mass is not feasible in many cases. Consequently, invertebrate samples are usually fixed soon after collection and mass is estimated from measurements of preserved organisms. Because mass determination is laborious and preservation often alters the mass of invertebrates, direct measurement may not be desirable. Thus, the fresh mass of preserved invertebrates is often estimated indirectly from relationships between fresh mass and linear body dimensions. These empirical relationships are widely used in many freshwater ecological studies. Although several studies have compiled mass–length relationships for taxa of specific localities (e.g. Mason, 1977; Smock, 1980; Meyer, 1989; Towers *et al*., 1994; Burgherr & Meyer, 1997), comparisons of mass predictions among studies have rarely been made.

The primary objective of the present study was to conduct a review of previously reported mass–length relationships to summarize results, compare predictions, and assess the methodology and assumptions which go into the construction and use of such models. Such a review would be useful in assessing the applicability of mass–length relationships beyond the studies from which these were developed. In addition, we wanted to determine the dry mass versus length relationships for some of the insect taxa most commonly found in the benthic community of Catamaran Brook, New Brunswick, Canada. These relationships are required for future assessments of benthic community structure and of the feeding ecology of benthivorous fishes.

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Materials and methods

We reviewed the primary literature in aquatic sciences to find studies which reported mass–length relationships for aquatic insects. In each case, they recorded the taxon, collection site, methods used in determining the relationship and the relationship itself. Some studies where organisms were grouped into size classes before mass determination were included, but studies that grouped organisms into instars or very large size classes were not. In some cases where mass–length relationships were not reported, the relationship was derived from data in figures or tables.

Catamaran Brook (46° 52.7′ N, 66° 06.0′ W) is a third-order stream draining into the Little Southwest Miramichi River in central New Brunswick, Canada. Detailed descriptions of the physical, chemical and biological conditions of the brook and its drainage basin are provided by Cunjak *et al*. (1990, 1993). All collections were made in the lower 300 m of Catamaran Brook, immediately upstream of its confluence with the Little Southwest Miramichi River. Sampling was conducted from mid-June to mid-July in 1995 and 1996. Invertebrates were collected in mid-stream in shallow (15–20 cm) riffle habitat by placing a 200-μm mesh Nitex® (Sefar Inc., Switzerland) drift net in the brook and gently disturbing the stream bed immediately upstream. Material trapped in the net was flushed into a shallow sorting tray and allowed to settle. Live organisms were removed with a pipette and transported in cool water to the laboratory, where these were processed within 3 h. Organisms were killed by placing them in a saturated antacid (sodium citrate) solution for about 1 min and identified (usually to genus) using the keys of Merritt & Cummins (1996). Only specimens with complete sets of intact body appendages were selected. Two linear dimensions were measured (± 0.04 mm) using a dissecting microscope and an ocular micrometer. Length was measured along the dorsal surface from the anterior edge of the head capsule to the posterior tip of the abdomen, excluding anal prolegs and cerci. Head capsule width was measured perpendicular to length at the widest point across the dorsal surface of the head. Individual organisms were transferred to pre-weighed (± 1.3 mg) aluminium pans, oven-dried at 60 °C for 24 h, moved to a desiccator for 1 h, then weighed (± 0.0001 mg) on a Cahn® C-33 Microbalance (Orion Research Inc., Beverly, MA).

Mass–length relationships were developed for all genera and families in which ten or more organisms were measured. Relationships at the familial level were developed using measured organisms from all genera in the family, including those genera in which less than ten individuals were measured. The present authors modelled dry mass (Y, mg) as a function of body length or head capsule width (X, mm) using a power model ($\ln Y = \ln b_0 + b_1 \cdot \ln X$) since this was the most commonly employed model in earlier studies (e.g. Smock, 1980; Meyer, 1989; Towers *et al*., 1994; Burgherr & Meyer, 1997). We compared the fitof the power model with those of three other models: (1) linear ($Y = b0 + b1 \cdot X$); (2) exponential ($\ln Y = \ln b_0 + b_1 \cdot X$); and (3) quadratic ($Y = b_0 + b_1 \cdot X + b_2 \cdot X^2$). The power model was considered appropriate unless one of these other models provided better uniformity in residuals versus predicted mass plots and accounted for a higher percentage of variation in mass (r^2). The fitted parameter estimates b_0, b_1 and b_2 were obtained by least-squares regression (GLM procedure; SAS Institute, 1985), and b_0 was adjusted for transformation bias where necessary (Bird & Prairie, 1985).

We assessed the variability in mass estimates by comparing predictions among several mass–length relationships (including those from Catamaran Brook taxa) within each of twelve families of benthic insects. Within each family, the relationships came from a variety of taxonomic levels (i.e. familial, generic and specific). We selected only those models which were constructed using ten or more fresh (i.e. not chemically preserved) specimens, and which related dry mass to total body length. For each family, coefficients of variation for predicted mass were determined at three body lengths (BL_1, BL_2 and BL_3). The intermediate body length (BL_2) was selected as the mid-point of overlap for the reported length ranges of organisms used to build the relationships (not all studies reported the length ranges of organisms used in model construction). This was considered the closest approximation to the mean size of organism used among studies. The smallest (BL_1) and largest (BL_3) body lengths were chosen as half and twice the intermediate body length, respectively. The ratio of highest to lowest predicted mass was also calculated at each of these three body lengths.

Results

The literature yielded a total of seventy-one publications (including the present study) which reported aquatic insect mass–length relationships or the data from which such relationships could be determined (Table 1; Appendices 1 & 2). Many additional studies indicated that mass–length relationships were used, but did not report these or referred to inaccessible sources (e.g. graduate theses, technical reports and unpublished data). Few studies were devoted specifically to the development of mass–length relationships of benthic insects, and the present authors found only seven earlier publications which reported such relationships for ten or more taxa (Table 1). Most mass–length relationships were reported as part of life history, growth, production or bioenergetics studies.

The methodology used in developing mass–length relationships has varied considerably. Out of the seventy-one studies reviewed, twenty-three used fresh specimens, twenty-five used chemically preserved (in formalin and/or alcohol) specimens, six used frozen specimens and seventeen did not explicitly state the treatment of samples. Most ($n = 50$) studies used total body length as the linear measurement, whereas nine used head capsule width, one used interocular width, one used labium length, and ten used both body length and some head capsule measurement. The linear size range of organisms used to build the relationships was indicated in forty-one out of the seventy-one studies reviewed. Mass was determined as dry mass ($n = 52$), ash-free dry mass ($n = 5$), wet mass ($n = 9$), or as both wet and dry mass ($n = 5$). In one study, dry mass was determined by freeze-drying. The most commonly reported procedure was oven-drying for 24 h at 60 °C, but temperatures varied from 37 to 105 °C and drying time from 2 to 72 h. A high proportion of studies (fifteen out of sixty-two) did not indicate the drying time and/or the temperature used, and few studies reported desiccation time following oven-drying. Mass is usually modelled as a power function of length for most taxa (Mackey, 1977; Smock, 1980; Balushkina, 1982; Meyer, 1989; Towers *et al.*, 1994; Burgherr & Meyer, 1997; Appendix 1), but linear, exponential, quadratic and polynomial models have also been used (Mason, 1977; Meyer, 1989; Burgherr & Meyer, 1997; Appendix 2).

The relationship between dry mass and body length was best described by a power model for eight genera and seven families of benthic insects sampled from Catamaran Brook (Table 2). For some taxa, the quadratic model was also able to provide a uniform scatter in residuals versus predicted mass plots, but it did not account for as much variation in mass as the power model. Coefficients of determination (r^2) were generally > 0.85, but were considerably lower for Chironomidae. For most taxa, body length explained more variation in dry mass than head capsule width (Table 2).

Variation in predicted dry mass at length within families was high, with coefficients of variation (CVs) usually > 25% (Fig. 1; Table 3). The ratio of highest to lowest mass predicted at a given length was two or more in most cases (Table 3). Within families, the highest CV was always associated with mass predictions at the highest or lowest body length (BL_1 or BL_3). Families with all relationships from a single genus (e.g. *Baetis* for Baetidae and *Isoperla* for Perlodidae) did not show appreciably lower CVs than families with relationships derived from different genera. For all families, the variation shown in Fig. 1 and Table 3 should be considered as conservative since the present authors excluded relationships from studies which used chemically preserved organisms. For Chironomidae, in particular, the variation should be considered very conservative since we also excluded relationships from two studies (Mason, 1977; Towers *et al.*, 1994) which predicted mass an order of magnitude higher than that of the remaining models. Relationships from some studies consistently predicted a higher mass at length across taxa relative to those of other studies. For example, relationships presented by Smock (1980) predicted consistently higher mass at length than those of Burgherr & Meyer (1997) for several families (Fig. 1).

Discussion

Mass–length relationships are a useful tool in ecological research. Estimating mass indirectly from linear measurements is more rapid than direct mass determination, particularly for smaller invertebrates. As a result, mass–length relationships have been determined for numerous taxa of terrestrial insects (Rogers *et al.*, 1976; Rogers *et al.*, 1977; Schoener, 1980; Sage, 1982; Sample *et al.*, 1993), freshwater zooplankton (reviewed by McCauley, 1984; Culver *et al.*, 1985;

Table 1 Studies reporting mass–length relationships for 10 or more taxa of aquatic insects. All organisms were dried for 24 h at 60 °C unless otherwise indicated

Source	Locality	Treatment	*Y* versus *X*	Families represented (taxa per family)
Mackey (1977)	Thames River, UK	Formalin-preserved	DM vs BL	Chironomidae (16)
Mason (1977)	Norfolk Broads, UK	Fresh, starved 48 h, dried to constant mass at 80 °C	DM vs BL	Baetidae (1), Caenidae (1), Coenagrionidae (1), Corixidae (1), Leptoceridae (1), Polycentropodidae (1), Ceratopogonidae (1), Chaoboridae (1), Chironomidae (6), plus 12 non-insect taxa
Smock (1980)	Haw, New Hope and Eno Rivers, NC, USA	Frozen, dried 4 h at 105 °C	DM vs BL	Baetidae (1), Isonychiidae (1), Heptageniidae (3), Ephemerellidae (1), Caenidae (1), Ephemeridae (1), Gomphidae (1), Aeshnidae (1), Coenagrionidae (1), Taeniopterygidae (2), Capniidae (1), Perlidae (3), Perlodidae (2), Veliidae (1), Gerridae (2), Corixidae (1), Sialidae (1), Corydalidae (2), Philopotamidae (1), Polycentropodidae (1), Hydropsychidae (3), Lepidostomatidae (1), Limnephilidae (1), Gyrinidae (1), Haliplidae (1), Dytiscidae (1), Elmidae (2), Ceratopogonidae (1), Chironomidae (2), Simuliidae (1), Tipulidae (1)
Balushkina (1982)	Various sites in E. Europe and Russia	Fresh or recently preserved, dried ? h at ? °C	DM or WM vs BL	Chironomidae (25)
Meyer (1989)	Steina stream, SW Germany	Frozen, dried 36h at 104 °C	DM vs BL and DM vs HW	Baetidae (5), Heptageniidae (3), Ephemerellidae (3), Caenidae (1), Leptophlebiidae (2), Taeniopterygidae (2), Nemouridae (5), Leuctridae (3), Perlidae (1), Perlodidae (2), Chloroperlidae (1), Philopotamidae (1), Psychomyidae (1), Hydropsychidae (1), Rhyacophilidae (1), Glossosomatidae (2), Limnephilidae (6), Sericostomatidae (1), Odontoceridae (1), Elmidae (3), Ceratopogonidae (1), Chironomidae (1), Simuliidae (1), Tipulidae (4), Athericidae (1), Empididae (1), plus three non-insect taxa
Towers *et al.* (1994)	Kahuterawa and Turitea streams, New Zealand	Fresh, dried 36 h at 104 °C	DM vs BL and DM vs HW	Siphlonuridae (1), Ameletopsidae (1), Coloburiscidae (1), Leptophlebiidae (2), Austroperlidae (1), Eustheniidae (1), Gripopterygidae (2), Corydalidae (1), Hydropsychidae (1), Hydrobiosidae (1), Conoesucidae (2), Helicopsychidae (1), Elmidae (1), Chironomidae (1), Simuliidae (1), Tipulidae (1), plus one non-insect taxon
Burgherr & Meyer (1997)	Necker River, Switzerland	Frozen on dry ice, dried 48 h at 60 °C	DM vs BL and DM vs HW	Baetidae (1), Heptageniidae (3), Leptophlebiidae (1), Nemouridae (3), Leuctridae (1), Perlidae (1), Perlodidae (1), Chloroperlidae (1), Hydropsychidae (1), Rhyacophilidae (1), Glossosomatidae (1), Hydraenidae (1), Elmidae (2), Blephariceridae (1), Chironomidae (3), Simuliidae (1), Tipulidae (2), Athericidae (1), plus one non-insect taxon

DM = dry mass, BL = body length, HW = head capsule width.

Table 2 Mass–length relationships for aquatic insects from Catamaran Brook, New Brunswick, Canada. Relationships at the generic level are presented for those genera for which ten or more individuals were measured. The relationships at the familial level are presented for those families for which more than one genus was examined (including genera for which ten or more individuals were measured)

Taxon	BL range (mm)	DM vs BL relationship	HW range (mm)	DM vs HW relationship
Ephemeroptera				
Baetidae	1.0–5.5	$DM = 0.00983 \cdot BL^{2.61}$ ($n = 103$, $r^2 = 0.90$)	0.30–1.0	$DM = 0.772 \cdot HW^{3.11}$ ($n = 103$, $r^2 = 0.87$)
Acentrella	1.0–4.8	$DM = 0.00962 \cdot BL^{2.75}$ ($n = 57$, $r^2 = 0.88$)	0.30–1.0	$DM = 0.701 \cdot HW^{3.29}$ ($n = 57$, $r^2 = 0.86$)
Baetis	1.1–5.5	$DM = 0.00946 \cdot BL^{2.44}$ ($n = 45$, $r^2 = 0.95$)	0.30–0.85	$DM = 1.07 \cdot HW^{3.40}$ ($n = 45$, $r^2 = 0.92$)
Heptageniidae	1.5–8.6	$DM = 0.0111 \cdot BL^{2.74}$ ($n = 37$, $r^2 = 0.98$)	0.70–2.5	$DM = 0.128 \cdot HW^{3.44}$ ($n = 37$, $r^2 = 0.97$)
Leucrocuta	1.5–7.5	$DM = 0.0106 \cdot BL^{2.79}$ ($n = 26$, $r^2 = 0.98$)	0.70–2.2	$DM = 0.134 \cdot HW^{3.40}$ ($n = 26$, $r^2 = 0.97$)
Ephemerellidae	1.6–7.1	$DM = 0.00928 \cdot BL^{2.90}$ ($n = 50$, $r^2 = 0.97$)	0.40–1.8	$DM = 0.549 \cdot HW^{3.35}$ ($n = 50$, $r^2 = 0.90$)
Drunella	2.3–7.0	$DM = 0.00902 \cdot BL^{3.00}$ ($n = 16$, $r^2 = 0.97$)	0.70–1.8	$DM = 0.368 \cdot HW^{3.78}$ ($n = 16$, $r^2 = 0.97$)
Serratella	1.6–4.8	$DM = 0.0104 \cdot BL^{2.83}$ ($n = 20$, $r^2 = 0.94$)	0.40–1.1	$DM = 0.676 \cdot HW^{3.67}$ ($n = 20$, $r^2 = 0.89$)
Leptophlebiidae				
Paraleptophlebia	1.8–7.1	$DM = 0.00940 \cdot BL^{2.51}$ ($n = 50$, $r^2 = 0.96$)	0.40–1.2	$DM = 0.622 \cdot HW^{3.23}$ ($n = 50$, $r^2 = 0.92$)
Trichoptera				
Philopotamidae				
Dolophilodes	2.8–9.4	$DM = 0.00408 \cdot BL^{2.82}$ ($n = 28$, $r^2 = 0.88$)	0.50–1.2	$DM = 0.997 \cdot HW^{3.25}$ ($n = 28$, $r^2 = 0.72$)
Diptera				
Chironomidae	2.0–6.0	$DM = 0.00215 \cdot BL^{2.71}$ ($n = 38$, $r^2 = 0.84$)	0.20–0.50	$DM = 4.86 \cdot HW^{3.15}$ ($n = 38$, $r^2 = 0.35$)
Tanypodinae	3.0–5.8	$DM = 0.00562 \cdot BL^{2.00}$ ($n = 16$, $r^2 = 0.62$)	0.25–0.50	$DM = 0.407 \cdot HW^{1.01}$ ($n = 16$, $r^2 = 0.14$)
Non-Tanypodinae	2.0–6.0	$DM = 0.00124 \cdot BL^{3.26}$ ($n = 22$, $r^2 = 0.85$)	0.20–0.35	$DM = 12.6 \cdot HW^{3.83}$ ($n = 22$, $r^2 = 0.23$)
Simuliidae				
Simulium	0.65–5.4	$DM = 0.00601 \cdot BL^{2.81}$ ($n = 30$, $r^2 = 0.98$)	0.10–0.60	$DM = 2.50 \cdot HW^{3.55}$ ($n = 30$, $r^2 = 0.89$)

DM = dry mass (mg); BL = body length (mm), HW = head capsule width (mm), n = number of individuals measured, and r^2 = coefficient of determination.

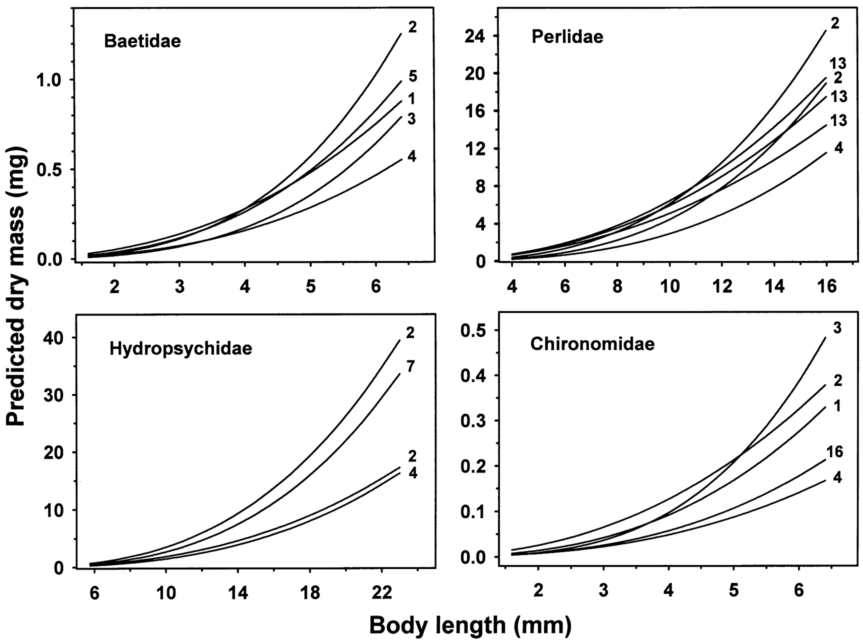

Fig. 1 Comparison of predicted dry mass versus body length relationships for various taxa within each of four families of aquatic insects. The numbers indicate the sources of the plotted relationships, as listed in the caption of Table 3.

Lawrence *et al.*, 1987) and aquatic insects (Tables 1 & 2; Appendices 1 & 2). These relationships have been used to estimate the mass of invertebrates from different geographical locations and/or to estimate the mass of taxa with similar body shapes. The present results indicate that the mass–length relationships of aquatic insects reported in different studies may yield quite different predictions, even for closely related taxa. Thus, the choice of a predictive model should be an important consideration in order to obtain accurate mass estimates.

Variation in the predictions of different mass–length relationships may be attributable to two sources: (1) methodological differences in the development or application of the relationships; and (2) true spatio-temporal or taxonomic variation in mass at length.

Preservation may bias the estimation of mass from length, but the direction and magnitude of this bias can vary with the type of preservative used, the duration of storage, and the size, condition and taxon of the specimens. For example, most benthic insects show marked reductions in dry mass following chemical preservation (Howmiller, 1972; Ladle *et al.*, 1972; Landahl & Nagell, 1978; Iversen, 1980; Giberson & Galloway, 1985; Leuven *et al.*, 1985), whereas large caddisfly larvae show only negligible changes (Ross & Wallace, 1983; MacKay, 1984). In addition, some invertebrates may exhibit significant length changes following chemical preservation (Britt, 1953; Kulka & Corey, 1982; Lasenby *et al.*, 1994), whereas others show no significant change in length (Giberson & Galloway, 1985; Heise *et al.*, 1988; Nolte, 1990). Alcohol appears to cause greater mass changes than formalin (Mills *et al.*, 1982; Leuven *et al.*, 1985). Furthermore, Lasenby *et al.* (1994) noted that the length of *Chaoborus* spp. increased (by about 11%) following preservation in ethanol, but decreased (by 8–14%) following preservation in formalin.

Mass and length changes caused by preservation create two problems. Firstly, mass–length relationships developed from preserved organisms may deviate from the true (i.e. fresh) relationship depending on the relative changes in mass and length. Secondly, using lengths of preserved organisms to predict mass from relationships constructed from fresh organisms may result in biased estimates of fresh mass. Because chemical preservation appears to cause relatively larger changes in mass than length, the best solution would be to develop and use mass–length relationships from fresh organisms, and correct the lengths of any preserved organisms used for mass prediction. Some studies have used frozen rather than fresh samples to develop mass–length relation-

Table 3 Coefficients of variation (CV) and the ratios of the highest to lowest predicted values (H:L) of dry mass at length predictions at three body lengths (BLs) using mass–length relationships of various studies

Family	Taxonomic relationships used (sources)	BL_1 (mm)	CV_1 (%)	$H:L_1$	BL_2 (mm)	CV_2 (%)	$H:L_2$	BL_3 (mm)	CV_3 (%)	$H:L_3$
Baetidae	*Baetis* (1–4), *B. quilleri* Dodds (5)	1.60	46.0	3.39	3.20	28.5	1.93	6.40	28.9	2.27
Heptageniidae	Heptageniidae (1), *Epeorus sylvicola* Pictet (3), *Heptagenia aphrodite* McDunnogh (2), *Rhithrogena* (4), *R. semicolorata* (Curtis) (3), *Stenonema* (2)	2.90	39.4	4.21	5.80	23.9	2.17	11.6	25.8	2.29
Ephemerellidae	Ephemerellidae (1), *Ephemerella* (3, 6), *E. temporalis* McDunnogh (2)	2.20	25.7	1.73	4.40	26.3	1.90	8.80	33.0	2.10
Leptophlebiidae	*Deleatidium* (7), *Habrophlebia lauta* Eaton (3, 8), *Leptophlebia vespertina* (L.) (9), *Paraleptophlebia* (1), *Zephlebia* (7)	2.75	36.4	2.62	5.50	24.6	1.87	11.0	27.1	1.96
Ephemeridae	*Ephemera danica* Müller (10, 11), *Hexagenia limbata* (Serville) (12), *H. munda* Eaton (2)	3.50	61.2	4.95	7.00	58.4	4.10	14.0	55.1	3.40
Perlidae	*Acroneuria abnormis* (Newman) (2), *A. evoluta* Klapalek (13), *Agnetina capitata* (Pictet) (13), *Neoperla* (13), *Perla grandis* Rambur (4), *Perlesta placida* (Hagen) (2)	4.00	48.0	3.68	8.00	29.6	2.49	16.0	25.2	2.13
Perlodidae	*Isoperla* (4), *I. clio* (Newman) (2), *I. grammatica* Poda (3), *I. namata* Frison (13), *I. signata* (Banks) (13)	4.00	52.4	3.20	8.00	18.3	1.59	16.0	95.4	1.69
Corydalidae	*Archichauliodes diversus* Walker (7), *Corydalus cornutus* (L.) (2, 14), *Nigronia serricornis* (Say) (2, 15)	10.8	28.4	1.93	21.5	5.63	1.16	43.0	29.9	2.00
Hydropsychidae	*Aoteapsyche* (7), *Cheumatopsyche* (2), *Hydropsyche* (2, 4)	5.75	34.9	2.35	11.5	38.7	2.39	23.0	43.7	2.42
Chironomidae	Chironomidae (1, 3, 4), Chironominae/Orthocladinae (2), *Chironomus salinarius* Kieffer (16)	1.60	64.9	3.53	3.20	42.1	2.80	6.40	40.5	2.89
Simuliidae	Simuliidae (2–4), *Austrosimulium* (7), *Prosimulium mixtum/fuscum* complex Syme & Davies (17, 18), *Simulium* (1), *S. vittatum* Zetterrstedt (18), *Stegopterna mutata* (Malloch) (17, 18)	1.70	72.6	10.4	3.40	49.4	4.11	6.80	45.8	3.82
Tipulidae	*Aphrophila neozelandica* (Edwards) (7), *Dicranota* (3, 4), *Hexatoma* (3, 4), *Pedicia* (3), *Pedicia hannai* Alexander (19), *Tipula abdominalis* (Say) (2)	6.80	66.0	6.22	13.6	41.8	4.08	27.2	76.5	16.9

The intermediate body length (BL_2) was selected as the mid-point of overlap for the reported size ranges of organisms used to build the relationships. The smallest (BL_1) and largest (BL_3) body lengths were chosen as half and twice the intermediate body length, respectively. The sources of the relationships are: (1) present study; (2) Smock (1980); (3) Meyer (1989); (4) Burgherr & Meyer (1997); (5) Fisher & Gray (1983); (6) Benke & Jacobi (1994); (7) Towers *et al.* (1994); (8) Wenzel *et al.* (1990); (9) Savage (1986); (10) Svensson (1977); (11) Tokeshi (1985); (12) Edsall *et al.* (1991); (13) Jop & Stewart (1987); (14) Knight & Simmons (1975b); (15) Knight & Simmons (1975a); (16) Drake & Arias (1995); (17) Merritt *et al.* (1982); (18) Morin *et al.* (1988); and (19) MacLean (1973).

ships (Brittain, 1978; Smock, 1980; Meyer, 1989; Wenzel *et al*., 1990; Dixon & Wrona, 1992; Burgherr & Meyer, 1997). Freezing in water causes both length reduction and dry mass loss in larval fish (Johnston & Mathias, 1993). Thus, the effects of freezing on length and mass of invertebrates may also be problematic.

The choice of length measurement and drying procedure should be considered in developing mass–length relationships. Relationships between mass and head measurements may be useful for studies predicting the mass of badly damaged organisms (e.g. analysis of fish gut contents) since the head capsule is usually less susceptible to damage and deformity than other body parts. Head capsule width is also less affected by chemical preservation than total body length (Britt, 1953). However, because of heavy sclerotization, head capsule width probably changes little within instars, even though body length and mass may change considerably. This stepwise growth pattern in head capsules may explain why head width often accounts for slightly less variation in body mass than total length (Meyer, 1989; Wenzel *et al*., 1990; Towers *et al*., 1994; Burgherr & Meyer, 1997; present study). Errors in length measurements in both model construction and model application can lead to errors in predicted mass, but these errors are generally small and the required precision in length measurement declines with increasing organism size (Bird & Prairie, 1985).

Oven-drying for 24–28 h at 60 °C followed by 1–2 h of desiccation is the most common method for drying aquatic insects as well as other invertebrates (McCauley, 1984). Few studies have compared aquatic insect dry masses derived from different drying or desiccation procedures. Dermott & Paterson (1974) observed significant differences in the masses of chironomid larvae dried at 60 and 100 °C. However, it has not been established if higher temperatures result in greater loss of water, greater loss of volatile organic matter or both. Gut contents can add to mass, and some studies have removed gut contents or allowed guts to clear before mass determination (e.g. Mason, 1977; Tokeshi, 1985; Dudgeon, 1989). The proportion of body mass attributable to gut contents probably varies considerably among taxa, habitats and sampling times. Gut contents accounted for 4% of total dry mass in larval *Chironomus plumosus* L. (Landahl & Nagell, 1978), but may constitute a much higher proportion of body mass in insects which feed on leaves and wood such as some caddis larvae (M. J. Winterbourn, personal communication).

Both the size range of organisms used to build mass–length relationships and the model-fitting procedure can affect model predictions. Depending on the form of the model used, model parameters estimated from a narrow size range of data may differ markedly from parameters estimated over a different or wider size range. For example, the slope parameter (b_1) of the power model tends to increase with instar number or length for larval Diptera (Dumont & Balvay, 1979; Merritt *et al*., 1982; Nolte, 1990). This indicates that the increase in body mass with respect to body length is more rapid in late instars than in early instars. Thus, predicting mass for late instars from a model developed for early instars or *vice versa* could lead to serious errors. In our analyses, the highest variation among mass predictions was always observed at body lengths above or below the midpoint of the common length range, and was probably associated with extrapolation error. The size range of organisms used may also affect the type of model selected. Growth which appears geometric over a wide length range may appear linear over a shorter length range. Finally, the method of parameter estimation may also pose problems. Power model parameters are usually estimated by least-squares regression of ln mass against ln length where b_1 is the slope and b_0 is estimated as the antilog of the intercept. However, this simple back-transformation will lead to underestimation of b_0 and a correction factor must be applied (Bird & Prairie, 1985). This adjustment may be substantial in some cases, but in our review of mass–length relationships, they found only one study other than their own which stated explicitly that this correction factor was applied (Morin *et al*., 1988). In our study, correction factor values ranged from 1.02 to 1.08 for dry mass versus body length relationships, and from 1.03 to 1.15 for most dry mass versus head width relationships, but up to 1.50 for dry mass versus head width relationships of non-Tanypodinae chironomids. An alternate approach to obtaining unbiased estimates of b_0 is to fit the power model by non-linear least-squares (e.g. NLIN procedure; SAS Institute 1985).

In addition to methodological problems in their development and application, mass–length relationships may differ in their predictions because of true spatio-temporal or taxonomic variation in invertebrate mass at length. Even closely related taxa may differ in mass at length. For example, different species of *Eusimulium* exhibit different mass at length characteristics (Schröder, 1987) and different species of Chironomidae also exhibit highly variable mass at length (Balushkina, 1982). The relatively low r^2-values for mass–length relationships of Chironomidae at the familial level seen in the present and earlier studies may indicate taxonomic variation because Chironomidae represent a large and diverse group, and individual relationships may include many different taxa. Some of the variation the we observed among model predictions may have been a result of taxonomic differences in mass at length because they grouped equations at the familial level. However, monogeneric groupings did not seem to exhibit markedly lower variation in their predictions (Table 3). Food availability may influence mass predictions in two ways. Firstly, larvae living in food-rich habitats may contain greater amounts of food in their guts (see above). Secondly, well-fed individuals usually exhibit higher condition (i.e. body mass at length independent of gut con-tents) (Baker, 1989). Some studies have noted intraspecific variation in mass at length between different habitats (Schröder, 1987; Short *et al*., 1987; Griffith *et al*., 1993). This may be attributable to differences in food availability or other physical, chemical and biological conditions. For example, Griffith *et al*. (1993) observed significant differences in the mass–length relationship of *Paracapnia angulata* Hanson from streams of different pH. In contrast, other studies have found little difference in mass–length relationships of benthic insects estimated from different habitats (Kovalak, 1978; Smock, 1980; Eggert & Burton, 1994).

Our analyses indicated that the variation among mass predictions of published mass–length relationships may be quite large. However, in most cases, we could not quantify the relative contributions to this variation of methodological differences, and of true spatio-temporal or taxonomic differences in mass at length. Standardizing the methods of collection, sample treatment and model development would greatly aid comparisons among mass–length relationships from different studies in future. The variability among model predictions poses problems for studies using published mass–length relationships and we offer the following recommendations. Ideally, mass–length equations should be developed for the taxon and habitat under study, preferably using fresh organisms over a wide size range. Parameters should be corrected for transformation bias where necessary. Full details of the measuring, drying, mass determination and model-fitting procedure should be published with the equation to aid comparisons among studies. Alternatively, if mass–length equations are borrowed from the literature, care must be taken in selection. For each taxon under study, we suggest using only equations of taxonomically similar organisms from limnologically similar habitats. The selected equation should have been constructed from organisms covering the size range for which predictions will be made. Equations developed from fresh organisms should be selected over those developed from chemically preserved organisms, although the latter may still be useful for certain studies. Regardless of whether mass–length relationships are developed or borrowed, correction factors for length changes caused by preservation should be estimated and applied (if necessary) to any preserved organism for which mass is to be predicted.

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Appendix 1 Summary of published power relationships between mass and linear measurements for various aquatic insect taxa. The relationships from those sources listed in Table 1 are not included for brevity. The formulae represent immature forms of the taxa. Wet masses (WM, mg) were determined after blotting, dry masses (DM, mg) were determined after drying for 24 h at 60 °C, total body lengths (BLs, mm) were measured from the anterior margin of the head capsule to the posterior margin of the terminal abdominal segment (excluding setae and appendages) and head capsule widths (HWs, mm) were measured at the widest part of the head unless otherwise indicated. Some studies used ash-free dry mass (AFDM, mg) instead of dry mass and some used interocular width (IOW, mm) instead of head width. For studies which reported relationships for both wet and dry mass (Brittain, 1978; Cianciara, 1980; Jop & Stewart, 1987; Edsall *et al*., 1991), only dry mass relationships are listed. Parameters are from the power equation $Y = b_0 \cdot X^{b1}$, where Y is mass (mg) and X is the linear measurement (mm). Studies reporting mass–length relationships of non-power form are listed in Appendix 2. Sample sizes (n) represent the total number of individuals used in building the relationship even if these were grouped prior to mass determination. Coefficients of determination (r^2) may be based on sample sizes < n if the relationship was fit to means rather than individual data points; (NA) data not available

Taxon	Source	Locality	Sample treatment	Y versus X	X range (mm)	b_0	b_1	n	r^2
Ephemeroptera									
Ameletidae									
Ameletus inopinatus Eaton	Brittain (1978)	Norway	Frozen in water, dried 3 h at 70 °C	DM vs BL	7.0–13	0.00224	2.90	26	0.81
Siphlonuridae									
Siphlonurus lacustris Eaton	Brittain (1978)	Norway	Frozen in water, dried 3 h at 70 °C	DM vs BL	3.0–17	0.000319	3.85	80	0.99
Baetidae									
Baetis	Benke & Jacobi (1986, 1994)	GA, USA	Fresh	DM vs HW	NA	1.27	3.33	49	0.96
	Breitenmoser-Würsten & Sartori (1995)	Switzerland	Presumably ethanol-preserved, dried ≈ 36 h at 70 °C	DM vs BL	NA	0.0100	2.55	NA	0.94
B. macani Kimmins	Brittain (1978)	Norway	Frozen in water, dried 3 h at 70 °C	DM vs BL	8.0–10	0.0147	2.10	12	0.96
B. pygmaeus (Hagen)	Lauzon & Harper (1988)	S Québec, Canada	NA	DM vs BL	NA	0.00395	2.38	NA	NA
B. quilleri	Fisher & Gray (1983)	AZ, USA	Presumably fresh, dried? h at? °C	DM vs BL	2.0–4.4	0.00517	2.83	12	0.94
Callibaetis floridanus Banks	Christman & Voshell (1992)	VA, USA	Formalin/ethanol-preserved	DM vs HW	≈ 0.45–1.7	0.351	2.69	16	0.97
Cloëon dipterum (L.)	Cianciara (1980)	E Poland	Formalin-preserved, dried to constant mass at 50 °C	DM vs BL	2.0–8.4	0.0010	3.68	1096	0.95
				DM vs HW	0.25–1.0	0.590	2.93	712	0.85
					0.90–1.3	0.956	3.28	384	0.73
Isonychiidae									
Isonychia spp.	Benke & Jacobi (1994)	GA, USA	Fresh	DM vs BL	NA	0.00306	2.92	123	0.97
Heptageniidae									
Ecdyonurus venosus group (Fabricius)	Wenzel *et al*. (1990)	SW Germany	Frozen in liquid nitrogen, dried 48 h at 50 °C	DM vs BL	NA	0.00430	3.35	58	0.98
				DM vs HW		0.121	3.13	65	0.97
Epeorus sylvicola	Wenzel *et al*. (1990)	SW Germany	Frozen in liquid nitrogen, dried 48 h at 50 °C	DM vs BL	NA	0.00874	2.89	30	0.97
				DM vs HW	NA	0.161	3.63	37	0.94
Heptagenia sp.	Benke & Jacobi (1994)	GA, USA	Fresh	DM vs HW	NA	0.186	2.94	11	0.98
Rhithrogena	Breitenmoser-Würsten & Sartori (1995)	Switzerland	Presumably ethanol-preserved, dried ≈ 36 h at 105 °C	DM vs BL	NA	0.0138	2.56	NA	0.96
R. jejuna Eaton	Kovalak (1978)	MI, USA	Formalin/ethanol-preserved	DM vs HW	0.6–2.4	0.128	3.59	≈ 110	NA
R. semicolorata group	Wenzel *et al*. (1990)	SW Germany	Frozen in liquid nitrogen, dried 48 h at 50 °C	DM vs BL	NA	0.00341	3.35	106	0.96
				DM vs HW	NA	0.139	3.80	106	0.92

Stenonema	Benke & Jacobi (1986, 1994)	GA, USA	Fresh	DM vs HW	NA	0.184	3.04	67	0.83
S. modestum (Banks)	Lauzon & Harper (1988)	S Québec, Canada	NA	DM vs BL	NA	0.00474	2.82	NA	NA
Ephemerellidae									
Drunella	Cummins (personal communication cited in Hawkins, 1986)	OR, USA	NA	DM vs BL	NA	0.00185	3.46	256	0.91
				DM vs HW	NA	0.434	3.62	256	0.92
Ephemerella spp.	Benke & Jacobi (1994)	–	Fresh	DM vs BL	NA	0.0124	2.51	32	0.86
E. deficiens Morgan	Kovalak (1978)	MI, USA	Formalin/ethanol-preserved	DM vs HW	0.4–1.2	0.404	3.36	≈ 70	NA
E. ignita (Poda)	Bass (1976)	Dorset, UK	Ethanol-preserved, dried 24 h at 105 °C	DM vs BL	0.7–8.0	0.0148	2.21	NA	0.98
E. lata Morgan	Kovalak (1978)	MI, USA	Formalin/ethanol-preserved	DM vs HW	0.7–1.4	0.299	3.25	≈100	NA
E. major Klapalek	Rosillon (1986)	Belgium	Formalin-preserved	WM vs BL	NA	0.0545	2.72	521	0.97
E. subvaria McDunnough	Waters & Crawford (1973)	MI, USA	Presumably fresh, centrifuged	WM vs BL	≈ 0.50–8.5	0.298	1.97	NA	0.99
	Kovalak (1978)	MI, USA	Formalin/ethanol-preserved	DM vs HW	0.3–2.0	0.475	3.36	≈ 160	NA
Eurylophella verisimilis (McDunnough)	Lauzon & Harper (1988)	S Québec, Canada	NA	DM vs BL	NA	0.00505	2.44	NA	NA
Tricorythidae									
Tricorythodes minutus Traver	McCullough *et al.* (1979)	ID, USA	Presumably fresh, dried? h at 50 °C	DM vs BL	2.5–6.0	0.00921	3.22	200	NA
Caenidae									
Caenis amica Hagen	Christman & Voshell (1992)	VA, USA	Formalin/ethanol-preserved	DM vs HW	≈ 0.30–1.1	0.188	3.22	17	0.98
Leptophlebiidae									
Habrophlebia lauta	Wenzel *et al.* (1990)	SW Germany	Frozen in liquid nitrogen, dried 48 h at 50 °C	DM vs BL	NA	0.00552	2.70	28	0.61
				DM vs HW	NA	0.869	3.17	36	0.47
H. vibrans Needham	Lauzon & Harper (1986)	S Québec, Canada	Presumably formalin-preserved, dried? h at 105 °C	DM vs BL	≈ 0.5–6	0.00349	2.42	NA	NA
	Lauzon & Harper (1988)	S Québec, Canada	NA	DM vs BL	NA	0.00284	2.49	NA	NA
Leptophlebia cupida (Say)	Clifford *et al.* (1979)	Alberta, Canada	Preserved, dried? h at? °C	DM vs BL	< 6.0	0.0045	2.23	NA	0.99
					>6.0	0.0002	4.01	NA	0.99
L. marginata (L.)	Brittain (1978)	Norway	Frozen in water, dried 3 h at 70 °C	DM vs BL	9.0–13	0.0000441	4.69	50	0.98
L. vespertina (L.)	Brittain (1978)	Norway	Frozen in water, dried 3 h at 70 °C	DM vs BL	4.0–11	0.000469	3.74	66	0.97
	Savage (1986)	Cheshire, UK	Fresh, dried 4 h at 105 °C	DM vs BL	≈ 1.1–8.0	0.00363	3.10	15	0.98
Paraleptophlebia mollis (Eaton)	Kovalak (1978)	MI, USA	Formalin/ethanol-preserved	DM vs HW	0.5–1.3	0.401	3.47	≈ 60	NA
Polymitarcyidae									
Ephoron album (Say)	Giberson & Galloway (1985)	Manitoba, Canada	Fresh	DM vs BL	≈ 1.0–14	0.002	3.05	NA	0.89
Ephemeridae									
Ephemera danica	Svensson (1977)	S Sweden	Fresh	DM vs BL	NA	0.00309	2.86	NA	NA

	Tokeshi (1985)	Norfolk, UK	Fresh, food-deprived for 48 h prior to drying	DM vs BL	NA	0.00316	2.86	NA	0.86
E. simulans Walker	Heise *et al*. (1988)	Manitoba, Canada	Formalin/ethanol-preserved	WM vs BL	NA	0.00614	3.13	33	0.99
Hexagenia limbata	Horst & Marzolf (1975)	KS, USA	Presumably fresh	WM vs BL	NA	0.0025	2.72	NA	0.94
	Heise *et al*. (1988)	Manitoba, Canada	Formalin/ethanol-preserved	WM vs BL	NA	0.0101	2.99	80	0.99
	Welch & Vodopich (1989)	TX, USA	Preserved, dried 24 h at 100 °C	DM vs BL	NA	0.000616	3.31	430	NA
	Edsall *et al*. (1991)	Great Lakes, Canada/USA	Fresh, dried 6 h at 100 °C, relationship uses preserved BL not fresh BL	DM vs BL	NA	0.000894	3.16	186	0.97
Odonata									
Aeshnidae									
Aeshna grandis L.	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	15–38	0.0623	2.68	13	NA
				DM vs HW	3.4–9.2	1.02	3.12	15	NA
Corduliidae									
Cordulia aenea L.	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried? h at ? °C	DM vs BL	1.7–21	0.0629	2.92	100	NA
				DM vs HW	0.57–6.7	0.0216	3.15	100	NA
Somatochlora aenea (L.)	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	8.5–20	0.0882	2.85	20	NA
				DM vs HW	2.9–6.6	0.248	2.97	20	NA
Libellulidae									
Sympetrum scoticum Donovan	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	2.7–18	0.0932	2.73	150	NA
				DM vs HW	1.5–5.6	0.496	3.39	50	NA
Lestidae									
Lestes sponsa (Fabricius)	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	4.9–21	0.00745	2.97	30	NA
				DM vs HW	1.0–3.2	0.609	3.44	30	NA
Coenagrionidae									
Coenagrion hastulatum Charpentier	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	1.8–22	0.0248	2.65	180	NA
				DM vs HW	1.0–3.2	0.616	3.23	40	NA
C. pulchellum (Van der Linden)	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	9.1–13	0.0918	2.10	27	NA
Erythromma naja (Hansemann)	Pavlov & Zubina (1990)	NW Russia	Presumably fresh, dried ? h at ? °C	DM vs BL	14–21	0.107	2.08	42	NA
				DM vs HW	0.7–3.7	0.838	3.17	107	NA
Pyrrhosoma nymphula (Sulzer)	Lawton (1971)	Durham, UK	NA	DM vs BL	1.3–2.7	0.00490	3.00	≈ 65	NA
				DM vs BL	2.7–10	0.00661	2.73	≈ 120	NA
Plecoptera									
Peltoperlidae									
Tallaperla maria Needham & Smith	Stout (1990)	NC, USA	Fresh, dried 24 h at 50 °C	DM vs BL	≈ 1–11	0.0141	2.62	289	0.89
Nemouridae									
Amphinemura delosa (Ricker)	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	0.5–6.4	0.0478	1.43	113	0.99
				DM vs IOW	0.3–0.7	1.50	2.59	113	0.99
Prostoia completa (Walker)	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	1.0–6.8	0.0435	1.79	63	0.96
				DM vs IOW	0.4–1.1	2.32	3.34	63	0.96

Capniidae									
Allocapnia rickeri Frison	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	1.0–6.2	0.0197	1.83	55	0.98
				DM vs IOW	0.2–0.6	0.00381	7.78	55	0.95
Paracapnia angulata Hanson	Griffith *et al*. (1993)	WV, USA, SFR stream	Formalin-preserved, dried 24 h at 60 °C	DM vs HW	NA	0.497	2.43	NA	NA
		WV, USA, WS4 stream	Formalin-preserved, dried 24 h at 60 °C	DM vs HW	NA	0.549	3.09	NA	NA
		WV, USA, WS3 stream	Formalin-preserved, dried 24 h at 60 °C	DM vs HW	NA	0.712	3.51	NA	NA
		WV, USA, HSR stream	Formalin-preserved, dried 24 h at 60 °C	DM vs HW	NA	0.364	2.44	NA	NA
Perlidae									
Acroneuria evoluta	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	0.5–21	0.0281	2.36	152	0.98
				DM vs IOW	0.3–3.2	0.592	3.75	151	0.99
A. lycorias (Newman)	Eggert & Burton (1994)	MI, USA, Ford River	Ethanol-preserved, dried ? h at ? °C	DM vs BL	NA	0.0129	2.8	NA	0.97
		MI, USA, Peshekee River	Ethanol-preserved, dried ? h at? °C	DM vs BL	NA	0.0101	2.9	NA	0.97
Agnetina capitata	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	1.0–19	0.0297	2.30	152	0.98
				DM vs IOW	0.4–2.9	1.13	3.23	88	0.99
Neoperla spp.	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	0.9–12	0.0307	2.22	88	0.99
				DM vs IOW	0.3–1.9	1.17	2.55	88	0.99
Perlodidae									
Isoperla namata	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs BL	1.0–12	0.0552	1.79	125	0.99
				DM vs IOW	0.4–1.7	1.17	2.47	125	0.99
Isoperla signata	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	DM vs IOW	0.2–1.9	0.0842	2.64	0.99	
Megaloptera									
Sialidae									
Sialis lutaria L.	Brooker (1979)	Essex, UK	Formalin/ethanol-preserved, dried ? h at 100 °C	DM vs BL	NA	0.0039	2.86	42	0.98
	Giani & Laville (1973)	S France	Presumably both fresh and formalin-preserved, dried 18 h at 105 °C	DM vs HW	3.0–18	0.276	2.95	NA	NA
Corydalidae									
Corydalus cornutus	Roell & Orth (1991)	WV, USA	Fresh	WM vs HW	NA	0.00494	2.70	45	0.89
	Knight & Simmons (1975b)	MI, USA	Fresh, dried 48 h at 104 °C	DM vs BL	13–85	0.000576	3.28	1423	0.97
	Short *et al*. (1987)	TX, USA	Formalin-preserved, dried to constant mass at 50 °C	DM vs HW	0.7–9.4	0.947	2.91	NA	0.99
	Brown & Fitzpatrick (1978)	TX, USA	Presumably fresh, dried ? h at ? °C	DM vs HW	0.50–10	0.761	2.87	445	0.92

Nigronia serricornis	Knight & Simmons (1975a)	MI, USA	Fresh, dried 48 h at 104 °C	DM vs BL	10–45	0.000398	3.45	867	0.92
Trichoptera									
Polycentropodidae									
Polycentropus flavomaculatus (Pictet)	Bass *et al*. (1982)	S UK	Fresh, dried 24 h at 105 °C	DM vs BL	3–13	0.00266	2.76	19	0.98
Stenopsychidae									
Stenopsyche marmorata Navás	Kocharina (1989)	E Russia	Presumably formalin-preserved, dried to constant mass at 80 °C	DM vs BL	2.0–50	0.056	2.29	50	NA
Hydropsychidae									
Arctopsyche palpata Martynov	Kocharina (1989)	E Russia	Presumably formalin-preserved, dried to constant mass at 80 °C	DM vs BL	0.50–25	0.059	2.54	50	NA
Hydropsyche orientalis Martynov	Kocharina (1989)	E Russia	Presumably formalin-preserved, dried to constant mass at 80 °C	DM vs BL	0.50–13	0.039	2.42	50	NA
Rhyacophilidae									
Rhyacophila vao Milne	Dixon & Wrona (1992)	Alberta, Canada	Frozen, dried 48 h at 37 °C	DM vs HW	0.16–0.90	6.80	4.12	613	0.78
Glossosomatidae									
Glossosoma nigrior Banks	Kovalak (1978)	MI, USA	Formalin/ethanol-preserved	DM vs HW	0.15–0.65	0.329	3.02	≈ 100	NA
Brachycentridae									
Brachycentrus subnubilus Curtis	Majecki *et al*. (1997)	Poland	Formalin-preserved	WM vs BL	≈ 2–14	0.0232	2.74	34	NA
Limnephilidae									
Platycentropus radiatus Say	Stout (1990)	NC, USA	Fresh, dried 24 h at 50 °C	DM vs BL	≈ 1–12	0.00919	2.70	300	0.89
Diptera									
Chaoboridae									
Chaoborus flavicans (Meigen)	Dumont & Balvay (1979)	France	Formalin-preserved, dried 2 h at 110 °C	DM vs HW	1.5–4.0	0.000677	1.48	NA	0.89
				DM vs HW	4.0–6.0	0.0000533	3.49	NA	0.98
				DM vs HW	6.0–8.0	0.0000252	3.92	NA	0.98
				DM vs HW	8.0–12	0.0000010	5.47	NA	0.99
C. punctipennis (Say)	Eaton (1983)	NC, USA	Ethanol-preserved, dried 24 h at 105 °C	DM vs BL	NA	0.000453	2.43	NA	0.89
Chironomidae	Potter & Learner (1974)	Wales, UK	Ethanol-preserved, dried 72 h at 60 °C	DM vs BL	2–19	0.00113	2.73	NA	0.96
	Huryn & Wallace (1986)	GA, USA	Formalin-preserved, dried 12 h at 65 °C	AFDM vs BL	0.88–5.8	0.000452	3.10	70	0.81
Procladius cinereus Goetghebuer	Grzybkowska (1985)	Poland	Formalin-preserved	WM vs BL	≈ 2–8	0.0077	2.84	60	0.61
Diamesa spp.	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	0.51–9.90	.00197	2.60	327	0.98
Corynoneura sp.(lobata)	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.1–2.9	0.00147	2.10	116	0.99

Thienemanniella sp. (partita)	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.1–2.8	0.00409	2.01	746	0.96
Eukiefferiella brehmi/gracei group	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.4–5.2	0.00201	2.24	61	0.92
E. devonica group	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.6–4.7	0.00494	2.34	16	0.86
Orthocladius spp.	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.4–5.7	0.00197	2.26	30	0.91
Synorthocladius semivirens (Kieffer)	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.5–3.7	0.00530	2.11	47	0.96
Chironomus	Butler (1982)	Alaska	Presumably fresh, dried ? h at? °C	DM vs BL	5–9	0.000762	3.07	21	0.72
				DM vs BL	> 10	0.0000428	4.15	38	0.93
C. salinarius	Drake & Arias (1995)	SW Spain	Fresh, dried 48 h at 80 °C	DM vs BL	NA	0.0012	2.79	947	0.99
Polypedilum spp.	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.4–7.9	0.000669	2.60	32	00.94
Tribelos sp.	Fisher & Gray (1983)	AZ, USA	Presumably fresh, dried ? h at ? °C	DM vs BL	2.1–4.4	0.000281	4.16	12	0.96
Micropsectra sp. (*atrofasciata*)	Nolte (1990)	Germany	Fresh, BL measured from antenna base to procercus	AFDM vs BL	1.2–8.6	0.000662	2.59	696	0.98
Simuliidae									
Boophthora erythrocephalum De Geer	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.25–0.60	1.9	2.76	60	0.53
Eusimulium costatum (Friederichs)	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.30–0.65	1.5	2.04	9	0.64
E. cryophilum (Rubzov)	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.30–0.65	0.97	2.16	15	0.62
E. vernum (Macquart)	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.30–0.60	0.49	3.73	17	0.56
Odagmia spinosa (Doby & Deblock)	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.25–0.80	4.2	3.86	205	0.79
Prosimulium mixtum/fuscum	Merritt *et al*. (1982)	MI, USA	Fresh	DM vs BL	NA	0.00122	3.19	612	0.94
	Morin *et al*. (1988)	S Québec, Canada	Fresh, dried 48 h at 60 (C	DM vs BL	NA	0.00136	3.05	144	0.95
P. tomosvaryi (Enderlein)	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.30–0.85	1.30	2.36	66	0.45
Simulium spp.	Wotton (1978)	Durham, UK	Presumably ethanol-preserved, dried ? h at ? °C	DM vs BL	1.0–7.0	0.00171	2.88	NA	0.98

	Edwards & Meyer (1987)	GA, USA	Formalin/ethanol-preserved, dried ? h at ? °C	AFDM vs BL	NA	0.0031	2.6424	0.90	
S. equinum (L.)	Ladle *et al*. (1972)	Dorset, UK	Formalin/ethanol-preserved, presumably corrected for loss in mass, dried 24 h at 105 °C	DM vs BL	NA	0.00546	2.50	NA	NA
S. ornatum Meigen	Ladle *et al*. (1972)	Dorset, UK	Formalin/ethanol-preserved, presumably corrected for loss in mass, dried 24 h at 105 °C	DM vs BL	NA	0.00658	2.31	NA	NA
S. rostratum (Lundstroem)	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.20–0.60	3.8	4.07	93	0.74
S. vittatum	Morin *et al*. (1988)	S Québec, Canada	Fresh, dried 48 h at 60 °C	DM vs BL	NA	0.00119	3.65	123	0.95
Stegopterna mutata	Merritt *et al*. (1982)	MI, USA	Fresh	DM vs BL	NA	0.00042	3.83	169	0.94
	Morin *et al*. (1988)	S Québec, Canada	Fresh, dried 48 h at 60 °C	DM vs BL	NA	0.00118	3.22	67	0.99
Wilhelmia	Schröder (1987)	Germany	Fresh, dried 24 h at 45 °C	DM vs IOW	0.25–0.60	2.1	2.73	149	0.72
Tipulidae									
Pedicia hannai antenatta	MacLean (1973)	Alaska	Fresh, BL measured as maximum extended length in locomotion, freeze-dried	DM vs BL	7.0–22	0.000175	3.51	NA	0.99
Athericidae									
Atherix spp.	Neveu (1977)	S France	Fresh, gives WM to DM conversion	WM vs BL	3.0–25	0.0746	2.50	77	0.94

Appendix 2 Summary of published non-power relationships between mass and linear measurements for various aquatic insect taxa. For brevity, the relationships from those sources listed in Table 1 are not included. The formulae represent immature forms. Wet masses (WMs, mg) were determined after blotting, dry masses (DMs, mg) were determined after drying for 24 h at 60 °C, total body lengths (BLs, mm) were measured from the anterior margin of the head capsule to the posterior margin of the terminal abdominal segment (excluding setae and appendages) and head capsule widths (HWs, mm) were measured at the widest part of the head unless otherwise indicated. Some studies used ash-free dry mass (AFDM, mg) instead of dry mass and some used labium length (LL, mm) instead of head width. The sample sizes (n) represent the total number of individual organisms used in building relationship, even if these were grouped prior to mass determination. Coefficients of determination (r^2) may be based on sample sizes < n if the relationship was fitted to means rather than individual data points; (NA) data not available

Taxon	Source	Locality	Sample treatment	Length range (mm)	Relationship
Ephemeroptera					
Potamanthidae					
Potamanthus luteus (L.)	Obrdlík *et al.* (1979)	Czech Republic	Formalin-preserved, dried ? h at ? °C	NA	$DM = 0.00551 + 0.00188 \cdot BL + 0.00018 \cdot BL^2$ (n = 112, r^2 = ?)
Odonata					
Gomphidae					
Heliogomphus scorpio Ris	Dudgeon (1989)	Hong Kong	Presumably fresh, gut contents removed, dried ? h at ? °C	NA	$\log_e DM = -1.73 + 1.30 \cdot LL$ (n = 155, r^2 = 0.93)
Onychogomphus sinicus Chao	Dudgeon (1989)	Hong Kong	Presumably fresh, gut contents removed, dried ? h at ? °C	NA	$\log_e DM = -1.45 + 1.35 \cdot LL$ (n = 165, r^2 = 0.94)
Lestidae					
Pyrrhosoma nymphula	Lawton (1971)	Durham, UK	NA	12–15	$DM = -29.9 + 2.90 \cdot BL$ (n = ?, r^2 = ?)
Plecoptera					
Perlodidae					
Isoperla signata	Jop & Stewart (1987)	OK, USA	Fresh, centrifuged, dried 24 h at 105 °C	0.7–13	$\log_e DM = -2.37 + 0.392 \cdot BL$ (n = 47, r^2 = 0.97)
Diptera					
Chironomidae					
Macropelopia nebulosa (Meigen)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	$AFDM = (0.149 + 0.0836 \cdot BL)^3$ (n = 39, r^2 = 0.88)
Procladius islandicus (Goetghebuer)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	$AFDM = (0.0441 + 0.0833 \cdot BL)^3$ (n = 69, r^2 = 0.88)
Cricotopus sylvestris (Fabricius)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	$AFDM = (0.0603 + 0.0791 \cdot BL)^3$ (n = 48, r^2 = 0.92)
C. tibialis Meigen	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	$AFDM = (0.0968 + 0.0688 \cdot BL)^3$ (n = 13, r^2 = 0.88)
Orthocladius (*Pogonocladius*) *consubrinus* (Holmgren)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	$AFDM = (0.0675 + 0.0803 \cdot BL)^3$ (n = 52, r^2 = 0.90)
O. oblidens (Walker)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	$AFDM = (0.0375 + 0.0988 \cdot BL)^3$ (n = 31, r^2 = 0.92)

Psectrocladius barbimanus (Edwards)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	AFDM = $(0.0652 + 0.0765 \cdot BL)^3$ (n = 70, r^2 = 0.92)
Chironomus anthracinus Zett	Johnson (1984)	Sweden	Preserved, corrected for loss in mass, BL measured to tip of anal gills, dried 2 h at 60 °C	NA	$\log_e$AFDM = –2.39 + 0.123 · BL (n = ?, r^2 = ?)
C. islandicus Kieffer	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	AFDM = $(0.0258 + 0.0618 \cdot BL)^3$ (n = 152, r^2 = 0.96)
C. plumosus L.	Johnson (1984)	Sweden	Preserved, corrected for loss in mass, BL measured to tip of anal gills, dried 2 h at 60 °C	NA	$\log_e$AFDM = –1.77 + 0.0735 · BL (n = ?, r^2 = ?)
Pseudochironomus richardsoni Malloch	Gresens (1997)	CA, USA	Fresh, dried ? h at ? °C	NA	$\log_e$AFDM = –5.14 + 0.499 · BL (n = 106, r^2 = 0.88)
Tanytarsus gracilentus (Holmgren)	Lindegaard & Jónasson (1979)	Iceland	Formalin-preserved	NA	AFDM = $(0.0442 + 0.0879 \cdot BL)^3$ (n = 135, r^2 = 0.94)
Stratiomyidae					
Hedriodiscus truquii (Bellardi)	Stockner (1971)	WA, USA	Fresh	≈ 9.0–35	WM = –46.9 + 6.02 · BL (n = ?, r^2 = 0.84)