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Abstract. We assessed the relative magnitude of various factors (year, preservation method, continent, investigator, and taxonomic level) affecting prediction of invertebrate dry mass (DM) in light of the variability of assessments of invertebrate density. We developed 34 length (L)–DM relationships for Oligochaeta and 17 freshwater invertebrate families belonging to Mollusca, Crustacea, and Insecta. Comparison of our predicted DM for reference-size individuals with values from 120 other published equations revealed that 31% of predicted values were within our 95% CI and 73% were within a 2× DM range (i.e., between 0.5× and 2×). Interannual differences in exponent (slope) or scale factor (intercept) of L–DM relationships were detected for 6 of the 7 taxa investigated, but represented only 3% of total variance in predicted DM. Similarly, preservation methods and measured body dimension each accounted for a small (0–3%) fraction of total variance. Variation among investigators (12–50%) and continents (1–17%) were more important and might have reflected methodological or regional and latitudinal differences. Increasingly precise taxonomical levels explained progressively lower proportions of the total variance, a result indicating that family or a more precise taxonomic level provided a robust estimate of most invertebrate DM even if the equations were derived from other sites. However, overall variability induced by L–DM relationships was smaller than variability in total invertebrate density among replicate samples (coefficient of variation [CV] = 19–97%), a result indicating that more effort should be devoted to improving the accuracy of invertebrate density estimates than to developing site-specific L–DM relationships to assess benthic biomass in freshwater.

Key words: freshwater benthic invertebrates, biomass, length–dry mass relationships, ash-free dry mass, comparison of model predictions, variance component, total density.

Assessment of invertebrate biomass is an important component of quantification of secondary production, energy budgets, trophic dynamics, and C cycling in aquatic ecosystems. At the community level, density alone is not a reliable indicator of habitat productivity, especially considering the generally negative relationship between density and body size across organisms

within aquatic communities (Cyr et al. 1997). Biomass usually is derived from an assessment of abundance, either directly from weighing the enumerated organisms (to obtain dry mass [DM]) or determination of their biovolume, or indirectly from measurement of linear body dimensions (L) to apply mass-conversion equations. Estimation of biomass from linear body dimensions is generally simpler and more accurate than direct measurement techniques (Stoffels et al. 2003). Biomass assessment typically is associated with 2 types of error: 1) sampling error in the total numbers and size distribution of organisms resulting from site-specific variability and 2) prediction error, including that arising from the use of a length–mass relationship developed for other times, places, populations, or species (Kimmerer et al. 2005).

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A number of environmental factors have been invoked to explain differences in L–DM relationships for a given taxon, leading to the development of a large number of such relationships. Variations in L–DM relationships for populations of the same species have been reported from different locations within the same watershed (González et al. 2002), but not consistently (Smock 1980). Such differences were attributed to physicochemical environment, trophic conditions, or genetic variation (Benke et al. 1999). Differences in the regressions for related invertebrates in streams and in the littoral zone of lakes suggest that equations should be restricted to the same region or water bodies with similar abiotic conditions (Baumgärtner and Rothhaupt 2003).

We focused on the macroinvertebrate assemblages found in the shallow, slow-flowing littoral zone of Lake Saint-Pierre (St. Lawrence River, Quebec, Canada). Comparatively little attention has been devoted to macroinvertebrate assemblages from river ecosystems in northern latitudes compared to planktonic assemblages from southern, lacustrine environments. Regression models for predicting biomass are more commonly available for lotic than lentic macroinvertebrate communities (Stoffels et al. 2003). Thus, we thought it important to develop specific L–DM relationships for the most common littoral macroinvertebrates in this large fluvial system to assess their variability locally and compared to previously published L–DM models.

Our initial objective was to develop L–DM relationships and to assess the proportion of organic (ash-free) mass for the major groups of macroinvertebrates of Lake Saint-Pierre to enable limnologists to transform invertebrate density into biomass estimates, which are more suitable for ecosystem studies. Analysis of samples collected in 2004 and 2006 also allowed us to evaluate interannual variability in L–DM relationships for 7 taxa. We compared our predictions of invertebrate DM for a given reference size to those published in earlier studies to quantify the proportion of variance in predicted DM associated with different taxonomic levels, preservation methods, continents of origin, and investigators. Last, we examined the variability in predicted DM caused by using different equations in the broader perspective of the inherent variability in density assessment to ascertain where effort should be allocated to assess the biomass of invertebrate assemblages properly.

Methods

Study area

Lake Saint-Pierre (LSP) is a large (~300 km^2) shallow (mean depth ≈ 3 m) fluvial lake of the St. Lawrence River. Littoral habitats of LSP consist of large beds of emergent and submerged aquatic vegetation subjected to a wide range (<0.1–1.5 m/s) of current speed, from lacustrine to fast-flowing conditions. This reach of the St. Lawrence River is under the influence of waters originating from Lake Ontario, the Ottawa River, and a number of smaller tributaries draining farmlands, which results in differences in water quality among neighboring locations (Hudon and Carignan 2008). Littoral habitats also support rich macroinvertebrate assemblages whose density, biomass, composition, and size structure vary spatially with water quality and habitat characteristics (Tessier et al. 2007, Tourville Poirier et al. 2010). Aquatic invertebrates are a major component of LSP ecosystems and are used to monitor changes in water quality and ecosystem health (Tall et al. 2008, Environment Canada 2010).

Sampling and laboratory analyses

We collected invertebrate samples in September–October 2004 and 2006 in emergent and submerged macrophyte beds of LSP (lat 46°10′N, long 72°50′W) with either a core sampler, a D-frame net (400-µm mesh), or a plastic box (volume = 5.7 L; Downing and Cyr 1985) with a 400-µm-mesh sieve. We preserved invertebrates (95% ethanol), stained (5% rose Bengal), and sorted them prior to identification. We identified taxa belonging to Mollusca, Crustacea, and Insecta to the family level, but we treated Oligochaeta as a single group (see Environment Canada 2010).

We obtained L–DM relationships of preserved specimens for the most commonly observed (>10% of individuals or present in >10% of samples) invertebrate groups in LSP. For most taxa, we measured total body length (BL) or shell height (SH, Gastropoda) (Table 1). We developed additional relationships with linear measurements of other morphometric characteristics, such as head capsule width (HW, Insecta), head height (HH, Gammaridae), or shell aperture width (AW, Gastropoda), to allow estimation of biomass of individuals with incomplete BL or SH (Stoffels et al. 2003). We selected individuals used for the L–DM measurements from several samples from different sites to cover the broadest size range available for each year. We measured the dimensions of preserved animals to the nearest 0.1 mm under a dissecting microscope (MZ12, Leica Microsystems, Wetzlar, Germany) fitted with a calibrated ocular micrometer. We digitized measurements of Oligochaeta and Crustacea (Amphipoda:Gammaridae and Isopoda:Asellidae) with an image analyzer (Image-Pro Plus, version 4.1; Media Cybernetics, Bethesda, Maryland).

TABLE 1. Description of the linear body dimensions (L) measured in mm for each taxon. BL = body length, SH = shell height, SW = shell width, AW = shell aperture width, HW = head width, HH = head height.

Class	Order	Family	L	Remarks
Oligochaeta			BL	Specimens with prostomium and pygidium were considered complete, and their entire body length was measured with a digitizer; curved individuals were measured with consecutive linear segments
Mollusca	Gastropoda	Ancylidae, Bithyniidae, Hydrobiidae, Physidae, Valvatidae, Viviparidae	SH	Height of the shell along its longest axis
Mollusca	Gastropoda	Ancylidae, Bithyniidae, Hydrobiidae, Planorbidae, Valvatidae, Viviparidae	AW	Width of shell aperture along its longest axis
Mollusca	Gastropoda	Planorbidae	SW	Maximum width of the shell lying on its side
Crustacea	Isopoda	Asellidae	BL	Measured from the anterior part of the head to the tip of the telson with a digitizer; curved individuals were measured with consecutive linear segments
Crustacea	Isopoda	Asellidae	HW	Head width measured as a straight line between the eyes with a digitizer
Crustacea	Amphipoda	Gammaridae	BL	Digitized following the curve of the body with consecutive linear segments from the anterior rostrum to the base of the telson
Crustacea	Amphipoda	Gammaridae	HH	Length between the posterior margin of the head and the mouth parts
Insecta	Ephemeroptera, Odonata, Hemiptera, Trichoptera, Lepidoptera, Diptera		BL	Distance between the anterior part of the head and the posterior part of the last abdominal segment without including caudal appendices; case-bearing caddisflies were extracted from their case
Insecta	Ephemeroptera, Odonata, Hemiptera, Trichoptera Lepidoptera, Diptera		HW	Width at the broadest part of the head capsule

We measured DM of organisms after measuring their dimensions. We placed intact, clean individuals on preweighed, precombusted (13-mm) glass microfiber filters (GFF). For smaller organisms (chironomids, oligochaetes), we used the same procedure with 5 individuals of similar length/GFF. We dried filters and organisms for 24 h at 50°C, transferred them to a desiccator (1 h), and weighed them (±1 µg) on a Cahn 26 microbalance (Orion Research Inc., Beverly, Massachusetts). Gastropod DM included shell because shell removal could have damaged small specimens (1.5–4.1 mm) and reduced the accuracy of the individual DM values.

Ash-free DM

We measured the ash content of organisms by weighing individuals after combustion at 500°C for 24 h and obtained ash-free DM (AFDM) by subtracting ash mass from DM. Our use of AFDM allowed us to account for the mass of inorganic constituents for each group of invertebrates. For example, gastropod shell mass can represent a significant proportion of their total DM. For each group of invertebrates, we estimated the ratio of AFDM/DM by calculating the ratio of the sum of all individual values of AFDM and DM (rather than the mean of individual ratios). We chose this method because it minimizes the relative influence of the smallest individuals, for which the error of AFDM measurement is probably most important, when calculating the ratio.

Data analysis

We $\log_{10}(x)$-transformed invertebrate L and DM measurements before calculating L–DM relationships

with linear least squares regression (SAS, version 9.2; SAS Institute, Cary, North Carolina). We used all data available (2004 and 2006) to obtain estimates of the slope (b) and intercept (a) of the regression equations between $\log_{10}(x)$-transformed body dimension (BL, SH, HH, HW, or AW; mm) and $\log_{10}(x)$-transformed DM (mg) for each taxon. All relationships were estimated in the form:

$$\log_{10}DM = \log_{10}a + b(\log_{10}L)$$

We excluded observations that generated studentized residuals >3 as outliers. We investigated possible variations in the L–DM relationships of organisms collected in different years with analysis of covariance (ANCOVA; including separate slopes analysis; SAS, version 9.2). We avoided the potential effect of interannual differences in the range of body dimensions by using only the size range for which data from both years overlapped in the multiple regression lines.

Back-transformation of means or predicted values from linear log-transformed data models underestimates the true location statistics on the original scale (Bird and Prairie 1985, Stoffels et al. 2003). We estimated the magnitude of this bias as the factor corresponding to Duan's (1983) *smearing estimate* for every regression model because it was the simplest (a multiplicative factor of predicted values) and most robust correction factor (Smith 1993).

Assessment of factors inducing variability in predicted DM

Predicted invertebrate DM (mg) published in earlier studies (see Appendix S1 for equations and references; available online from: http://dx.doi.org/ 10.1899/11-120.1.s1) were presented in the form:

$$DM = aL^b$$

We compared predicted DM values derived from our equations with values predicted by equations developed by other investigators by assessing the predicted DM of an organism of a given size (reference size) with all available equations. We used a reference size in the middle of the common size range from all studies to avoid extreme sizes where the coefficient of variation (CV) is largest (Johnston and Cunjak 1999). For each taxon, we calculated *relative predicted DM* as the ratio of expected DM values predicted with other equations with the value obtained with our equations (predicted value ± 95% confidence interval [CI]) to visualize their distribution and relative magnitude.

We assessed the relative contribution of different environmental factors to the variability in predicted DM with variance component analysis (JMP, version 8.0; SAS Institute, Cary, North Carolina) on 4 subsets of data for which a sufficient number of equations were available. These equations included equations from our study ($n = 14$; effects of year, class, and body dimension), Insecta ($n = 76$; effects of family, continent, and investigator), Chironomidae ($n = 44$; effects of subfamily, preservation method, continent, and investigator), and Amphipoda ($n = 12$; effects of genus, preservation method, and investigator). We used relative predicted DM values for the analysis of our study and Insecta subsets when comparisons involved organisms covering a wide range of sizes (among different classes or families). We $\ln(x)$-transformed all values before analysis to ensure homoscedasticity. We calculated within-subset CV (%) as $100(e^{\sigma} - 1)$.

We assessed within- and among-site variability in total invertebrate density from the mean and variance among replicate samples collected in LSP with D-frame nets in August 2004 (Tall et al. 2008; $n = 9$ sites, 3 replicate samples/site) and August–September 2006 (Tourville Poirier 2009; $n = 12$ sites, 5 replicate samples/site). We estimated the constant CV (% σ/ mean) of total invertebrate densities among replicate samples with a log–log regression between mean and variance after checking that the slope did not differ significantly from 2. We restricted our analysis to total invertebrate density to maximize its range after noting that abundant taxa had similar variance to mean relationships.

Results

L–DM relationships

We estimated 34 L–DM relationships for Oligochaeta and 17 invertebrate families belonging to Mollusca, Crustacea, and Insecta (Table 2). All relationships but 1 (Tipulidae HW) were significant and explained between 11.8 (Caenidae HW) and 97.7% (Physidae SH) of the variance of individual data sets. Intercepts ($\log_{10}a$) ranged from −3.52 (Ceratopogonidae BL) to 0.41 (Ceratopogonidae HW), and slopes (b) ranged from 0.87 (Caenidae HW) to 3.51 (Pyralidae HW). All relationships obtained for gastropods, derived either from AW or SH measurements, explained a high proportion of variance in DM ($r^2 > 0.91$). Relationships predicting DM of crustaceans performed equally well from measurements of BL, HW (Isopoda, $r^2 > 0.90$), or HH (Amphipoda, $r^2 > 0.92$). For insects, relationships predicting DM derived from BL generally were stronger than those from HW, except for Leptoceridae (Table 2). L–DM relationships

TABLE 2. Parameters of the regression equations ($\log_{10}DM = \log_{10}a + b[\log_{10}L]$) predicting dry mass (DM, mg) from linear body dimension (L, mm) for Lake Saint-Pierre invertebrates, using combined data for 2004 and 2006. For each taxon and body dimension, values are given for the number of observations (n), size range (minimum [Min], maximum [Max]), y-axis intercept ($\log_{10}a$) and standard error (a SE), slope (b) and standard error (b SE), coefficient of determination (r^2), root mean square residual (RMSE), and the correction factor to convert $\log_{10}$ predicted DM values to mass (smearing factor; Duan 1983). Body dimensions include total body length (BL), head height (HH), head width (HW), shell aperture width (AW), and shell height (SH). All relationships are highly significant ($p < 0.001$) except for Caenidae HW ($p = 0.03$) and Tipulidae HW ($p = 0.1$; indicated as n.s.). Percent ash-free dry mass relative to total dry mass (% AFDM) is shown with the number of individuals measured (n).

Eq.	Taxon	L	n	Min	Max	$\log_{10}(a)$	a SE	b	b SE	r^2	RMSE	Smearing factor	% AFDM (n)
1	Oligochaeta	BL	47	1.96	62.1	−2.23	0.11	1.54	0.12	0.777	0.2624	1.20	76.4 (46)
	Mollusca/Gastropoda												
2	Ancylidae	AW	134	0.80	5.9	−1.54	0.02	2.70	0.04	0.965	0.1282	1.04	
3	Ancylidae	SH	90	0.42	3.7	−1.01	0.02	3.13	0.08	0.945	0.1676	1.08	34.4 (82)
4	Bithyniidae	AW	19	1.25	4.1	−0.11	0.06	2.76	0.16	0.943	0.1006	1.02	
5	Bithyniidae	SH	77	1.80	7.8	−0.57	0.05	2.50	0.09	0.912	0.0958	1.02	17.8 (17)
6	Hydrobiidae	AW	91	0.38	1.9	−0.05	0.01	2.48	0.06	0.945	0.1041	1.03	
7	Hydrobiidae	SH	153	0.80	4.6	−0.74	0.02	2.82	0.05	0.957	0.1160	1.04	27.1 (83)
8	Physidae	SH	50	1.98	10.3	−1.34	0.05	3.05	0.07	0.977	0.0924	1.02	
9	Planorbidae	AW	34	0.28	8.9	−0.04	0.04	2.65	0.10	0.953	0.2125	1.12	
10	Planorbidae	SW	93	0.70	17.0	−1.12	0.03	2.90	0.05	0.969	0.1289	1.04	17.9 (28)
11	Valvatidae	SH	59	1.52	3.7	−0.93	0.05	3.18	0.12	0.921	0.0808	1.02	
12	Viviparidae	SH	59	2.08	15.2	−0.64	0.07	2.60	0.09	0.932	0.1613	1.07	
	Crustacea/Isopoda												
13	Asellidae	BL	133	1.72	11.4	−2.11	0.06	2.60	0.07	0.908	0.1702	1.08	68.0 (95)
14	Asellidae	HW	88	0.35	1.5	−0.05	0.02	3.39	0.12	0.903	0.1847	1.09	
	Crustacea/Amphipoda												
15	Gammaridae	BL	148	1.81	13.0	−2.17	0.05	2.39	0.05	0.929	0.1437	1.05	73.1 (95)
16	Gammaridae	HH	93	0.29	1.6	−0.11	0.02	3.00	0.08	0.939	0.1471	1.06	
	Insecta/Ephemeroptera												
17	Caenidae	BL	40	1.13	4.8	−2.28	0.06	2.70	0.14	0.902	0.1386	1.05	92.9 (39)
18	Caenidae	HW	39	0.24	0.9	−0.87	0.14	0.87	0.39	0.118	0.4198	1.57	
	Insecta/Odonata												
19	Coenagrionidae	BL	23	1.50	13.3	−2.31	0.13	2.53	0.14	0.935	0.1629	1.06	98.6 (24)
20	Coenagrionidae	HW	24	0.60	2.8	−0.82	0.10	2.65	0.31	0.768	0.3040	1.32	
	Insecta/Hemiptera												
21	Corixidae	BL	45	2.17	8.3	−2.33	0.09	3.31	0.14	0.928	0.1169	1.04	96.1 (43)
22	Corixidae	HW	49	0.83	2.8	−0.65	0.05	3.14	0.23	0.802	0.1995	1.10	
	Insecta/Trichoptera												
23	Leptoceridae	BL	30	1.68	9.2	−2.14	0.17	2.34	0.31	0.673	0.3029	1.25	97.0 (29)
24	Leptoceridae	HW	30	0.16	0.7	0.02	0.12	2.31	0.27	0.716	0.2819	1.19	
	Insecta/Lepidoptera												
25	Pyralidae	BL	25	1.67	15.0	−1.70	0.14	1.95	0.16	0.859	0.2319	1.14	97.5 (24)
26	Pyralidae	HW	23	0.42	1.4	0.16	0.08	3.51	0.42	0.767	0.3032	1.24	
	Insecta/Diptera												
27	Ceratopogonidae	BL	22	2.03	9.8	−3.52	0.18	2.70	0.23	0.875	0.1460	1.05	
28	Ceratopogonidae	HW	22	0.09	0.2	0.41	0.44	2.41	0.57	0.471	0.2978	1.22	
29	Chironomidae larvae	BL	102	1.50	15.8	−2.40	0.08	1.99	0.12	0.736	0.2543	1.17	89.4 (56)
30	Chironomidae larvae	HW	62	0.09	0.6	0.19	0.16	2.30	0.25	0.581	0.3690	1.34	
31	Chironomidae pupae	BL	13	1.75	3.8	−2.34	0.22	2.53	0.47	0.728	0.1508	1.05	94.9 (13)
32	Chironomidae pupae	HW	14	0.20	0.8	−0.52	0.14	1.48	0.31	0.661	0.2020	1.10	
33	Tipulidae	BL	22	2.32	11.7	−2.52	0.34	2.44	0.44	0.605	0.3422	1.34	87.9 (22)
34	Tipulidae	HW	22	0.20	0.8	−0.25	0.28	$1.14^{n.s.}$	0.65	0.133	0.5073	2.10	

derived for body parts (HH, HW, or AW) had a smaller range of variation with DM than BL.

Slopes derived from BL–DM relationships ranged from 1.54 (Oligochaeta) to 3.31 (Corixidae). Slopes derived from body-part–DM relationships ranged from 0.87 (Caenidae) to 3.51 (Pyralidae). Worm-shaped invertebrates (Oligochaeta, Diptera larvae) had lower slopes ($b \leq 2$) than thicker-bodied insect families (Corixidae, Pyralidae) or sphere-shaped gastropods (Ancylidae, Physidae, or Valvatidae) ($b \geq 3$).

Duan's (1983) smearing factor, a multiplier of the transformed predicted DM accounting for the bias

TABLE 3. Results of the between year (2004 vs 2006) comparison of intercepts ($\log_{10}a$) and slopes (*b*) for the regression equations ($\log_{10}DM = \log_{10}a + b[\log_{10}L]$) predicting dry mass (DM) from linear body dimension (L, mm) of invertebrates sampled in Lake Saint-Pierre for the overlapping ranges of body size sampled in both years (*n* = number of observations). The probability of difference between the 2 years for the intercepts ($\log_{10}a$) and slopes (*b*) are shown. The DM predicted (pred) from L–DM relationships for 2004 and 2006 is provided for an individual organism of a reference size (Ref, mm) in the middle of the observed size distribution. Analysis of covariance (ANCOVA) is not possible for cases in which the slopes (*b*) of the regression equations differ significantly (probability of interannual difference in slope [*p*] < 0.05), thus not fulfilling the prerequisite conditions for ANCOVA.

| | | *n* | | $\log_{10}a$ | | *b* | | *p* | | | Pred DM | | |
| | | 2004 | 2006 | 2004 | 2006 | 2004 | 2006 | $\log_{10}a$ | *b* | | 2004 | 2006 | |
Taxon	L	2004	2006	2004	2006	2004	2006	$\log_{10}a$	*b*	Ref	2004	2006	ANCOVA?
Gammaridae	BL	83	54	−2.30	−1.75	2.54	1.93	0.038	<0.001	5	0.30	0.40	No
Asellidae	BL	32	37	−1.31	−0.36	1.66	0.69	0.005	0.047	5	0.71	1.32	No
Hydrobiidae	SH	40	49	−0.89	−0.44	3.11	2.24	<0.001	<0.001	2	1.10	1.71	No
Planorbidae	SW	24	60	−1.03	−1.04	2.57	2.80	<0.001	0.035	3	1.55	2.01	No
Ancylidae	AW	58	46	−1.50	−1.66	2.66	2.84	0.004	0.189	3	0.59	0.51	Yes
Bithyniidae	SH	16	57	−0.82	−0.59	2.91	2.59	0.005	0.169	3	3.75	4.44	Yes
Chironomidae larvae	BL	57	43	−2.52	−2.24	2.17	1.77	0.645	0.127	3.3	0.04	0.04	Yes

induced by the use of log-transformation, ranged from 1.02 (Bithyniidae SH) to 2.1 (Tipulidae HW) (Table 2). Most values (26 of 34) were ≤1.20, indicating that predicted DM values were generally within 20% of those derived from uncorrected equations.

Proportion of organic matter

We estimated the proportion of organic matter assessed from the ratio of AFDM/DM for 15 taxa (Table 2). Organic mass made up ~76% of Oligochaeta DM. Gastropoda organic mass was ~18 and ~34% of DM, depending on the relative importance of their mineral shell. The highly mineralized shell of Bithyniidae and Planorbidae reduced their % organic matter (~18%) in contrast with the more delicate shell of Ancylidae (~34%). Crustacea and Insecta generally had high % organic matter (>68%) because of their relatively low mineral content.

Comparison of L–DM relationships over different years

Separate relationships predicting DM from L for the same taxa sampled in 2004 and 2006 could be calculated in 7 cases for which a sufficient number of organisms were available. We used these samples to assess interannual differences in slope and intercept (Table 3). Examination of the data points for each organism revealed the issues commonly encountered with such comparisons (Fig. 1A–G). BL–DM regressions for Amphipoda sampled in 2004 and 2006 had differing slopes and intercepts (Table 3) although the overlapping size range for both years spanned over an order of magnitude (Fig. 1A). In the absence of a

justification to prefer one year over the other, we calculated a single BL–DM regression line for Amphipoda (Table 2) with all available data points, including 11 values outside the overlapping size range of 2004 and 2006 (*n* = 148; Table 2). Predicted DM for a 5-mm-long gammarid amphipod was 0.32 mg (all data points; Appendix S1), in contrast with 0.30 and 0.40 mg from equations derived for 2004 and 2006 data, respectively (Table 3).

We applied the same rationale to Isopoda, Hydrobiidae, and Planorbidae L–DM relationships, which showed significant interannual differences in both slopes and intercepts (Table 3). However, in these 3 cases, the size ranges of 2004 and 2006 overlapped only partially and included some outlying values (Fig. 1B–D). For each of these 3 organisms, including all available data points in a single regression line (Table 2, Appendix S1) markedly increased the size range and yielded better-fitted (higher r^2) relationships that were representative of all available data. An extreme example of the bias induced by using a narrow size range is that of DM predicted for a 5-mm-long Isopoda (1.39 mg and 2.58 mg for 2004 and 2006 data, respectively) derived from the relatively narrow BL range (overlapping range of 6.1–10.4 mm for 2004–2006, $r^2 = 0.39$). These values contrast sharply with the 0.51 mg DM predicted for the same size Isopoda derived from the regression line using all data points (1.7–11.4 mm BL; Fig. 1B), with a corresponding rise in r^2 to 0.91 (Table 2, Appendix S1).

The relationships predicting DM from Ancylidae AW (Fig. 1E) and Bithyniidae SH (Fig. 1F) did not differ significantly in slope (Table 3), allowing a formal ANCOVA of interannual differences in DM
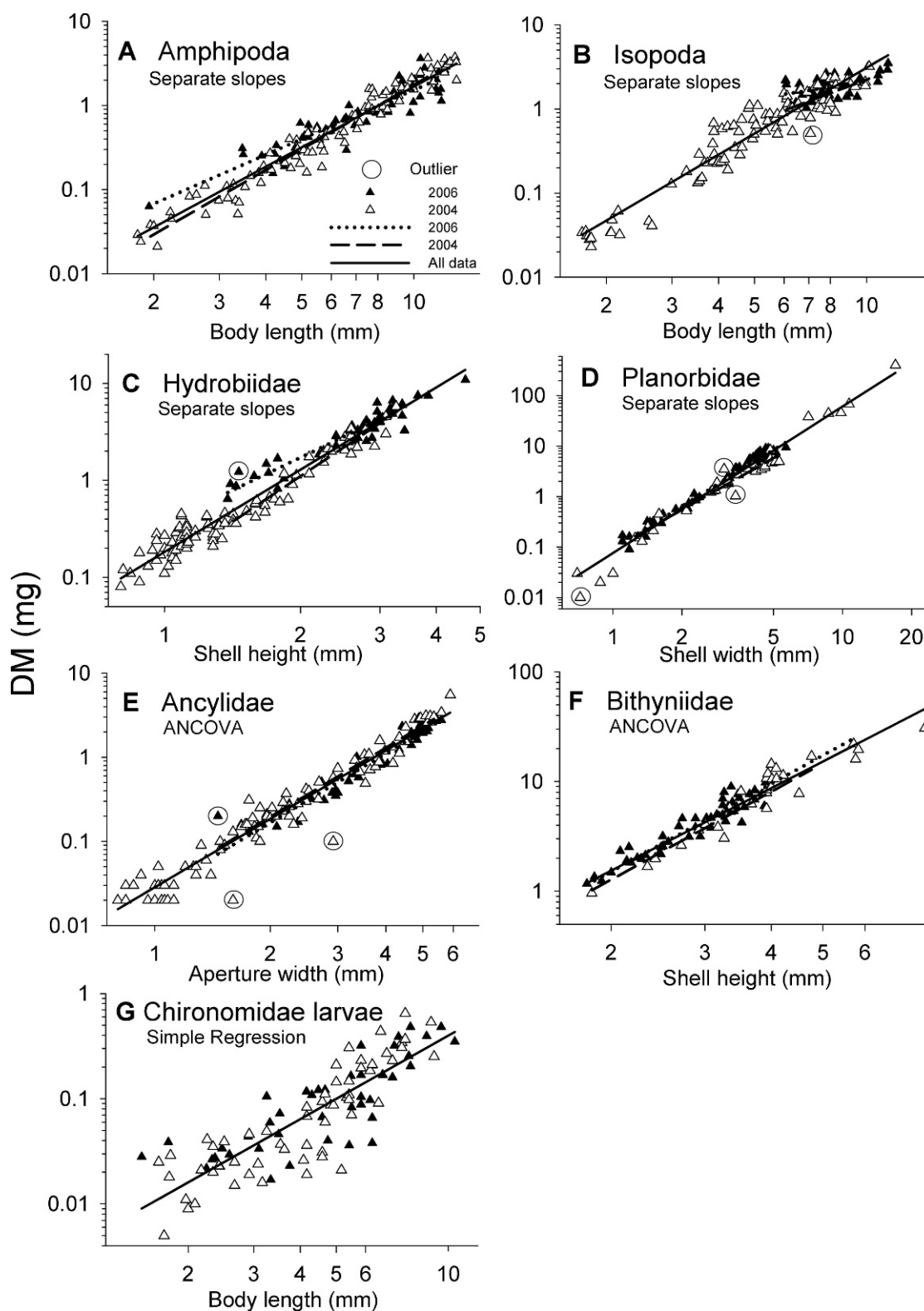
Fig. 1. Log-scale linear regressions predicting individual dry mass (DM) from body dimensions of Amphipoda (A), Isopoda (B), Hydrobiidae (C), Planorbidae (D), Ancylidae (E), Bithyniidae (F), and Chironomidae larvae (G) from the Saint Lawrence River sampled in autumn 2004 and 2006. Samples were analyzed separately by year and together. Separate analyses were done on overlapping size ranges (shown as the extent of lines). Outliers were excluded from regressions. For each graph, we specified whether slopes differed between years (separate slopes) or not (analysis of covariance) or if data were best described by a simple regression line (simple regression).

Table 4. Results of the analysis of covariance (ANCOVA) comparing the intercepts ($\log_{10}a$) given a common slope (b) for the regression equations ($\log_{10}DM = \log_{10}a + b[\log_{10}L]$) between dry mass (DM, mg) and linear body dimension (L, mm) for invertebrates sampled in 2004 and 2006 in Lake Saint Pierre. p is given for the intercept (a). AW = shell aperture width, SH = shell height, BL = total body length.

Taxon	L	n		p	b	$\log_{10}a$		Smearing factor	Interpretation of ANCOVA results
		2004	2006			2004	2006		
Ancylidae	AW	58	46	0.0040	2.73	−1.53	−1.60	1.03	For a given AW, DM 2004 > 2006
Bithyniidae	SH	16	57	0.0051	2.66	−0.70	−0.62	1.02	For a given SH, DM 2004 < 2006
Chironomidae	BL	57	43	0.6473	2.01	−2.42	−2.40	1.16	For a given BL, DM 2004 = 2006

for a given size (Table 4). However, for both taxa, the (statistically significant; Table 4) difference in regression-line intercepts between years was much smaller than the within-year scatter of data points (Fig. 1E, F). For example, predicted DM for a Bithyniidae gastropod with a 3 mm-high shell was 4.25 mg (all data points; Appendix S1), but was 3.75 and 4.44 mg, respectively, from equations derived from ANCOVA with data from 2004 and 2006 equations (Table 3, Appendix S1).

Chironomidae larvae sampled in 2004 and 2006 spanned 1 order of magnitude in BL and 2 in DM (Fig. 1G). Slopes and intercepts did not differ between years (Table 3). DM values were very scattered (Fig. 1G) for both years and reduced the statistical power of ANCOVA tests (Table 4). The results supported using 1 L–DM relationship for all data points (Table 2).

Factors inducing variability in DM predictions

We found 120 L–DM relationships in the published literature for organisms for which similar relationships were developed in our study (Appendix S1). Predicted DM values from published equations at reference sizes for Isopoda BL, Caenidae BL and HW, Leptoceridae BL and HW, Pyralidae BL, and Tipulidae BL showed little dispersion around our DM values. In contrast, predicted DM from published equations for Amphipoda BL, Isopoda HW, Ceratopogonidae BL, and Chironomidae BL and HW together ranged from 0.003 to 16.6× our predicted DM values.

Overall, DM estimated from 37 of the 120 equations (31%) fell within the 95% CI for the predicted mean value at the reference size, whereas 87 (73%) were within a 2× DM range (i.e., 0.5–2× our predicted DM values; Fig. 2). Smaller (0.003–2×) or larger (2–16.6×) values appeared equally on both sides of the 2× range (Fig. 2). These results show that in ~3 of 4 cases, DM

of individuals in the middle of the size range can be predicted without excessive bias from equations derived from taxa belonging to the same class or family.

We used variance components analysis on 4 subsets of data to investigate the relative ability of different factors to induce variability in predicted DM values (Table 5, Appendix S1). The 4 data subsets showed moderate (36%: our study) to high (Insecta: 124%; Chironomidae: 147%) CVs (Table 5), reflecting the span of DM values under study (Fig. 2). We made use of the equations obtained for 7 taxa belonging to 3 classes collected in 2004 and 2006 (n = 14 equations = 2 y × 7 taxa belonging to 3 classes) for which 2 different body dimensions were measured. Measurement based on different body dimensions within each class represented 0% of total variance. The component of variance for class was 32% of overall variance. Only 3% of the variance was attributable to yearly effects, within class differences, and body dimension.

Similarly, variability in relative DM for Insecta (n = 76 BL–DM equations) was mostly attributable to differences among the 7 families (10%) and 17 investigators (12%), with a small fraction (1%) of total variance ascribable to their continent of origin (Table 5). Within the Chironomidae family (n = 44 BL–DM equations), variability of predicted DM values was attributable to the effects of continent (17% of overall variance), investigator (12%), and preservation method (3%). Within the Amphipoda (n = 12 BL–DM equations), variability among the 9 investigators (50% of total variance) was more important than variability among genera and preservation methods (0%) (Table 5). All data subsets had a large (50–77%) residual variance component, as well as substantial (36–147%) CVs.

In comparison, mean total invertebrate density in LSP collected over the same years and with the same sampling gear spanned 3 orders of magnitude across sites (Fig. 3). Variance in density among replicate
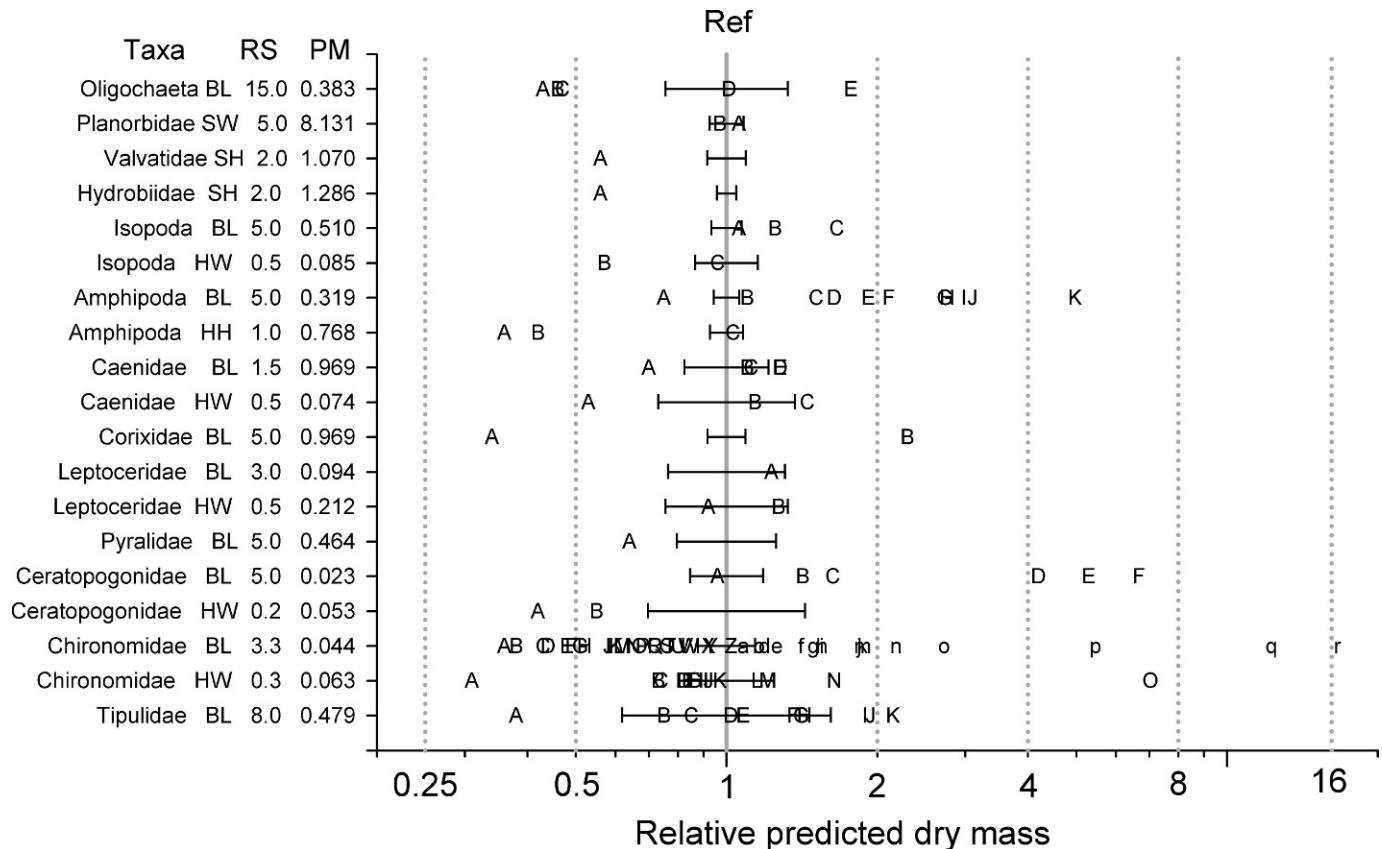
FIG. 2. Relative predicted dry mass (DM, mg) for a reference-size (RS) individual obtained with equations predicting DM from measurements of body dimensions. Letters refer to published equations identified in Appendix S1. For each organism and body dimension, we show the ratio of DM values derived from previously published equations relative to the mean DM predicted (PM) from our equations (Table 2). A relative predicted DM = 1 is indicated by the vertical line labeled ref. Horizontal bars represent 95% confidence limits of our mean DM predicted for an RS individual. Vertical lines at 0.5 and 2.0 show the 2× range of values around the reference DM. Body dimensions (mm) include total body length (BL), head height (HH), head width (HW), and shell height (SH). One value for Isopoda HW (A = 0.003) is outside the scale of the figure.

samples at any given site varied as the square of mean density, congruent with a uniform CV of 44% (range: 19–97%; Fig. 3).

Discussion

We presented 34 L–DM relationships for 18 taxa commonly encountered in LSP, including 7 families of gastropods, for which only a small number of examples are available in the published literature (Appendix S1). Most (30 of the 34) relationships had high r^2 values (0.60–0.98), with correspondingly low (1.02–1.34) smearing factors correcting for log-transformation. Our use of collections of invertebrates from late summer probably influenced the nature of the L–DM relationships (relatively high DM/unit body size) because this period represents the end of the growth season in northern latitude. For many univoltine species, individuals collected in later summer would

be at the maximum of their body reserves to survive through winter, and few individuals would be in early (spring) life-history stages (Karatayev et al. 2011). Moreover, our use of a 400-µm-mesh net (as in most studies; Carter and Resh 2001) favored collection of large individuals for the development of L–DM relationships. Thus, we did not examine the potential for seasonal variability in L–DM relationships. Nevertheless, predicted DM from our equations were in the middle of the range of predicted values from other published equations, 72% of which were within a 0.5–2× range of our values.

Values for % organic matter measured in our study were very close to those reported for marine polychaetes (75.7%), isopods (63%), and amphipods (72.9%) (Ricciardi and Bourget 1998). In contrast, % organic mass of freshwater oligochaetes in our study (76.4%) was markedly higher than that reported for marine oligochaetes (32.3%) (Ricciardi and Bourget 1998).

TABLE 5. Percentage of variance component (% var) and coefficient of variation (% CV = $100[e^{\sigma} - 1]$) associated with factors influencing the assessment of freshwater invertebrate dry mass (DM). The variance component was calculated for the predicted DM value for reference-sized individuals derived from the equations (Eq) available in the published literature (Appendix S1). All analyses were carried out on predicted DM values after ln(x)-transformation to homogenize variance. Relative DM values were used for comparisons among classes (our study) and families (Insecta), to remove the overwhelming effect of absolute size differences between vastly different taxonomic groups. Nested factors are indicated in brackets. For each factor, the groups under comparison are identified and the number of predicted DM values in each group is specified (in brackets). BL = total body length, SW = shell width, SH = shell height, AW = shell aperture width.

Relationship: taxon	% var	CV	Eq	Groups (number of predicted DM values)	Data source
This study		36	14		
Class	32			Mollusca (8), Insecta (2), Crustacea (4)	Fig. 1
Body dimension (within class)	0			BL (6), SW (2), SH (4), AW (2)	Appendix S1
Year (within class and body dimension)	3			2004 (7), 2006 (7)	
Unexplained residual	65				
BL–DM: Insecta		124	76		Appendix S1
Family	10			Caenidae (6), Ceratopogonidae (7), Chironomidae (44), Corixidae (3), Leptoceridae (2), Pyralidae (2), Tipulidae (12)	
Continent	1			Europe (18), North America (54), South America (2), Oceania (2)	
Investigator	12			17 investigators	
Unexplained residual	77				
BL–DM: Chironomidae		147	44		Appendix S1
Subfamily	0			Chironominae (15), Orthocladiinae (8), Tanypodinae (9), combined (12)	
Preservation method	3			Fresh/frozen (22), formaldehyde (15), ethanol (2), combined (5)	
Continent	17			Europe (19), North America (22), South America (1), Oceania (2)	
Investigator	12			15 investigators	
Residual (unexplained)	67				
BL–DM: Amphipoda		74	12		Appendix S1
Genus	0			*Crangonyx* (2), *Gammarus* (6), *Hyalella* (1), *Pontoporeia* (3)	
Preservation method	0			Fresh or frozen (8), formaldehyde (2), ethanol (2)	
Investigator	50			9 investigators	
Residual (unexplained)	50				

Percent organic content reported for freshwater insects, calculated from ash content for Lepidoptera (17.7% ash content = 82.3% AFDM), Coleoptera (8.0% = 92% AFDM), Trichoptera (8.5% = 91.5% AFDM), Ephemeroptera (7.2% = 92.8% AFDM), and Diptera (4.2% = 95.8% AFDM) (Benke et al. 1999), agreed well with the ranges for the same taxa (74–97.5%) in our study.

Differences in % AFDM among similar organisms could result from the presence of indigestible inorganic material in the gut, differences in mineral content of the exoskeleton or shell (Benke et al. 1999, Stoffels et al. 2003), or differences in diet or dissolved mineral content in water. Accurate measurement of AFDM is difficult for small organisms and those for
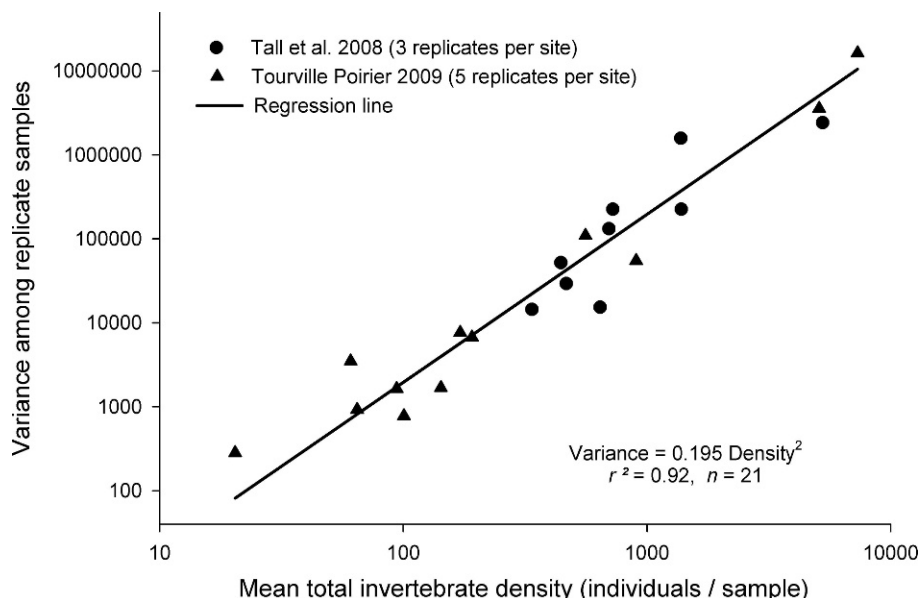
FIG. 3. Relationship between mean and variance of total invertebrate density sampled with D-frame nets in Lake Saint-Pierre in August 2004 (Tall et al. 2008; $n = 9$ sites) and August–September 2006 (Tourville Poirier 2009; $n = 12$ sites). The regression line corresponds to a constant coefficient of variation of 44.2%.

which ash content is within the error margin of high-precision scales. Percent AFDM provides a more accurate estimation of the proportion of diet that can be readily assimilated than does DM, but one could argue that DM provides a more realistic estimate of gut contents when whole organisms are ingested.

Factors inducing variability in DM predictions

Examination of variance components for different data subsets allowed us to highlight the relative magnitudes of factors related to the variability of DM predictions. We used 4 data subsets that included a sufficient number of independent observations to assess the effects of interannual differences, taxonomic level, continent, preservation method, and investigator. Our selection of reference-sized individuals in the *middle* of the size range was an attempt to characterize mean predicted DM for typical organisms rather than to find the largest discrepancies, which would occur toward the extremes of the size range. The range of variability associated with each subset and factor provided only an indication of the relative magnitude of co-occurring effects, which was somewhat blurred by the constantly high (>50%) proportion of residual variance. Nevertheless, we are confident our results will guide future decisions regarding allocation of efforts to maximize the precision of benthic invertebrate biomass assessment.

Interannual variability in L–DM relationships.—Our ANCOVA results showed that for gastropods, signif-

icant interannual differences in L–DM relationships could be detected by returning to the same location in the LSP system. Environmental characteristics during the growth season (April–September) in 2004 and 2006 might explain such patterns. For example, mean water temperature (15.3 and 16.5°C) and mean water level (4.92 and 4.76 m asl) differed between the growth seasons in 2004 and 2006, respectively (Hudon et al. 2010). However, differences in predicted DM were in opposite directions for Ancylidae (DM in 2004 > 2006) and Bithyniidae (DM in 2004 < 2006), so their ecological significance remains to be assessed.

In spite of their statistical significance, interannual differences in L–DM relationships were small in absolute terms, accounting for only ~3% of total variance in our study. The largest interannual differences in predicted DM were detected for taxa measured over a relatively narrow size range (e.g., Isopoda BL, Planorbidae shell width [SW]), which emphasizes the need to cover the broadest possible range to maximize r^2 value and, thus, improve the accuracy of DM predictions.

Effect of preservation method.—The effect of preservation method on individual length and DM has long been a subject of concern. This concern has led to detailed studies of the effects of freezing, formalin, and ethanol preservation on L–DM relationships. Preservation in ethanol causes a 7 to 37% loss in individual DM that differs significantly among taxa, concentration, and duration of preservation (How-

miller 1972, Mills et al. 1982, Leuven et al. 1985). However, in other studies, biomass loss over time was minor (Gaston et al. 1996), and formalin preservation had little effect on biomass loss (Stoffels et al. 2003, Wetzel et al. 2005). Loss of body mass appears to be particularly important for chironomid larvae and tubificid worms (Smock 1980, Mills et al. 1982, Benke et al. 1999, Stoffels et al. 2003).

However, our analysis showed that preservation effects were modest in comparison with those of other factors. Preservation effects represented 3% and 0% of total variance in predicted DM for reference-size Chironomidae and Amphipoda, respectively. Nevertheless, variability caused by loss of body mass attributed to preservation appears to be of the same order of magnitude because interannual differences in predicted DM, so studies in which the most precise determination of biomass is required should use fresh rather than preserved specimens (Smock 1980, Mills et al. 1982, Benke et al. 1999, Stoffels et al. 2003).

Effects of continent and investigator.—We made use of the impressive body of knowledge derived from published studies documenting L–DM relationships for freshwater invertebrates collected in North America (Tudorancea et al. 1979, Smock 1980, Marchant and Hynes 1981, Johnston and Cunjak 1999, Benke et al. 1999), South America (Miserendino 2001), Europe (Meyer 1989, Wenzel et al. 1990, Burgherr and Meyer 1997, González et al. 2002, Baumgärtner and Rothhaupt 2003), and Oceania (Towers et al. 1994, Stoffels et al. 2003) (Appendix S1). Continent accounted for 1% (Insecta BL) and 17% (Chironomidae BL) of total variance. Europe and North America were, by far, the best represented continents, and a very small number of equations originated from Oceania ($n = 2$) and South America ($n = 1–2$ depending on taxa).

Depending on the data subset, between 12% (Insecta BL, Chironomidae BL) and 50% (Amphipoda BL) of total variance in predicted DM was explained by differences among the 9–17 investigators. This variability could have arisen from methodological differences among laboratories, such as inclusion/exclusion of antennae, rostrum, telson, or abdominal setae, the number of linear segments measured, and use of a micrometric ocular or an image analyzer. This level of variability is probably maximal for BL of twisted or curved organisms such as Chironomidae or Amphipoda, whose measurement depends on the number of linear segments used to assess total body length. This observation emphasizes the very simple, but essential need to document carefully body dimensions, measurement methods, and statistical analyses (size range, data transformation, identification of outliers, regression r^2) used. Differences

among investigators also could have indirectly reflected regional or latitudinal differences among collection sites in North America and Europe.

Effect of taxonomic level.—For most taxa, DM values predicted by our equations were near the middle of the overall range of DM values. Values predicted by 31% of the 120 published equations were within our 95% CIs and 73% were within a 0.5–2× range of our predicted DM values. DM prediction was best for reference-sized Planorbidae BL, Isopoda BL, Caenidae BL and HW, Leptoceridae BL and HW, Pyralidae BL, and Tipulidae BL, but the small number of equations (1–4/taxon) somewhat limits this interpretation. The most notable outliers belonged to Amphipoda BL (5 of 14 values, 2.7–4.97× differences), Ceratopogonidae BL (3 of 6 values, 4.2–6.7× differences), and Chironomidae BL (3 of 44 values, 5.46–16.61× differences). The wide range of predicted DM of Chironomidae and the scatter of our L–DM measurements may have resulted from the presence of many morphologically distinct genera and species (Johnston and Cunjak 1999) in this large family. Taxa with marked body curvature had the widest range of predicted DM, a result that emphasizes the inherent variability related to measurement of the linear body dimension selected.

Variance component analysis of relative predicted DM within Insecta showed that 10% of the variance was assignable to differences among families and 12% was linked to variation among investigators. Within more precise taxonomic groups, Chironomidae subfamilies and Amphipoda genera, the effect of taxon on relative predicted DM was undetectable when estimated beside the effects of investigator, continent, or preservation method. These results indicate bias associated with estimating insect DM with an equation from a different insect family. However, all equations from Chironomidae subfamilies may adequately predict DM for taxa belonging to this family. In practical terms, family-level or more specific equations ideally should be used to predict DM for insects. Thus, previously published equations at the insect-family level probably provide valid estimates of DM even when the equations were derived from other sites (e.g., Benke et al. 1999).

Macroinvertebrate L–DM relationships: how specific should they be?

Our results were especially useful for assessing our ability to detect significant spatial and temporal variations in the biomass of common invertebrate taxa in a large northern river system. Beyond estimating and comparing regression-equation pa-

rameters for a range of taxa, we identified the range of expected DM values predicted from different equations for different invertebrates at the same reference size. This exercise allowed us to identify the relative importance of factors causing variability in predicted DM estimates for different data subsets.

We stress that estimates of DM, biomass, and production of benthic invertebrates rely on accurate assessments of density and size distributions (Kimmerer et al. 2005), both of which may span several orders of magnitude in variability caused by a range of environmental and human factors. For example, the overall effects of sampling gear, sorting and preservation techniques, substratum, current speed, water depth, seasonal variations, etc. led Hynes (1970, p. 246) to comment "many investigators have had doubts about the validity of quantitative sampling because not only are the techniques known to be variously selective, but the variances of samples that they do obtain are usually so large that only very wide limits of confidence are possible". Depending on the density of each taxon and the surface area sampled, Downing (1979) needed 2 to 45 replicate samples to reach 20% precision on density, a prerequisite seldom fulfilled in field studies. In LSP, the CV of mean total abundance of benthic invertebrates spanned 19 to 97% when sampled with D-frame nets in emergent vegetation and 17 to 108% when sampled with sediment corers (Tall et al. 2008). Thus, the variability arising from the use of L–DM relationships is compounded by comparatively more important errors originating from estimation of density and size distribution of organisms (Kimmerer et al. 2005).

Debate regarding the relative magnitude of each factor taken individually remains considerable (Smock 1980). Differences in L–DM relationships within a single taxon have been attributed to a wide range of environmental factors related to habitat productivity, food availability, or condition of other organisms (Short et al. 1987, Griffith et al. 1993, Johnston and Cunjak 1999). Our study puts into perspective the amount of variability at play at each step of the process leading to quantitative assessment of biomass (standing stock) and production of benthic freshwater invertebrates that cover a wide range of body length (0.2–60 mm), DM (0.01–>1 mg), and density (up to 4 orders of magnitude in no./m^2).

Assessment of DM is only one element of variability that must be dealt with when estimating invertebrate biomass. Interannual differences, preservation methods, and measured body dimension each accounted for a small (0–3%) fraction of total variance in predicted DM. Differences among investigators (12–50%) and among continents (1–17%) accounted for a higher proportion of total variance, possibly because of methodological or regional and latitudinal differences. Increasingly precise taxonomic levels explained progressively lower proportions of the total variance, a result suggesting that family or a more precise taxonomic level will provide suitable DM estimates for most invertebrates. However, overall variability caused by L–DM relationships was smaller than variability in total invertebrate density among replicate samples, so more effort should be devoted to improving the accuracy of estimates of invertebrate density than to the development of site-specific L–DM relationships when assessing benthic invertebrate biomass in freshwater.

Acknowledgements

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