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Relationships between length and weight of freshwater macroinvertebrates in Japan

Hitoshi Miyasaka · Motomi Genkai-Kato · Yo Miyake · Daisuke Kishi · Izumi Katano · Hideyuki Doi · Shin-ya Ohba · Naotoshi Kuhara

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Abstract Relationships between weight (W; dry weight) and length (L; head capsule width, total body length or head carapace length) were examined in 31 Japanese freshwater macroinvertebrate taxa, using the form $W = aL^b$. The relationships were expressed as data of the lowest taxonomic level and data of higher taxonomic levels. The length–weight relationships obtained in this study were similar to those obtained in North America and Europe at the lowest taxonomic level, whereas they could be different from those obtained in North America and Europe at the higher taxonomic levels. We suggest that researchers should make their own regressions for a target taxon or use the regression for the same taxon as possible lower taxonomic level in the local area.

Keywords Head capsule width · Body length · Weight · Freshwater macroinvertebrates · Stream

H. Miyasaka (✉)
Center for Marine Environmental Studies, Ehime University, 2-5 Bunkyo-cho, Matsuyama, Ehime 790-8577, Japan
e-mail: predator@sci.ehime-u.ac.jp

M. Genkai-Kato
Center for Ecological Research, Kyoto University, Otsu, Shiga, Japan

Y. Miyake
Graduate School of Science and Engineering, Ehime University, Matsuyama, Ehime, Japan

D. Kishi
Gero Branch, Gifu Prefectural Research Institute for Freshwater Fish and Aquatic Environments, Gero, Gifu, Japan

I. Katano
Aqua Restoration Research Center, Kakamigahara, Gifu, Japan

H. Doi
Faculty of Agriculture, Ehime University, Matsuyama, Ehime, Japan

S. Ohba
Graduate School of Natural Science and Technology, Okayama University, Okayama, Japan

N. Kuhara
Chitose Board of Education, Chitose, Hokkaido, Japan

Introduction

Estimates of biomass are essential for studies modeling the structure, animal growth, production and energy flow of ecosystems. The relationship between body mass and length is a useful tool in ecological research (e.g., Culver et al. 1985; Kawabata and Urabe 1998; Miyasaka et al. 2007). A parabolic or power curve, in the form $W = aL^b$, has most often been used to estimate weight W from length L in studies of freshwater macroinvertebrates (e.g., Baumgärtner and Rothhaupt 2003; Genkai-Kato and Miyasaka 2007). Benke et al. (1999) and Johnston and Cunjak (1999) reviewed the length–weight relationships of stream invertebrates in North America and Europe. Freshwater macroinvertebrates distributed only in Asia were not included in the literature, and, consequently, their weights have been inferred from the published equations for related taxa (Kawabata et al. 2002). However, the validity of this approach has not been verified. To improve the situation, relationships between weight and length (head capsule width, body length or head carapace length) were examined for 31 taxa of common benthic macroinvertebrates in Japanese aquatic environments. Subsequently, length–weight relationships grouped according to higher taxonomic levels were also examined, using two methods (regression method and arithmetic mean method) to obtain the regression constants (*a* and *b*). Our main goal in this paper was to establish a handy tool for the estimation of the dry weight of aquatic invertebrates.

Methods

Sampling of freshwater macroinvertebrates was conducted at five locations in Japan (Tables 1, 2). Sampling of macroinvertebrates of 22 taxa was conducted in Horonai Stream (42°43′ N, 141°36′ E), Tomakomai, Hokkaido, northern Japan. One ephemeropteran species and one trichopteran species were collected from the following streams of Shiretoko, Hokkaido: Rusha Stream (44°12′ N, 145°12′ E), Idashubetsu Stream (44°07′ N, 145°06′ E), Funbe Stream (44°03′ N, 144°59′ E), Oshokomanai Stream (44°02′ N, 144°58′ E), Onnebetsu Stream (44°01′ N, 144°56′ E) and Nukamappu Stream (43°55′ N, 144°51′ E). One ephemeropteran species and three trichopteran species were collected from Agi-gawa River (35°26′ N, 137°25′ E) and Inuma-gawa Stream (35°26′ N, 137°26′ E) in Ena, Gifu, central Japan. One trichopteran species was collected from Shigo-gawa Stream (34°23′ N, 136°01′ E) in Higashi Yoshino, Nara, central Japan. Two hemipteran species, one belostomatid and one nepid species, were collected from rice fields in Hyogo, central Japan. All freshwater macroinvertebrates, except for hemipteran species, were collected in a Surber net sampler (25 cm × 25 cm quadrat area, 225 μm mesh). Hemipteran species were caught by hand.

Specimens were preserved in 5% buffered formalin solution in the field, except for hemipteran species. We assumed that formalin-preserved invertebrates provided dry weight estimates close to those of fresh invertebrates (Leuven et al. 1985). We identified them to the lowest taxonomic level possible, using a binocular dissecting microscope (SMZ-U, Nikon, Tokyo, Japan) according to the taxonomical keys of Kawai (1985) and Kawai and Tanida (2005). We measured all individual specimens whose head contained chitin for head capsule width to the nearest 0.1 mm, using the binocular dissecting microscope with an ocular micrometer. Other specimens whose head contained little chitin (i.e., Athericidae and Oligochaeta) were measured for total body length to the nearest 0.1 mm with the binocular dissecting microscope. One ephemeropteran species and two trichopteran species were measured for both head capsule width and total body length. One amphipod species was measured for head carapace length (from the top of rostrum to the end of head carapace) to the nearest 0.1 mm with the binocular dissecting microscope. All specimens, except for hemipterans, were then dried at 60°C for 24 h, cooled in a desiccator and weighed to the nearest 0.01 mg on an electronic balance (AB135-S, Mettler Toledo, Greifensee, Switzerland). Live specimens of hemipteran species were measured for total body length to the nearest 0.1 mm with a digital caliper (Digimatic Caliper, series no. 500, Mitsutoyo, Kawasaki, Japan) and wet weight to the nearest 0.1 g with an electronic balance (Pocketablescale Handymini 1476, Tanita, Tokyo, Japan).

Length–weight relationships (*a* and *b* values) were calculated by linear regression from the formula: $\ln W = \ln a + b \ln L$, where W was dry or wet weight and L was head capsule width, total body length, or head carapace length. All coefficients of determination (r^2) were significant at the $P < 0.01$ level. For all macroinvertebrate taxa obtained in the lowest taxonomic level, coefficients of determination and number of samples were $r^2 > 0.50$ and $n > 10$, respectively. The b value represents the rate of increase (i.e., slope) of weight against length in the log-transformed relationship (i.e., $\ln W = \ln a + b \ln L$), whereas the constant a represents the weight of an organism at a unit length (i.e., 1 mm).

Results and discussion

We obtained the relationships between head capsule width and dry weight of 24 freshwater macroinvertebrate taxa (Table 1), between total body length and dry weight relationships of seven taxa, between head carapace length and dry weight relationships of one taxon, and between total body length and wet weight relationships of two taxa (Table 2). These relationships were shown as data of the lowest taxonomic level (we defined the word "taxon" as the taxonomic level as low as we could identify). The relationships of individuals grouped according to the six major orders of aquatic insects were also examined (Table 3).

For one ephemeropteran species, *Uracanthella punctisetae*, and two trichopteran species, *Goera japonica* and *Micrasema quadriloba*, we obtained the relationships between head capsule width and dry weight and between total body length and dry weight (Tables 1, 2). Coefficients of determination (r^2) of these relationships took similar values (0.66–0.89), independent of the measurement of head capsule width or total body length as the length (L), which conforms to the results obtained for four perlid plecopteran species (Genkai-Kato and Miyasaka 2007). This suggests that head capsule width and total body length are both reliable measurements to calculate dry weight in Ephemeroptera, Trichoptera and Plecoptera. Relationships between total body length and dry weight were available for organisms whose body shapes were

Table 1 Results of relationships between head capsule width and dry weight of 24 freshwater macroinvertebrate taxa. We defined the word "taxon" as the taxonomic level as low as we could identify (e.g., "*Rhyacophila* spp." was counted as one taxon). *a*, *b* Constants in $W = aL^b$, where *W* and *L* correspond to dry weight and head capsule width, respectively; *n* number examined

Taxon	*n*	*a*	*b*	r^2	Length (mm)		Weight (mg)		Sampling site and date
					Mean ± SD	Range	Mean ± SD	Range	
Ephemeroptera									
Leptophlebiidae									
Paraleptophlebia westoni	40	0.016	2.975	0.67	1.9 ± 0.5	0.8–3.0	0.14 ± 0.10	0.01–0.42	TK
Ephemeridae									
Ephemera japonica	22	0.117	2.257	0.91	2.7 ± 1.4	0.6–4.8	1.68 ± 1.63	0.06–4.63	TK
Ephemerellidae (three taxa)	125	0.277	1.486	0.58					
Ephemerella aurivillii	17	0.037	2.635	0.53	1.5 ± 0.3	1.2–2.2	0.12 ± 0.07	0.03–0.33	TK
Drunella spp.	34	0.038	2.961	0.96	4.1 ± 1.3	1.8–6.3	3.43 ± 3.40	0.25–13.08	TK
Uracanthella punctisetae	74	0.380	2.368	0.66	1.1 ± 0.22	0.7–1.6	0.51 ± 0.29	0.07–1.30	EN
Ameletidae									
Ameletus spp.	32	0.156	1.910	0.86	2.5 ± 0.9	0.6–3.5	1.10 ± 0.69	0.03–2.27	TK
Baetidae (two taxa)	61	0.201	1.796	0.78					
Baetis thermicus	31	0.091	2.720	0.86	1.9 ± 0.6	0.5–3.0	0.79 ± 0.83	0.04–3.21	TK
Baetiella japonica	30	0.512	3.020	0.87	0.6 ± 0.2	0.3–1.0	0.16 ± 0.14	0.01–0.52	ST
Heptageniidae (two taxa)	63	0.013	2.741	0.89					
Epeorus latifolium	27	0.002	3.785	0.87	6.4 ± 1.5	2.2–9.0	2.97 ± 2.86	0.13–10.58	TK
Cinygmula sp.	36	0.012	2.941	0.79	2.8 ± 0.8	1.2–4.7	0.35 ± 0.31	0.04–0.98	TK
Plecoptera									
Chloroperlidae	30	0.060	2.340	0.83	2.3 ± 0.8	0.8–3.2	0.55 ± 0.46	0.04–1.58	TK
Perlodidae	33	0.010	3.590	0.97	4.1 ± 2.3	1.7–10.9	4.91 ± 9.40	0.04–51.30	TK
Megaloptera									
Sialidae	14	0.102	2.586	0.83	3.0 ± 1.5	1.0–5.2	3.39 ± 5.02	0.17–19.07	TK
Trichoptera									
Brachycentridae									
Micrasema quadriloba	71	1.336	3.021	0.78	0.5 ± 0.1	0.2–0.7	0.20 ± 0.16	0.01–0.60	HY
Goeridae									
Goera japonica	54	3.458	4.164	0.85	1.0 ± 0.2	0.4–1.3	4.31 ± 3.60	0.10–13.80	EN
Glossosomatidae									
Glossosoma sp.	26	0.272	3.212	0.62	1.2 ± 0.3	0.5–1.7	0.84 ± 0.78	0.04–2.87	TK
Limnephilidae (two taxa)	65	0.070	3.644	0.93					
Dicosmoecus jozankeanus	35	0.246	2.836	0.70	4.8 ± 0.7	2.5–5.8	22.79 ± 10.43	2.42–50.00	TK
Hydatophylax festivus	30	0.062	3.795	0.84	2.1 ± 0.9	0.9–4.6	5.53 ± 18.00	0.02–81.20	TK
Rhyacophilidae									
Rhyacophila spp.	30	0.309	2.716	0.78	1.7 ± 0.6	0.9–3.2	2.21 ± 3.15	0.17–16.29	TK
Stenopsychidae									
Stenopsyche marmorata	27	1.659	3.358	0.92	1.2 ± 0.7	0.3–3.2	11.18 ± 33.32	0.01–174.43	ST
Coleoptera									
Hydrophilidae	17	0.066	3.829	0.72	1.7 ± 0.5	1.1–3.3	1.35 ± 3.62	0.10–15.26	TK
Diptera									
Chironomidae									
Orthocladiinae	33	0.114	1.696	0.80	1.2 ± 0.5	0.4–2.0	0.18 ± 0.14	0.02–0.51	TK
Dixidae	31	0.111	3.775	0.63	1.0 ± 0.2	0.7–1.2	0.14 ± 0.12	0.02–0.43	TK
Simuliidae	31	0.079	2.497	0.53	1.2 ± 0.3	0.7–1.6	0.16 ± 0.13	0.03–0.67	TK

TK Tomakomai on 25 July and 10 August 1995; *EN* Ena on 18 March and 22 August 2005; *ST* Shiretoko on 26–30 August 1999; *HY* Higashi Yoshino on 30 June, 29 July, 30 September 2002, 22 and 26 March 2003

Table 2 Results of relationships between total body length and dry weight for seven taxa, head carapace length and dry weight for one taxon, and total body length and wet weight for two taxa. We defined the word "taxon" as the taxonomic level as low as we could identify. *a*, *b* Constants in $W = aL^b$, where *W* and *L* correspond to weight and length, respectively; *n* number examined

Taxon	*n*	*a*	*b*	r^2	Length (mm)		Weight (mg)		Sampling site and date
					Mean ± SD	Range	Mean ± SD	Range	
Length = total body length; weight = dry weight									
Oligochaeta	30	0.008	1.888	0.90	8.9 ± 9.7	1.0–37.0	0.95 ± 1.56	0.01–5.98	TK[a]
Ephemeroptera									
Ephemerellidae									
Uracanthella punctisetae	74	0.021	2.315	0.71	3.8 ± 0.8	2.3–5.5	0.51 ± 0.29	0.07–1.30	EN
Trichoptera									
Brachycentridae									
Micrasema quadriloba	71	0.019	2.631	0.76	2.2 ± 0.7	0.7–3.3	0.20 ± 0.16	0.01–0.60	HY
Glossosomatidae (two taxa)	77	0.022	2.524	0.65					
Glossosoma altaicum	39	0.011	2.998	0.64	5.2 ± 1.0	2.1–6.8	1.85 ± 1.09	0.10–3.80	EN
Glossosoma ussuricum	38	0.041	2.066	0.66	4.7 ± 1.2	2.3–6.9	1.17 ± 0.86	0.20–3.60	EN
Goeridae									
Goera japonica	54	0.025	2.575	0.89	6.6 ± 2.4	1.8–11.3	4.31 ± 3.60	0.10–13.80	EN
Diptera									
Athericidae	30	0.007	2.648	0.76	4.2 ± 0.6	3.3–5.3	0.35 ± 0.12	0.15–0.55	TK
Length = head carapace length; weight = dry weight									
Amphipoda									
Anisogammaridae									
Jesogammarus jesoensis	32	0.106	2.424	0.90	2.1 ± 1.0	0.6–4.1	1.07 ± 1.21	0.04–3.97	TK
Length = total body length; weight = wet weight									
Hemiptera									
Belostomatidae									
Kirkaldyia (=*Lethocerus*) *deyrolli*	120	0.023	2.988	0.84	5.94 ± 0.48	5.05–6.70	4.9 ± 1.3	2.7–7.4	HG
Nepidae									
Laccotrephes japonensis	51	0.020	2.981	0.77	3.21 ± 0.24	2.82–3.76	0.7 ± 0.2	0.4–1.0	HG

TK Tomakomai on 25 July and 10 August 1995; *EN* Ena on 18 March and 22 August 2005; *ST* Shiretoko on 26–30 August 1999; *HY* Higashi Yoshino on 30 June, 29 July, 30 September 2002, 22 and 26 March 2003; *HG* Hyogo on 3–16 March 2003, 16 and 30 May 2006

[a] Collected in riffle habitats in Horonai Stream

Table 3 Relationships between head capsule width and dry weight of individuals grouped according to the six major orders of aquatic insects, by regression and arithmetic mean methods. We defined the word "taxon" as the taxonomic level as low as we could identify. *a*, *b* Constants in $W = aL^b$, where *W* and *L* correspond to dry weight and head capsule width, respectively; *n* number examined

Taxon	*n*	Regression method			Arithmetic mean method	
		a_r	b_r	r^2	a_m	b_m
Ephemeroptera (ten taxa)	343	0.161	1.448	0.51	0.136 ± 0.055	2.757 ± 0.163
Plecoptera (six taxa)[a]	307	0.032	4.371	0.75	0.205 ± 0.062	3.145 ± 0.182
Megaloptera (one taxon)	14	0.103	2.586	0.83	0.103	2.586
Trichoptera (seven taxa)	273	0.768	2.115	0.71	1.049 ± 0.464	3.300 ± 0.197
Coleoptera (one taxon)	17	0.066	3.829	0.72	0.066	3.829
Diptera (three taxa)	95	0.099	2.024	0.59	0.101 ± 0.011	2.656 ± 0.605

[a] Data from two taxa (this study) and four taxa (Genkai-Kato and Miyasaka 2007) were combined

slender and whose heads contained little chitin (i.e., Athericidae and Oligochaeta) (Table 2). Two hemipteran species, *Kirkaldyia* (= *Lethocerus*) *deyrolli* and *Laccotrephes japonensis*, had almost cubic length–weight relationships ($b \approx 3$), although wet weight was used for body mass (Table 2).

When using head capsule width as the length (*L*), we found that *b* varied in a wide range among taxa at the lowest taxonomic level (1.696–4.164, Table 1). This variation would be due to insects with relatively small heads compared to their bodies. We suggest that body length is the better predictor of body mass for aquatic insects with small heads.

There are two methods to obtain the regression constants, *a* and *b*, at the order taxonomic level (Table 3): a_r and b_r, length–weight regression using all individual data of the order (regression method); a_m and b_m, arithmetic means of the *a* and *b* values at the lowest taxonomic level (i.e., $a_m = \sum_{i=1}^{n} a_i/n$ and $b_m = \sum_{i=1}^{n} b_i/n$, where *n* is the number of the lowest taxa of the order; arithmetic mean method). The arithmetic mean *b* values (b_m) were close to the cubic relationship (b_m = 2.586–3.829), whereas the regression *b* values (b_r) deviated from the cubic relationship for some orders (i.e., Ephemeroptera 1.448, Plecoptera 4.371). Consequently, the length–weight relationships can differ between the regression method (Fig. 1a) and the arithmetic mean method (Fig. 1b) for some orders. The deviation from the cubic relationship in the regression method is attributed to the species-specific length–weight relationship and body size range (Fig. 2). Here, we explain why this deviation occurred, using simple examples. In Baetidae, the regression line for the larger-bodied species, *Baetis thermicus*, lay below that for the other species, *Baetiella japonica* (Fig. 2a). In this case, although the *b* values were similar at the species level (*b* = 2.72 for *B. thermicus* and 3.02 for *B. japonica*), the combined b_r value at the family Baetidae level was considerably smaller (1.796). On the other hand, in Plecoptera, the regression line for the larger-bodied group Perlidae lay above that of non-Perlidae (Fig. 2b). In this case, the combined b_r value at the order level was considerably higher (4.371), although the *b* values were similar at the lower taxonomic level (*b* = 3.449 for Perlidae and 2.884 for non-Perlidae). Notice that the *a* value for the larger-bodied species (*a* = 0.091, *B. thermicus*) was smaller than that for the other species (0.512, *B. japonica*) in the former case (Fig. 2a), whereas the *a* value for the larger-bodied group (0.202, Perlidae) was greater than for the other group (0.031, non-Perlidae) in the latter case (Fig. 2b).

There was no marked difference in regression slope (*b* value) between aquatic insects in Japan and North America when we used the arithmetic mean method to calculate the b_m values at the order level. For example, b_m values in North America are 3.3 for Ephemeroptera, 3.1 for Plecoptera, and 3.3 for Trichoptera (Benke et al. 1999). We obtained 2.757 for Ephemeroptera, 3.145 for Plecoptera, and 3.3 for Trichoptera (see Table 3). On the other hand, when we adopted the regression method, the b_r value could differ considerably from those in North America and

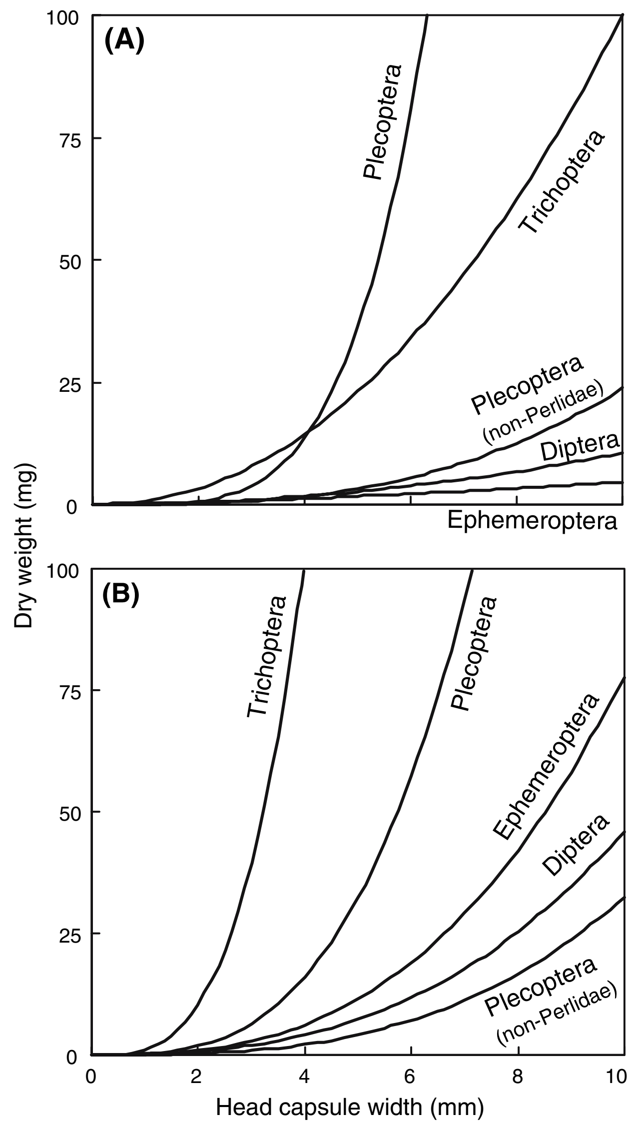

Fig. 1 Regression curves of dry weight versus head capsule width according to insect order obtained by the regression method (**a**) and by the arithmetic mean method (**b**). Curves for Plecoptera (non-Perlidae) were drawn based on data of two taxa (Chloroperlidae and Perlodidae) measured in this study. Curves for the order Plecoptera were based on data of the two taxa (Chloroperlidae and Perlodidae) and four perlid taxa (*Oyamia lugubris*, *Paragnetina tinctipennis*, *Kamimuria tibialis* and *Kamimuria uenoi*) from Genkai-Kato and Miyasaka (2007)

Europe. We obtained b_r = 1.448 for Ephemeroptera, b_r = 4.371 for Plecoptera and b_r = 2.115 for Trichoptera (see Table 3). For Ephemeroptera, b_r = 1.8 (Baumgärtner and Rothhaupt 2003) in Europe and b_r = 3.6 (Smock 1980) in North America. For Plecoptera, b_r = 2.7 (Meyer 1989) in Europe and b_r = 2.5 (Smock 1980 in North America. For Trichoptera, b_r = 2.7 (Meyer 1989) and b_r = 2.8 (Baumgärtner and Rothhaupt 2003) in Europe, and b_r = 2.8 (Smock 1980) in North America. These comparisons between the methods to obtain the regression constants,

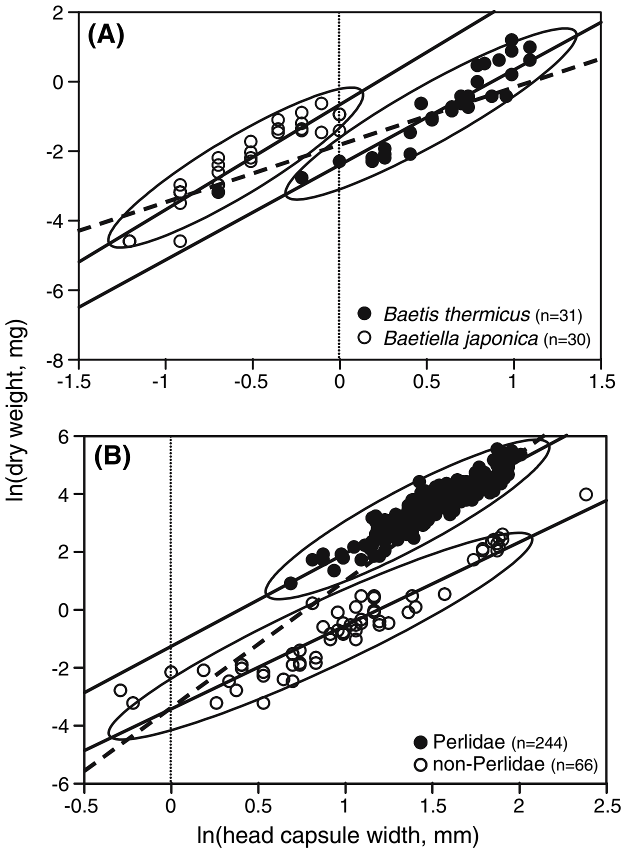

Fig. 2 Log-transformed relationships between dry weight and head capsule width of two taxonomic groups. **a** Family Baetidae, including *Baetiella japonica* and *Baetis thermicus*. **b** Order Plecoptera, including non-Perlidae (data measured in this study) and Perlidae (data based on Genkai-Kato and Miyasaka 2007) groups. *Solid lines* represent the regression line for each taxonomic group. *Broken lines* represent the regression line for the family Baetidae (**a**) and for the order Plecoptera (**b**). Note that the slopes of the regression lines correspond to the b values and the y-intercepts of the regression lines at ln (head capsule width) = 0 correspond to the ln a values

a and b, at the higher taxonomic level and between aquatic insects in Japan and other areas in the world, imply that the arithmetic mean method is more reliable in the estimation of dry weight from length when generic length–weight equations are unavailable or when organisms are only identified to the family or order level. However, in order to reduce errors in estimating the biomass, we suggest that researchers should make their own regressions for a target taxon or use the regression for the same taxon as possible lower taxonomic level in the local area.

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References

Baumgärtner D, Rothhaupt K (2003) Predictive length–dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. Int Rev Hydrobiol 88:453–463

Benke AC, Huryn AD, Smock LA, Wallace JB (1999) Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J N Am Benthol Soc 18:308–343

Culver DA, Boucherle MM, Bean DJ, Fletcher JW (1985) Biomass of freshwater crustacean zooplankton from length–weight regressions. Can J Fish Aquat Sci 42:1380–1390

Genkai-Kato M, Miyasaka H (2007) Length–weight relationships of four predatory stonefly species in Japan. Limnology 8:171–174

Johnston TA, Cunjak RA (1999) Dry mass–length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. Freshw Biol 41:653–674

Kawabata K, Urabe J (1998) Length–weight relationships of eight freshwater planktonic crustacean species in Japan. Freshw Biol 39:199–205

Kawabata K, Narita T, Nagoshi M, Nishino M (2002) Stomach contents of the landlocked dwarf ayu in Lake Biwa, Japan. Limnology 3:135–142

Kawai T (1985) An illustrated book of aquatic insects of Japan. Tokai University Press, Tokyo

Kawai T, Tanida K (2005) Aquatic insects of Japan: manual with keys and illustrations. Tokai University Press, Tokyo

Leuven RSEW, Brock TCM, van Druten HAM (1985) Effects of preservation on dry- and ash-free dry weight biomass of some common aquatic macro-invertebrates. Hydrobiologia 127:151–159

Meyer E (1989) The relationship between body length parameters and dry mass in running water invertebrates. Arch Hydrobiol 117:191–203

Miyasaka H, Genkai-Kato M, Goda Y, Omori K (2007) Length–weight relationships of two grapsid crab species in Japan. Limnology 8:81–83

Smock LA (1980) Relationships between body size and biomass of aquatic insects. Freshw Biol 10:375–383