LIVE MASS AND LENGTH-MASS ALLOMETRY
OF ADULT ODONATES COLLECTED IN EAST-CENTRAL
MISSISSIPPI, UNITED STATES

J.T. BRIED[1], L.W. BENNETT[2] and G.N. ERVIN[1,3]

[1] Department of Biological Sciences, Mississippi State University, P.O. Box GY,
Mississippi State, MS 39762, United States
e-mail: jtb117@msstate.edu

[2] College of Veterinary Medicine, Mississippi State University, Box 6100,
Mississippi State, MS 39762, United States
e-mail: Tox@cvm.msstate.edu

[3] e-mail: gervin@biology.msstate.edu

Live mass was recorded for over 290 adult Odon. during peak flight season in Mississippi. Total live mass is reported for 19 spp., along with a quantitative species subset analysis of inter- and intraspecific sex partitioned mass. Fresh mass was significantly correlated with species and sex in Anisoptera (p = 0.021) and Zygoptera (p = 0.001), based on separate species-level analyses of the Libellulidae (n = 6 spp.) and Coenagrionidae (n = 4 spp.), respectively. Total live mass also was correlated with total body length in the libellulid dragonflies (r^2 = 0.59-0.94, p<0.0001-0.03) and length-mass slopes were not significantly different among species. Limitations and cautions of mass prediction via proportionate size dimension(s) are discussed, some advantages of working with adults as opposed to larvae and measuring fresh mass as opposed to dry mass are described, and further study of length-mass relationships in adult Odon. is encouraged.

INTRODUCTION

Insect mass is measured either directly as fresh or preserved weight, or indirectly as an estimate of a closely correlated size dimension parameter, such as length of body and/or wing. Length-mass regressions can yield useful mass predictive equations (MILLER, 1976; SAMPLE et al., 1993; BENKE et al., 1999; HALE et al., 2004). For example, they may facilitate more efficient (rapid, non-laborious) determination of secondary production by circumventing the processing time and need for laboratory equipment that accompanies direct mass measurement (SAMPLE et al., 1993). Regressions for aquatic insects in North America are scarce (BENKE et al.,

1999) and exist only for dried or chemically treated larval stages (SMOCK, 1980; BURGHERR & MEYER, 1997; BENKE et al., 1999).

Measuring live mass of adult Odonata and other aerial insects has several advantages for mass prediction. Molting may cause a temporary decline in specific gravity of aquatic insect larvae, because the cast exuviae reduces mass-volume ratio relative to that of the premolt instar. Therefore, greater length-mass variability and diminished accuracy of mass prediction will result from pooling specimen data collected both near and distant to molting periods (BENKE et al., 1999). Another disadvantage to working with larval aquatic insects is that obtaining ash free dry mass is required to negate the effects of attached silt and other water-borne inorganic materials (BENKE et al., 1999). The procedure is time consuming relative to live-mass measurement and is unnecessary for aerial adults, except to determine gut contents. Preservation methods often destroy lipids (thus, induce loss of tissue mass) and different techniques, such as acetone vs. alcohol, produce equations that are not interchangeable (DERMOTT & PATERSON, 1974; SMOCK, 1980; GONZALEZ et al., 2002). In addition, live mass measurement avoids or minimizes a death toll, unlike all insect preservation techniques.

Biomass data of Odonata are used in studies of ontogeny, reproductive fitness, flight biophysics and energetics, physiological ecology, and behavioral ecology (MAY, 1976, 1984; ANHOLT et al., 1991; BAKER et al., 1992; DUNHAM, 1993; CORDERO, 1994; WAKELING, 1997). However, there exists a paucity of descriptive odonate mass data (BECKEMEYER, 1999; but see ANHOLT et al., 1991) and allometry between total mass and body length has not been reported for freshly captured adult stages. The need to fill this information gap is underscored by overwhelming evidence that the Odonata are strong candidates as indicators of ecological integrity (e.g., SAMWAYS, 1993; SAMWAYS & STEYTLER, 1996; CHOVANEC & RAAB, 1997; STEWART & SAMWAYS, 1998; CHOVANEC & WARINGER, 2001; BRIERS & BIGGS, 2003) and the assessment of ecosystem functions, such as production, generally lags behind structural investigations (BENKE, 1984; AINSLIE, 1994; GESSNER & CHAUVET, 2002).

The specific objectives of the present study were to (1) compile live-mass data for adult dragonflies and damselflies and quantitatively compare select species, and (2) analyze relationships between fresh-body length and biomass in a small suite of dragonflies as a first-step feasibility test for mass prediction. Our discussion covers some fine points of mass prediction using length, both in general and as pertains to Odonata.

METHODS

On 11 July and 19-20 August 2003, adult odonates were collected from 17 locations within the Noxubee National Wildlife Refuge, Noxubee Co., MS, USA (33°17'N, 88°48'W). Sampled habitats included reservoir littoral zones and spillways, bottomland hardwood forest, cypress-tupelo sloughs, roadside ditches, and open fields adjacent to lentic breeding habitat, spread across approximately 45 km².

All encountered Odonata were captured with aerial nets during a 1 h period at each location and processed within 0.5 h. Therefore, the amount of time between capture and weighing of any individual never exceeded 1.5 h. Netted individuals were immediately inspected to facilitate prompt release of animals in poor condition (e.g., tattered wings, missing body parts). Specimens were inserted into separate glassine envelopes and transported to a temperature--controlled facility located within 9.6 km of all collection sites. The catch was sorted by species and by gender within species, and individuals were weighed to 0.01 mg (Fisher Scientific accu-124D electronic balance). Specimens were gently blotted with Kimwipes immediately prior to weighing to minimize exoskeletal moisture effects. Body length (mm) was measured from frons to abdominal apex, excluding the caudal appendages (i.e., cerci, epi-, and paraprocts). Odonata were kept alive and returned to capture locations immediately after processing. Collections at a given location were never repeated.

Data were pooled across all sampling locations and for the mid July and August dates. We statistically crossed select species with sex using factorial ANOVA and made LSD multiple comparisons to rank mean response
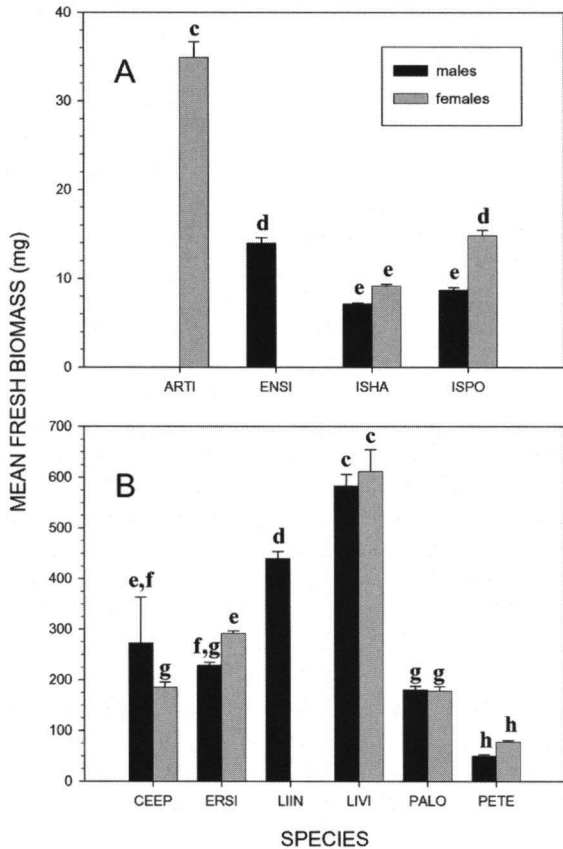

Fig. 1. Average total fresh mass of select adult Odonata collected in the Noxubee NWR. Panel A are damselflies: ARTI = *Argia tibialis*; ENSI = *Enallagma signatum*; ISHA = *Ischnura hastata*; ISPO = *Ischnura posita*. Panel B are dragonflies: CEEP = *Celithemis eponina*; ERSI = *Erythemis simplicicolis*; LIIN = *Libellula incesta*; LIVI = *Libellula vibrans*; PALO = *Pachydiplax longipennis*; PETE = *Perithemis tenera*. Within panels, species/sexes sharing any lower-case letter are not significantly different ($\alpha = 0.05$). Error bars are $\pm$ 1 SE.

(biomass). Separate analyses were conducted for the suborders Zygoptera and Anisoptera. Biomass is obviously size-dependent, but the aim here was to differentiate fresh mass variability within species and among taxonomic relations. Length-mass correlation in select dragonflies (sexually mature, n > 5 replicates) was tested with a series of gender segregated simple linear regressions. Natural log, $\log_{10}$ and base-specified logarithmic transformations of data produced similar fits; natural log regressions are reported here. Analysis of covariance (ANCOVA) was used to compare sex-specific regression slopes among species, using length as the covariate and mass as the response. Analyses were performed with SAS V8.01 (SAS Institute Inc., Cary) and Data Desk 6.0 (Data Description, Inc., Ithaca).

RESULTS

TOTAL LIVE MASS

A total of 296 adult specimens among 19 species were weighed. Species having n ≥ 5 mature individuals were used for fresh mass comparisons. Overall, gender and species interacted significantly to affect mass in both libellulid dragonflies (p = 0.021) and coenagrionid damselflies (p = 0.001); overall p-values were corrected for missing sex levels (Fig. 1).

Reproductively mature Odonata can be sexually dimorphic in terms of fresh mass. For the damselflies (Fig. 1A), *Ischnura posita* sexes differed (p < 0.0001) where as those of I. hastata did not. Fresh mass of *Argia tibialis* exceeded all other damselflies and results for this species apply to immature females. With respect to dragonflies (Fig. 1B), male and female *Libellula vibrans* weighed significantly more than any other species, including males of the congener *L. incesta*, but genders of *L. vibrans* were not significantly different from each other. *Pachidiplax longipennis* and *Perithemis tenera* also did not show significant mass differentiation by sex, but males and females in *Celithemis eponina* and *Erythemis simplicicolis* were dissimilar (p = 0.0071 and p = 0.0198, respectively). Interestingly, males of *C. eponina* and *E. simplicicolis* were more similar to males and females of each other's species than to females of their own species (Fig. 1B). *C. eponina* was the only species in which males significantly outweighed females.

Live-mass data for additional species captured during this study are listed in Table I. Mature adults were those fully hardened with the coloration typical of re-

Table I
Fresh (live) biomass of adult Odonata collected in east-central Mississippi, USA.
Data are given as mean mass (mg) for any n > 1; values in parentheses indicate n observations.
mM = mature males; tM = teneral males; mF = mature females; tF = teneral females

Species	Biomass
Argia apicalis (Say)	mM = 37.88 (1)
Argia tibialis (Rambur)	mM = 26.30 (1); tM = 22.25 (1)
Dromogomphus spinosus (Selys)	mF = 571.57 (1)
Enallagma signatum (Hagen)	mF = 18.58 (3)
Epitheca princeps Hagen	mM = 486.70 (3)
Erythemis simplicicolis (Say)	tF = 132.69 (1)
Erythrodiplax minuscula (Rambur)	mM = 86.87 (1)
Ischnura ramburii (Selys)	mM = 32.09 (2); mF = 47.31 (3); tF= 22.05 (1)
Lestes disjunctus Selys	mF = 77.11 (1)
Lestes rectangularis Say	mM = 55.76 (1)
Libellula incesta Hagen	mF = 432.50 (2)
Libellula lydia Drury	mM = 362.44 (2); mF = 362.44 (2); tF = 206.86 (6)
Pachydiplax longipennis (Burmeister)	tF = 78.63 (5)
Tramea carolina (Linnaeus)	mM = 319.38 (2)

productively active individuals (ANHOLT et al., 1991), where as tenerals had soft bodies, cryptic coloration, and glassy wings.

<div align="center">LENGTH-MASS CORRESPONDENCE</div>

Length-mass regressions are given for the same 6 anisopteran species as depicted in Figure 1B. A total of 118 data points, spread unevenly among the 6 Anisoptera, were used for length-mass regressions by species and intraspecific sex (Fig. 2).

All correlations were significant and had a p-value range from <0.0001 to 0.03. Total body length accounted for 59-94% of the variation in biomass. Female *Celithemis eponina* and male/female *Pachydiplax longipennis* displayed the strongest correlations (r^2 = 0.94 and 0.93/0.91, respectively) between body length and fresh
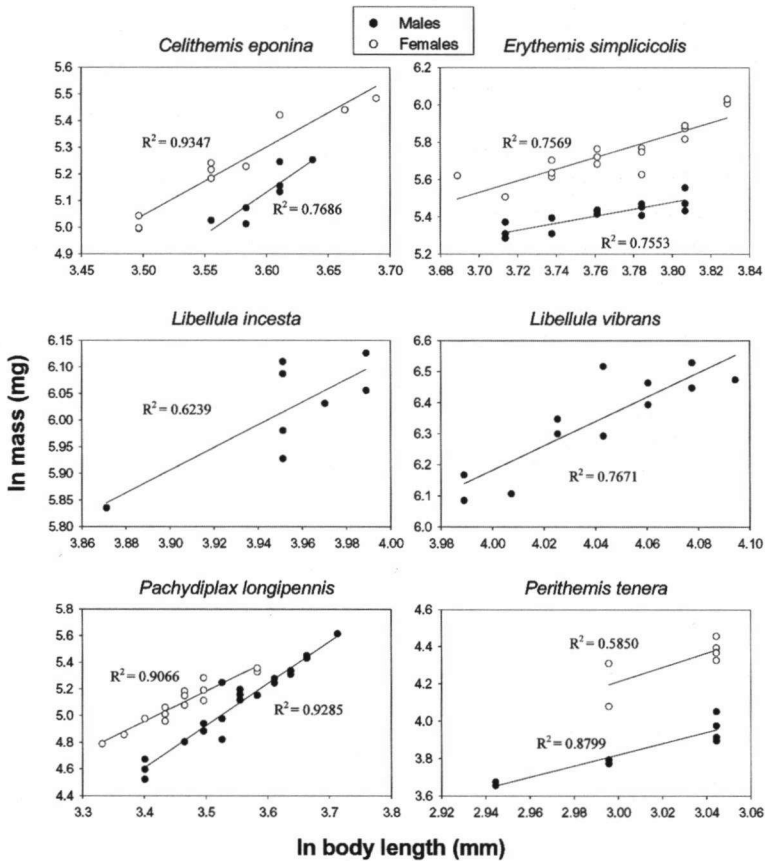

Fig. 2. Transformed total body length vs. fresh mass for select adult Anisoptera collected in the Noxubee NWR. All correlations are significant (α = 0.05).

mass. Data distributions in *Perithemis tenera* and male *Libellula incesta* were poor due to tied length values and outliers and should therefore be interpreted with caution. Lengths of *P. tenera* and *L. incesta* were non-normal (p > 0.2, Shapiro-Wilk test, PROC UNIVARIATE, SAS). Length-mass patterns were congruent among the remaining sex partitioned species (Length × Species, p > 0.05, Tab. II) and correlations for pooled data were strong (Fig. 3).

DISCUSSION

TOTAL LIVE MASS

As with previous studies (ANHOLT et al., 1991; DUNHAM, 1993; BECKE-MEYER, 1999), our results demonstrate that total fresh mass may differ inter- and intraspecifically in adult Odonata.

All damselfly species used in the comparative mass analysis belonged to Coenagrionidae (Fig. 1A) while all dragonflies belonged to Libellulidae (Fig. 1B). Both families are highly speciose in North America, which increases the likelihood of mass differentiation among member taxa. For example, *Argia* exhibit larger overall body size than confamilial *Ischnura* or *Enallagma*, thus explaining why teneral *A. tibialis* were more massive than the three mature coenagrionids (Fig. 1A). Separating specimens by age is at least somewhat subjective and we elected to minimize potential age bias with a teneral vs. mature dichotomy. DUNHAM (1993) reported little intermediate-level (immature) mass gain in *Pachydiplax longipennis* and found strong dissimilarity only between teneral and mature age classes.

Fresh mass heterogeneity was observed at the generic level, as exemplified by the differences between *Libellula vibrans* and male *L. incesta* and between the two *Ischnura*, although only with respect to female *I. posita*. Mean mass of mature *L. lydia* (362.44 mg average for both sexes) is much less than for the two measured congeners (Tab. I). Of course, one might expect interspecific differences within these particular genera from a small diversity sample since both have high representation in North America (23 *Libellula* spp, 14 *Ischnura* spp).

Sexually dimorphic fresh mass was observed in 3 of the 7 species analyzed intraspecifically (Fig. 1). Sex-specific mass differences are known for the Odonata (ANHOLT et al., 1991; DUNHAM, 1993; CORDERO, 1994), as well as various other insect taxa (e.g., wasps, MACKAUER, 1996). ANHOLT et al. (1991) determined that in 63% of 54 adult odonate species examined, females significantly outweighed males at maturity. Differential mass gain among males and females corresponds to where mass is allocated for increasing reproductive fitness. In females, increased abdomen size means greater capacity for larger eggs and clutch sizes (CORDERO, 1994), where as male size and flight muscle likely correlate to territorial ability and thus, indirectly, to reproductive success (ANHOLT et al., 1991; DUNHAM, 1993). This explanation is congruent with the finding of CORDERO (1994) in which fe-

males of a coenagrionid damselfly exhibited higher abdominal mass relative to males, while male thoracic mass exceeded that of females.

It should be noted that in the current study, species mass data were pooled for individuals collected across 17 localized habitat areas during mid July and August. As such, observed mass patterns might reflect weighing multiple cohorts of a species within or among sites, which may in turn add variance to water:tissue mass ratios. However, no relevant information, at least to our knowledge, has been published for adult Odonata. Mass patterns are poorly understood among spatially disjunct populations of aquatic insects (SMOCK, 1980; DUNHAM, 1993; BENKE et al., 1999). DUNHAM (1993) determined that *Pachydiplax longipennis* males caught in Florida exhibited greater mass gain relative to females through to maturity, where as the present study and ANHOLT et al. (1991) found no significant sex difference among populations collected in Mississippi and New Jersey, respectively. If macro-spatial scale is a primary mass regulatory factor, it seems Mississippi and Florida results should be more congruous, based on latitudinal geography alone and barring differences in methods of weight measurement. Of course our results do not represent actual mass gain or average mass over the adult life span, as may be attained from mark-recapture or other time series sampling methods. A possible cause for discrepancy between the current study and that of DUNHAM (1993) is that our data were obtained from three collection dates over ~1 mo period and not throughout the flight season.

In general it is difficult to make comparisons among the total mass of species examined in this study with that reported in the literature because authors either examined different species, neglected total body mass measurement, or reported dry weights for the few taxa that overlapped this study.

Table II

Analysis of covariance to test deviation in length-mass pattern (slope) among males and females of several libellulid dragonflies. Length and mass data were normally distributed in each species/sex. Type I-IV sum of squares produced the same results ($\alpha = 0.05$)

Source	DF	Type I SS	Mean Square	F Value	Pr > F
Males, y = mass					
Length	1	14.2856	14.2856	3020.46	< 0.0001
Species	3	0.5502	0.1834	38.78	< 0.0001
Length×Species	3	0.0360	0.0120	2.54	0.0680
Females, y = mass					
Length	1	4.3204	4.3204	1129.44	< 0.0001
Species	2	0.0875	0.0438	11.44	0.0002
Length×Species	2	0.0128	0.0064	1.68	0.2020

LENGTH-MASS CORRESPONDENCE

MAY (1981) summarized allometry among a variety of body dimensions in adult Odonata. However, all data were pooled for an untold variety of species and taxonomic levels, and body length measurements were not taken.

Our results suggest strong linear relationships between fresh body length and total mass in adult Anisoptera. The six test species provided a wide range of mature adult size differences and are among the common North American representatives of the most speciose dragonfly family, the Libellulidae. Tenerals were omitted and genders were analyzed separately within species because of known dissimilarity between sexually mature versus immature age classes (e.g., degree of chitinization, SMOCK, 1980) and between male versus female mass gain in adult Odonata (AN-HOLT et al., 1991; DUNHAM, 1993).

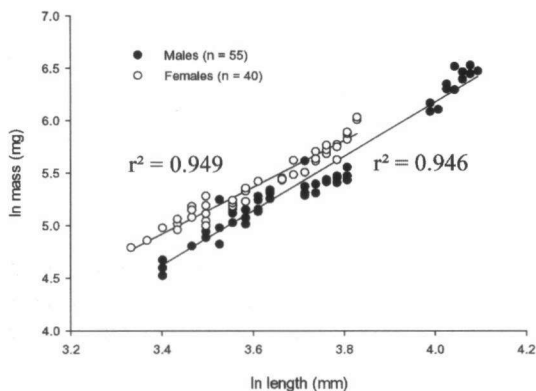Note that data distributions for *Libellula incesta* and *Perithemis tenera* (Fig. 2) are composed of overlapping length values. This reflects the coarse measurement scale (i.e., nearest 1 mm) necessary for field measurement. SMOCK (1980) measured larval odonate lengths to 0.1 mm. In the interest of quick and non-destructive collection of fresh mass data, say as a tool for rapid assessment of aquatic ecosystem function, 0.5 to 1.0 mm resolution is probably the finest for accurate field measurement.

Fig. 3. Transformed total body length vs. fresh mass pooled among males of *Celithemis eponina*, *Erythemis simplicicolis*, *Libellula vibrans*, and *Pachydiplax longipennis* and females of *C. eponina*, *E. simplicicolis*, and *P. longipennis*. p < 0.0001 for both sexes.

Patterns of length-mass gain (regression slope) were congruent amongst analyzed sex-specific libellulid species (Tab. II). This suggests that a single collective length-mass equation is sufficient for predicting fresh mass in each of these taxa. The pooled length-mass correlation was strong (Fig. 3) and could provide rough mass estimation for the tested sex-divided species, and for other morphologically and taxonomically related species. Of course at familial resolution, greater morphological variation should exist than at generic or species levels. Therefore, if mass prediction is desired then analyses of too few species within a highly speciose family will reduce extrapolation power directed towards the fraction of unsampled species within that family. Quality of mass prediction from higher taxonomic level regressions, such as for families or orders, is linked to

adequate representation of species diversity and will always be less powerful than well replicated species-level analyses. Such consideration is crucial for reliable mass prediction from length measurements (see next section).

MASS PREDICTION USING LENGTH

Reliable length-mass equations may accelerate biomass and production estimates for Odonata and other invertebrate taxa (e.g., earthworms, HALE et al., 2004). JOHNSON et al. (2000) used a species-specific mayfly length-mass equation provided in BENKE et al. (1999) to aid estimation of annual secondary production of freshwater marsh in West Virginia, USA. SCHEFFER et al. (1984) used equations published by SMOCK (1980) to link insect production with vegetative physiognomy. GLADDEN & SMOCK (1990) and DUFFY & LaBAR (1994) were able to accelerate the weighing process by performing length-mass regressions on initial collections to generate equations for predicting mass in their subsequent samples; sampling effort here could have been minimized further if corresponding length--mass equations were already available in the literature.

Length-mass equations use constants derived from plotting mass as a power function of body length:

[Eq. 1] $$M = aL^b$$

or, in linear form:

[Eq. 2] $$\ln M = \ln a + b \ln L$$

where M is organism mass (mg), L is length (mm), and a and b are constants. The exponent b of the power model becomes the slope in the linear transformation, while $\ln a$ is the intercept or elevation. Equations usually are presented as a, b constants $\pm$ S.E. (see SMOCK, 1980; BENKE et al., 1999).

We provide regression parameters for the studied relationships in Table III. These equations should only be used for comparisons in future studies and not for predicting mass. Greater replication is needed before predictive equations for the studied taxa may be used in practice. Furthermore, unknown differences in biometric relationships between geographically isolated populations (SMOCK, 1980; BENKE et al., 1999) could affect robustness of equations. Spatially and/or temporally disparate populations of aquatic insects are generally exposed to unequal environmental conditions that may affect growth and length-mass relationships. Odonatology needs systematic investigation of adult length-mass patterns across spatio-temporal gradients.

Predicting biomass using equations 1 and 2 requires the linear dimension L (body length in this study), which may be attained from, (1) averaging lengths from a subset of live individuals captured onsite, (2) the primary literature as available, (3) taxonomic keys, which often provide range and/or mean linear dimensions, or (4) preserved museum specimens. Surrogate size dimension metrics (e.g., wing length) may also be used in the case of adult odonates (see MAY, 1981; CORDERO, 1994).

Table III

Parameter estimates for length-mass relationships in the taxa studied. Equations are shown strictly for demonstrative and comparative purposes and should not be used for actual estimation of mass (see text). Parameters for the Libellulidae are averages across the six species shown. n refers to the number of individuals used and *range* represents the min-max lengths (nearest 1.0 mm) of each sample

Taxa	Sex	Power Model a	b	Linear (ln) Model a ± 1 SE	b ± 1SE	r^2	n	Range
Celithemis eponina	M	0.0013	3.268	6.378 ± 2.824	3.197 ± 0.785	0.76	7	35-38
	F	0.0307	2.440	3.926 ± 0.855	2.563 ± 0.239	0.94	10	33-40
Erythemis simplicicolis	M	0.1939	1.874	1.687 ± 1.119	1.886 ± 0.298	0.75	15	41-45
	F	0.0008	3.424	5.978 ± 1.776	3.111 ± 0.471	0.76	16	40-46
Libellula incesta	M	0.1094	2.083	2.388 ± 2.665	2.127 ± 0.674	0.59	8	48-54
	F	na	na	na	na	na	na	na
Libellula vibrans	M	0.0002	3.680	3.926 ± 0.855	2.563 ± 0.239	0.76	12	54-60
	F	na	na	na	na	na	na	na
Pachydiplax longipennis	M	0.0027	3.099	6.126 ± 0.715	3.157 ± 0.201	0.93	21	30-41
	F	0.0877	2.176	2.752 ± 0.727	2.267 ± 0.210	0.90	14	28-36
Perithemis tenera	M	0.0044	3.075	5.187 ± 1.362	3.002 ± 0.453	0.85	8	19-21
	F	0.0009	3.731	7.341 ± 4.395	3.851 ± 1.450	0.59	7	20-21
Libellulidae	M	0.0520	2.847	4.282 ± 1.556	2.655 ± 0.126	na	6	19-60
	F	0.0300	2.943	4.999 ± 2.107	2.948 ± 0.727	na	4	20-46

Wing length may be an easier field measurement than body length for living dragonflies because wings are easier to immobilize and measure with one set of hands.

It is recommended that mass be estimated using available species-level predictive equations involving a linear dimension (BENKE et al., 1999), namely body length for adult dragonflies. Family level equations have lower predictive ability and are only recommended for use when generic or species-specific equations are not available for the taxa under study (SMOCK, 1980; BURGHERR & MEYER, 1997; BENKE et al., 1999) and the researcher is too constrained by logistical matters (e.g., lack of time or personnel) to generate specific equations. If higher taxonomic equations must be used, then combined length-width measurements, rather than length alone, should help control for morphological variation (SAMPLE et al., 1993).

Fresh and preserved insect specimens differ in total biomass. Estimating biomass from collections of preserved specimens is met with the following uncertainties and potential disadvantages: (1) different preservation techniques may yield different specimen weights (GONZALEZ et al., 2002); acetone treatment is common in adult dragonfly preservation and likely extracts lipids (ANHOLT et al., 1991), (2) specimen quality, including mass, is probably associated with length of time in storage, (3) geographic identity of the collection (SMOCK, 1980; DUNHAM, 1993; BENKE et al., 1999), and (4) logistical concerns, such as finding the same species in collections, and enough replicates of those species, that were observed onsite. Creating dry-mass equations for each preservation method is impractical but necessary in order to have reliable species-specific equations. Currently there

are no standard procedures for converting fresh mass to preserved mass and vice-versa. Until the relationship (or lack thereof) between fresh versus preserved mass for adult odonates is better understood, equations for the two should not be used interchangeably.

Appropriate construction and application of length-mass equations, in Odonata as well as insects in general, requires prior separation of specimen quality (fresh vs. preserved), life stage (larva vs. adult), maturation stage (e.g., teneral adult vs. mature adult), gender, and taxonomic level. Another potential consideration is the geographic and temporal context of target populations. Secondary production represents a process attribute of ecosystems and can be used to diagnose functional integrity and performance of those ecosystems (e.g., JOHNSON et al., 2000; ZIMMER et al., 2001; CARLISLE & CLEMENTS, 2003). Applied secondary production research in aquatic systems will no doubt benefit by studying length-mass relationships in Odonata. These insects are easy to identify/sample in adult form and their mature mass is an integrated response to both an aquatic and terrestrial existence. Regression equations can help provide reliable mass information and are attractive for their speed and simplicity.

REFERENCES

ANHOLT, B.R., J.H. MARDEN & D.M. JENKINS, 1991. Patterns of mass gain and sexual dimorphism in adult dragonflies (Insecta: Odonata). *Can. J. Zool.* 69: 1156-1163.
AINSLIE, W.B., 1994. Rapid wetland functional assessment: It's role and utility in the regulatory arena. *Water Air Soil Pollut.* 77: 433-444.
BAKER, R.L., M.R.L. FORBES & H.C. PROCTOR, 1992. Sexual differences in development and behavior of larval Ischnura verticalis (Odonata: Coenagrionidae). *Can. J. Zool.* 70: 1161-1165.
BECKEMEYER, R.J., 1999. Measurements of total fresh mass for some species of Odonata from the Great Plains of the United States. *Notul. odonatol.* 5: 35-36.
BENKE, A.C., 1984. Secondary production of aquatic insects. *In:* D.M. Rosenberg & D.H. Resh, [Eds], *The ecology of aquatic insects,* pp. 289-322, Praeger Scientific, New York.
BENKE, A.C., A.D. HURYN, L.A. SMOCK & J.B. WALLACE, 1999. Length-mass relationships for freshwater macroinvertebrate communities in North America with particular reference to the southeastern United States. *Jl N. Am. benthol. Soc.* 18: 308-343.
BRIERS, R.A. & J. BIGGS, 2003. Indicator taxa for the conservation of pond invertebrate diversity. *Aquat. Conserv. Marine Freshw. Ecosyst.* 13: 323-330.
BURGHERR, P. & E.I. MEYER, 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Arch. Hydrobiol.* 139: 101-112.
CARLISLE, D.M. & W.H. CLEMENTS, 2003. Growth and secondary production of aquatic insects along a gradient of Zn contamination in Rocky Mountain streams. *Jl N. Am. benthol.l Soc.* 22: 582-597.

CHOVANEC, A. & R. RAAB, 1997. Dragonflies (Insecta: Odonata) and the ecological status of newly created wetlands - Examples for long-term bioindication programmes. *Limnologica* 27: 381-392.

CHOVANEC, A. & J. WARINGER, 2001. Ecological intergrity of river-floodplain systems-Assessment by dragonfly surveys (Insecta:Odonata). *Regulated Rivers Mngmt Res.* 17: 493-507.

CORDERO, A., 1994. Reproductive allocation in different-sized adult Ischnura graellsii (Rambur) (Zygoptera: Coenagrionidae). *Odonatologica* 23: 271-276.

DERMOTT, R.M. & C.G. PATERSON, 1974. Determining dry weight and percentage dry matter of chironomid larvae. *Can. J. Zool.* 52: 1243-1250.

DUFFY, W.G. & D.J. LaBAR, 1994. Aquatic invertebrate production in southeastern USA wetlands during winter and spring. *Wetlands* 14: 88-97.

DUNHAM, M., 1993. Changes in mass, fat content, and water content with growth in adult Pachydiplax longipennis (Odonata: Libellulidae). *Can. J. Zool.* 71: 1470-1474.

GESSNER, M.O. & E. CHAUVET, 2002. A case for using litter breakdown to assess functional stream integrity. *Ecol. Appls* 12: 498-510.

GLADDEN, J.E., & L.A. SMOCK, 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. *Freshw. Biol.* 24: 533-545.

GONZALEZ, J.M., A. BASAGUREN & J. POZO, 2002. Size-mass relationships of stream invertebrates in a northern Spain stream. *Hydrobiologia* 489: 131-137.

HALE, C.M., P.B. REICH & L.E. FRELICH, 2004. Allometric equations for estimation of ash-free dry mass from length measurements for selected European earthworm species (Lumbricidae) in the Western Great Lakes Region. *Am. Midl. Nat.* 151: 179-185.

JOHNSON, B.R., D.C. TARTER & J.J. HUTCHENS, Jr, 2000. Life history and trophic basis of production of the mayfly Callibaetis fluctuans (Walsh) (Ephemeroptera: Baetidae) in a mitigated wetland, West Virginia, USA. *Wetlands* 20: 397-405.

MACKAUER, M., 1996. Sexual size dimorphism in solitary parasitoid wasps: Influence of host quality. *Oikos* 76: 265-272.

MAY, M.L., 1976. Warming rates as a function of body size in periodic endotherms. *J. comp. Physiol.* 111: 55-70.

MAY, M.L., 1981. Allometric analysis of body and wing dimensions of male Anisoptera. *Odonatologica* 10: 279-291.

MAY, M.L., 1984. Energetics of adult Anisoptera, with special reference to feeding and reproductive behavior. *Adv. Odonatol.* 2: 95-116.

MILLER, W.E., 1976. Wing measure as a size index in Lepidoptera: The family Olethreutidae. *Ann. ent. Soc. Am.* 70: 253-256.

SAMPLE, B.E., R.J. COOPER, R.D. GREER & R.C. WHITMORE, 1993. Estimation of insect biomass by length and width. *Am. Midl. Nat.* 129: 234-240.

SAMWAYS, M.J., 1993. Dragonflies (Odonata) in taxic overlays and biodiversity conservation. *In*: K.J. Gaston, T.R. New & M.J. Samways, [Eds], *Perspectives on insect conservation*, pp. 111-123, Intercept, Andover / Hampshire, UK.

SAMWAYS, M.J. & N.S. STEYTLER, 1996. Dragonfly (Odonata) distribution patterns in urban and forest landscapes, and recommendations for riparian management. *Biol. Conserv.* 78: 279-288.

SCHEFFER, M., A.A. ACHTERBERG & B. BELTMAN, 1984. Distribution of macro-invertebrates in a ditch in relation to the vegetation. *Freshw. Biol.* 14: 367-370.

SMOCK, L.A., 1980. Relationships between body size and biomass of aquatic insects. *Freshw. Biol.* 10: 375-383.

STEWART, D.A. & M.J. SAMWAYS, 1998. Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. *Conserv. Biol.* 12: 683-692.

WAKELING, J.M., 1997. Odonatan wing and body morphologies. *Odonatologica* 26: 35-52.

ZIMMER, K.D., M.A. HANSON, M.G. BUTLER & W.G. DUFFY, 2001. Size distribution of aquatic invertebrates in two prairie wetlands, with and without fish, with implications for community production. *Freshw. Biol.* 46: 1373-1386.