

*Estimating benthic invertebrate  
production in lakes: a comparison of  
methods and scaling from individual taxa  
to the whole-lake level*

**Aquatic Sciences**  
Research Across Boundaries

ISSN 1015-1621  
Volume 73  
Number 1

Aquat Sci (2010) 73:153-169  
DOI 10.1007/  
s00027-010-0168-1



**Your article is protected by copyright and all rights are held exclusively by Springer Basel AG. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

# Estimating benthic invertebrate production in lakes: a comparison of methods and scaling from individual taxa to the whole-lake level

Katrina J. Butkas · Yvonne Vadeboncoeur ·  
M. Jake Vander Zanden

Received: 2 March 2010 / Accepted: 11 October 2010 / Published online: 3 November 2010  
© Springer Basel AG 2010

**Abstract** Studies of aquatic invertebrate production have been primarily conducted at the level of individual taxa or populations. Advancing our understanding of the functioning and energy flow in aquatic ecosystems necessitates scaling-up to community and whole-lake levels, as well as integrating across benthic and pelagic habitats and across multiple trophic levels. In this paper, we compare a suite of non-cohort based methods for estimating benthic invertebrate production at subpopulation, habitat, and whole-lake levels for Sparkling Lake, WI, USA. Estimates of the overall mean benthic invertebrate production (i.e. whole-lake level) ranged from 1.9 to 5.0 g DM m<sup>-2</sup> y<sup>-1</sup>, depending on the method. Production estimates varied widely among depths and habitats, and there was general qualitative agreement among methods with regards to differences in production among habitats. However, there were also consistent and systematic differences among methods. The size-frequency method gave the highest, while the regression model of Banse and Mosher (Ecol Monogr 50:355–379, 1980) gave the lowest production estimates. The regression model of Plante and Downing (Can J Fish Aquat Sci 46:1489–1498, 1989) had the lowest

average coefficients of variation at habitat (CV = 0.17) and whole-lake (CV = 0.08) levels. At the habitat level, variance in production estimates decreased with sampling effort, with little improvement after 10–15 samples. Our study shows how different production estimates can be generated from the same field data, though aggregating estimates up to the whole-lake level does produce an averaging effect that tends to reduce variance.

**Keywords** Benthic secondary production · Zoobenthos · Production to biomass ratio · Methods · Benthic trophic pathways

## Introduction

Studies of lake ecosystems have focused predominantly on pelagic production and processes (Reynolds 2008; Kalff 2002; Dodson 2005). Yet benthic habitats often contribute a large fraction of lake autochthonous primary production (Vadeboncoeur et al. 2003). Benthic primary production can be an important trophic pathway supporting fishes in lakes (Weidel et al. 2008; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). There is growing recognition that benthic invertebrates play a central role in channeling energy flow through lake food webs and supporting the production of higher trophic levels (Johannsson et al. 2000; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002; Reynolds 2008; Weidel et al. 2008).

Unfortunately, our understanding of energy flow in lakes, and the role of benthic secondary production in particular, is quite limited. Research from the International Biological Program era (1964–1974) produced a number of benthic invertebrate production measurements for lakes

---

K. J. Butkas · M. J. Vander Zanden (✉)  
Center for Limnology, University of Wisconsin-Madison,  
680 N. Park St., Madison, WI 53706, USA  
e-mail: mjvanderzand@wisc.edu

Y. Vadeboncoeur  
Department of Biological Sciences 235A BH,  
Wright State University, Dayton, OH 45435, USA

*Present Address:*  
K. J. Butkas  
4477 County Rd 32, Bloomfield, NY 14469, USA

(summarized in Waters 1977; Plante and Downing 1989; Lindegaard 1994; Gratton and Vander Zanden 2009), though many of the studies focused on a single taxon (Waters 1977; Plante and Downing 1989). Developing a broader understanding of energy flow in lake ecosystems necessitates expanding from populations and individual taxa, to that of communities and ecosystems, which relatively few studies have done (Strayer and Likens 1986; Babler et al. 2008). It also requires considering benthic invertebrate production within a broader food web context, through simultaneous production estimates for other trophic groups in benthic and pelagic habitats (Lindegaard 1994; Vander Zanden et al. 2006).

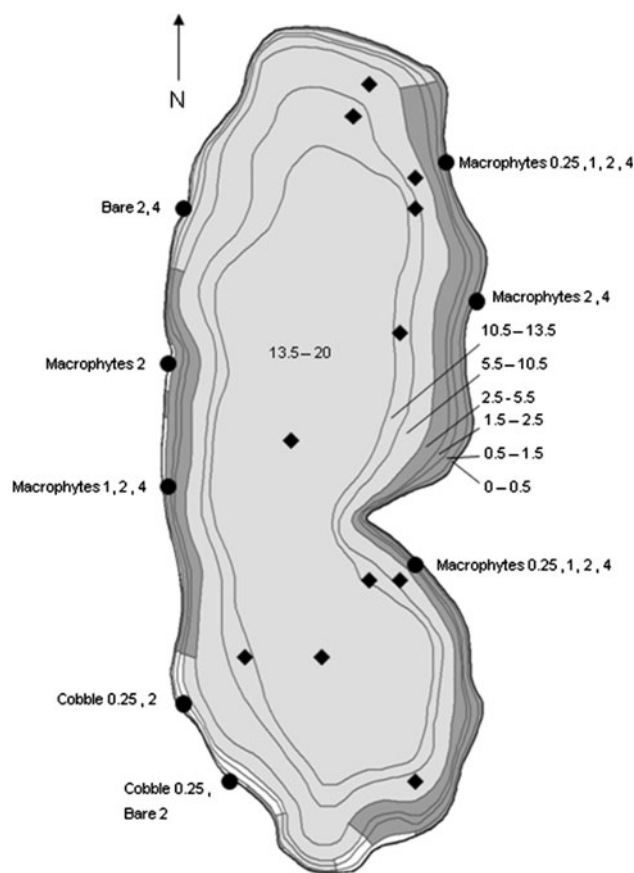
Habitat-level benthic invertebrate production estimates are typically generated by summing production estimates for individual invertebrate taxa within a specific habitat or site (Carlisle and Clements 2003; Woodcock and Huryn 2007; Babler et al. 2008). Whole-ecosystem estimates can then be generated by multiplying habitat-level estimates by the area of each habitat within an ecosystem, and summing across habitats. Most methodological studies have focused on developing and evaluating methods for estimating production for individual taxa (Waters and Crawford 1973; Benke 1979; Banse and Mosher 1980; Plante and Downing 1989; Brey et al. 1996; Stockwell and Johannsson 1997; Blukacz et al. 2005). Few studies have evaluated fundamental statistical and sampling issues such as estimation error and sampling effort associated with estimating invertebrate production at the whole-ecosystem level (Brey et al. 1996; Stockwell and Johannsson 1997), and no studies to date have done so for benthic invertebrates in lakes.

The goal of this paper is to address several fundamental issues associated with scaling benthic invertebrate production from individual taxa, to habitats, to the whole-lake level. Specifically, we develop a large benthic invertebrate dataset from Sparkling Lake, WI, USA and use it to accomplish three objectives: (1) to compare benthic invertebrate production derived using four different methods at the level of individual taxa, habitats, and an entire lake, (2) to estimate uncertainty associated with habitat-specific and whole-lake benthic invertebrate production estimates, and (3) to assess the relationship between sampling effort and error for habitat-level production estimates.

## Materials and methods

### Study system

Sparkling Lake is a dimictic, mesotrophic seepage lake in Vilas County, WI, USA (46°00'N, 89°42'W) and a core



**Fig. 1** Bathymetry, substrate type, and sampling sites for Sparkling Lake, WI, USA. Depths are in meters. *Light gray* sediment, *dark gray* macrophytes, *white* cobble. *Dots* indicate shallow-water (<5.5 m) sampling sites (sediment, macrophyte or cobble substrates), *diamonds* indicate deeper-water (>5.5 m) sampling sites (sediment only). Where multiple samples were taken at a site, substrate-depth combinations are indicated

study lake for the North Temperate Lakes Long-Term Ecological Research Program (NTL-LTER, Fig. 1). It has a surface area of 64 ha, a maximum depth of 20 m, and a littoral zone (defined as  $\geq 1\%$  of surface irradiance reaches the bottom) that extends to 14 m. Three distinct habitat types occur between the lake edge and 5.5 m: cobble, macrophyte beds, and unconsolidated sandy sediments (hereafter referred to as 'sediments'). Between 0 and 1 m, periphyton mats on sand and cobble are thin and inconspicuous, and macrophytes are scarce. At depths greater than 1 m, a thick (>1 cm) layer of periphyton covers cobbles and sand, and macrophytes are diverse and abundant. Below 5.5 m, the only habitat is unconsolidated sandy sediment, which becomes increasingly organic with depth. Periphyton occurs on the sediments down to approximately 13 m. The profundal zone (>14 m) consists entirely of fine organic sediments and can become hypoxic or anoxic during summer (<http://lter.limnology.wisc.edu/>).



## Field sampling and lab processing

Our sampling was designed to account for the habitat heterogeneity of Sparkling Lake. We defined 11 substrate-depth combinations (hereafter referred to as 'habitats'; Fig. 1). Shallow-water habitats (0–5.5 m) were as follows: macrophytes 0–0.5 m, macrophytes 0.5–1.5 m, macrophytes 1.5–2.5 m, macrophytes 2.5–5.5 m, cobble 0–0.5 m, cobble 0.5–2.5 m, sediment 0.5–2.5 m, and sediment 2.5–5.5 m. We also sampled sediment at 5.5–10.5 m, 10.5–14 m, and 14–20 m (profundal zone). Each habitat generally had multiple sampling sites at various locations within the lake: we sampled a total of 37 sampling sites (Fig. 1). Samples were collected on seven occasions during the summer of 2005 (June 9–13, June 22–23, July 6–8, July 21–25, August 2–3, August 19–21, August 26–27), and a total of 212 benthic invertebrate samples were collected.

At sites <5.5 m, SCUBA divers pressed lengths of PVC pipe part way into the sediment. Surface sediments within the enclosed area were agitated and suctioned into Nitex® bags using an air lift mechanism provided by a SCUBA tank (Taylor et al. 1995). We sampled a 0.12 m<sup>2</sup> area using a 500 µm mesh for large-bodied taxa (Amphipoda, Gastropoda, Trichoptera, Ephemeroptera, Megaloptera, Odonata, Hemiptera, Coleoptera). Smaller-bodied taxa (Diptera, Oligochaeta, Sphaeriidae, Hydrachnidia) were collected from a 0.018 m<sup>2</sup> area using a 250 µm mesh. Invertebrates were picked by eye for the 500 µm samples and using a dissecting scope for 250 µm samples. At sites deeper than 6 m, we used an Ekman grab (0.023 m<sup>2</sup>) and sieved samples through a 250 µm mesh. All small and large-bodied taxa visible using a dissecting scope were picked from the Ekman samples. Many of the 250 µm and Ekman samples were ¼ subsampled to expedite sample processing.

Invertebrates were identified to the lowest practical taxonomic level. Mollusks, crustaceans and insects were generally identified to family or genus. However, Oligochaetes and mites (Hydrachnidia) were not identified beyond these coarse taxonomic groupings. All individuals were counted and measured for length using an ocular micrometer. For most taxa, length was converted to individual dry mass (DM) according to regressions in Benke et al. (1999). For unionid mussels and crayfish, we applied our own unpublished length-weight regressions. For planorbid snails, we used a length-weight regression from P. Johnson (unpublished data). For mites, we used a length-weight equation from Baumgärtner (2004).

## Production estimates for taxon-habitat combinations:

Annual production ( $P$ , g DM m<sup>-2</sup> y<sup>-1</sup>) was estimated for each taxon in each of the 11 previously-defined habitats

(e.g. *Stenonema* in cobble at 0–0.5 m). Each individual production estimate was based on an average of 19 samples. Hereafter, we refer to individuals of a taxon occurring in a habitat or substrate-depth combination as a 'subpopulation'. The term 'population' is often used to refer to a group of inter-breeding individuals of a species. In this case, all the individuals in the lake would likely comprise the population.

Production was estimated using four methods: (1) the allometric-based approach of Banse and Mosher (1980; B&M), (2) the allometric-based approach of Plante and Downing (1989; P&D), (3) a compilation of literature  $P/B$  values ( $P/B$ ), and (4) the size-frequency method (SF). We could not detect cohorts in our data, and were thus unable to apply the well-known (and more direct) cohort methods (Waters and Crawford 1973; Benke 1984). Different methods were compared by calculating the ratio of the larger to the smaller estimate (i.e., values always  $\geq 1.0$ ).

## Regression model estimates

To estimate  $P$  from the regression models and the  $P/B$  method, mean annual biomass ( $B$ , g DM m<sup>-2</sup>), maximum mass per individual ( $M_{\max}$ , mg DM individual<sup>-1</sup>), and average mass per individual ( $M_{\text{avg}}$ , mg DM individual<sup>-1</sup>) were estimated for each taxon in each habitat.  $B$  was estimated as the average biomass of a taxon in a habitat.  $M_{\max}$  and  $M_{\text{avg}}$  were the maximum and average individual masses from all individuals of a taxon measured from a habitat. Production for individual taxa was estimated from Eq. 1 in Plante and Downing (1989; P&D):

$$\text{Log } (P) = 0.06 + 0.79 \times \text{Log } (B) - 0.16 \times \text{Log } (M_{\max}) + 0.05 \times T \quad (1)$$

where  $T$  is mean annual surface water temperature (11.2°C for Sparkling Lake in 2005, <http://lter.limnology.wisc.edu/>). All logarithms in this paper are base 10.

To estimate production using the Banse and Mosher (1980) regression model (B&M, Eq. 1 from that study), we converted individual body masses in Banse and Mosher (1980) from kilocalories to milligrams using conversions in Cummins and Wuycheck (1971) and refit the model to allow comparisons among methods. The new B&M model is:

$$\text{Log } P/B = 0.62 - 0.31 \times \text{Log } (M_{\text{mat}}) \quad (2)$$

where  $M_{\text{mat}}$  is mass at maturity in mg DM individual<sup>-1</sup>. We estimated  $M_{\text{mat}}$  as  $M_{\max}$  for insects and as  $M_{\text{avg}}$  for non-insects, which is how Banse and Mosher (1980) estimated  $M_{\text{mat}}$  for their model. To estimate  $P$  using B&M, estimated  $P/B$  was multiplied by our estimate of  $B$  for each taxon-habitat combination.

### *P/B* estimates

The *P/B* method assumes that the ratio of annual production to mean biomass is approximately constant for a species or closely related taxa. Production,  $P$  (g DM m<sup>-2</sup> y<sup>-1</sup>), is thus estimated by multiplying a literature *P/B* by the mean biomass,  $B$  (g DM m<sup>-2</sup>). We compiled *P/B* values from the literature for lentic, north-temperate zoobenthos (Neess and Dugdale 1959; Potter and Learner 1974; Momot and Gowing 1977; Waters 1977; Strayer et al. 1981; Lafont 1987; Plante 1987; Lindegaard 1992; Phillips 1997; Eleutheriadis and Lazaridou-Dimitriadou 2001, Karatayev et al. *unpublished*, Babler et al. 2008). Some of these sources are compilations of literature *P/B* values and we were careful to not include the same data more than once. If a literature source gave more than one *P/B* for a taxon-lake combination (i.e. multiple years or depths), we took the average of the values. Literature *P/B* values were grouped into the following taxonomic groups: Amphipoda, Anisoptera, Ceratopogonidae, Coleoptera, Decapoda, Ephemeroptera, Gastropoda, Hydrachnidia, Isopoda, Megaloptera, non-Tanypodinae Chironomidae, Oligochaeta, Sphaeriidae, Tanypodinae Chironomidae, Trichoptera, Turbellaria, Unionidae, and Zygoptera. To estimate production for sub-populations (i.e., a taxon within a habitat), we multiplied the average *P/B* for the taxonomic group by the estimated  $B$ .

### Size-frequency estimates

SF is a non-cohort based method based on the assumption that mortality of an average cohort and individual growth can be inferred from an average size-frequency distribution (see Benke 1984). This method can only be applied if the average population density decreases in consecutive size classes. Knowledge of generation time is also required to calculate the cohort production interval (CPI) for each taxon. For SF estimates, we used the following calculation from Benke (1984):

$$365/\text{CPI} \sum_{i=1}^{i=n} \bar{M}_{i,i+1} \times (N_i - N_{i+1}) \times n \quad (3)$$

CPI is the median period required for the completion of somatic growth of the individuals comprising a cohort (Huryn 1996),  $n$  is the number of length classes chosen (typically 10),  $\bar{M}$  is the average mass per individual in a length class, and  $N$  is the average population density in a length class. CPI values were estimated based on the literature (Stead et al. 2005; Babler et al. 2008). SF production estimates were generated for the 30 taxon-habitat combinations with appropriate size-frequency distributions. There was a very close relationship between SF-based production estimates and  $B$ .

$$\text{SF estimate} = 7.29 \times B, r^2 = 0.96 \quad (4)$$

Using this equation, we estimated production for the remaining 209 taxon-habitat combinations for which the SF method could not be applied. In doing this, we applied the regression model to values that were well outside (generally below) the range of values used to develop the model. We do this here for illustrative reasons—it was the only way that the SF method could be used to estimate production at the habitat and whole-lake level.

### Habitat-specific and whole-lake production estimates

Habitat-specific production, the sum of all taxon-specific estimates within a given habitat, was estimated for each of the 11 habitats using each of the four methods. Whole-lake production was estimated by weighting habitat-specific production estimates by the area of each habitat and summing across habitats.

To calculate habitat areas, we estimated the total area at each depth interval (Fig. 1) using a digital bathymetric map of Sparkling Lake and the 3D analyst tool in ArcGIS (ESRI 2008). The locations of different substrate types within each depth interval were estimated from habitat maps generated using handheld GPS units, snorkeling surveys, and underwater photographs taken at sampling locations. We used the cut polygons feature in ArcGIS (ESRI 2008) to delineate different substrate patches and to estimate their contribution to the total area for each depth interval.

### Uncertainty in habitat and whole-lake estimates: regression models

We used nonparametric bootstrapping to quantify uncertainty in habitat-specific and whole-lake production estimates. Bootstrapping is an appropriate solution to the problem of estimating uncertainty for derived quantities that come from a series of intermediate steps with correlated and/or nonlinear input variables (Efron and Tibshirani 1986; Blukacz et al. 2005). For habitat-level production estimates using B&M and P&D, we estimated variance due to uncertainty in regression coefficients (model uncertainty) and variance due to uncertainty in the estimates of  $B$ ,  $M_{\text{max}}$ , and  $M_{\text{mat}}$  (data uncertainty). To estimate data uncertainty, we sampled our original observations (quadrat or Ekman samples) in each habitat with replacement. Values associated with a single quadrat or Ekman sample ( $B$ ,  $M_{\text{max}}$ , or  $M_{\text{mat}}$ ) were kept together in this analysis, acknowledging the covariance in the estimates of measured variables ( $B$ ,  $M_{\text{max}}$ , or  $M_{\text{mat}}$ ). The number of observations was equal to the original number taken in each habitat. The data associated with this new set of observations was used to estimate  $B$ ,  $M_{\text{max}}$ ,  $M_{\text{mat}}$ , and production from B&M and

P&D for each taxon–habitat combination, and habitat-specific production for each habitat. We repeated this procedure 1,000 times, producing 1,000 estimates of habitat-specific production for each habitat. Data uncertainty was estimated as the variance of these estimates (Efron and Tibshirani 1986; Manly 1998). Variation in biomass ( $B$ ) dominated data uncertainty, as there was little difference between estimates based on biomass ( $B$ ) alone or simultaneous consideration of biomass ( $B$ ) and body mass ( $M$ ).

We estimated model uncertainty for habitat-specific estimates from each regression model following a bootstrapping procedure in Draper and Smith (1998). We refit each regression model to its original dataset (taken from Banse and Mosher 1980 or Plante 1987) and obtained the residuals. For each model, residuals were sampled with replacement and applied randomly to the original fitted values. Each regression model was refit to this new data and regression coefficients obtained. This procedure was repeated to generate 1000 sets of coefficients for each model. These sets of regression coefficients were applied to the original estimates of individual body mass ( $M_{\max}$  or  $M_{\text{mat}}$ ) and  $B$  to generate 1,000 bootstrap estimates of  $P$  for each taxon-habitat combination. The variance of these bootstrap estimates was the model uncertainty for each taxon, and is approximately equivalent to standard (parametric) estimates of the variance of predicted values (see formula in Draper and Smith 1998). This variance was summed across all taxa within a habitat to approximate model uncertainty for a habitat.

Total variance was estimated as the sum of model and data uncertainty. Habitat-specific production estimates from bootstrapping the predictor variables ( $B$ ,  $M_{\max}$ ,  $M_{\text{mat}}$ ) and the regression coefficients were normally distributed, thus the 95% confidence interval was estimated as  $1.96 \times$  the square root of the total variance (Manly 1998). To scale up to the whole lake, the variance in whole-lake production for the two regression models was estimated by multiplying the variance for each habitat-specific estimate by the square of the habitat area and summing across habitats.

Uncertainty in habitat-specific and whole-lake estimates:  $P/B$ s

To estimate data uncertainty for the  $P/B$  method, we used bootstrap estimates of  $B$  (described previously). Each bootstrap estimate of  $B$  was multiplied by the appropriate average literature  $P/B$ . The resulting  $P$  estimates were summed across all taxa within each habitat. The variance of the resulting 1,000 habitat-specific estimates was the data variance.

To estimate model uncertainty, we held  $B$  constant, using the mean value for a taxon-habitat combination. A  $P/B$  was randomly selected with replacement from the

appropriate set of literature  $P/B$ s for each taxon and multiplied by  $B$  to estimate  $P$ . Taxon-specific estimates of  $P$  were summed to generate habitat-specific  $P$  estimates and this process was repeated 1,000 times to generate 1,000 estimates of  $P$  for each habitat. The variance was the model uncertainty for  $P/B$  habitat-specific estimates. To estimate total uncertainty (model and data uncertainty), we simultaneously bootstrapped  $B$  and  $P/B$  values (described above). Habitat-specific production estimates were log-normally distributed, thus the habitat-specific estimate was the average logarithm of the 1,000 bootstrap estimates backtransformed. The variance from bootstrapping both  $B$  and  $P/B$ s was used to generate 95% confidence intervals (back transformed from  $1.96 \times$  the square root of the variance of the logarithms of the bootstrap estimates, Manly 1998). We used the bootstrapped habitat-specific estimates to estimate whole-lake production and its 95% confidence limits. For each bootstrap run, habitat-specific estimates were multiplied by habitat area and summed to generate a whole-lake estimate.

#### Sampling effort and uncertainty

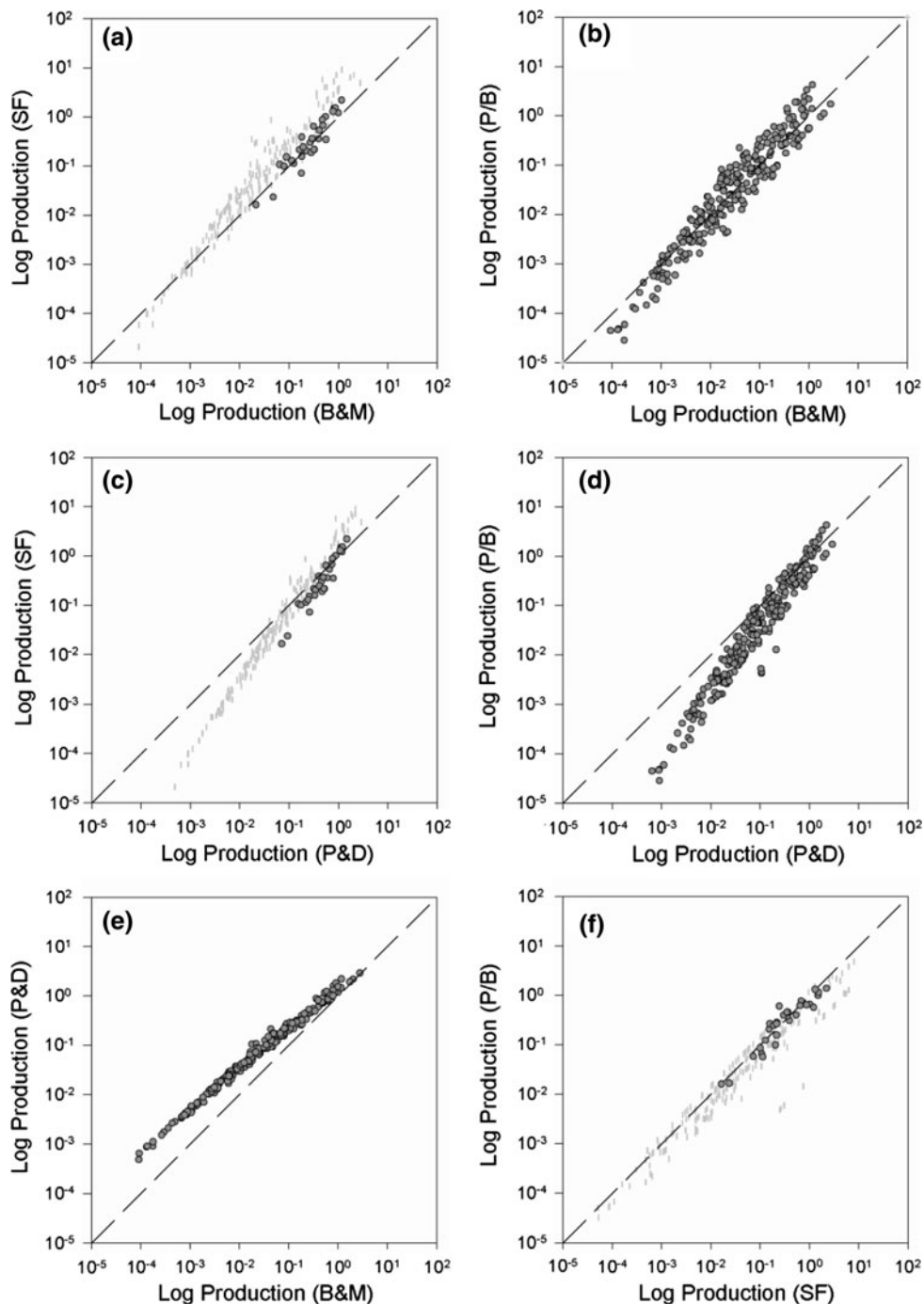
We quantified the relationships between sampling effort and data uncertainty for habitat-specific production estimated using P&D. We examined data uncertainty because it is the source of uncertainty that an investigator can control, and comprises  $\sim 88\%$  of the total uncertainty (see “Results”). We used the bootstrap procedure for estimating data uncertainty described previously (nonparametric bootstrap of  $B$  and  $M_{\max}$ ) and varied the sampling effort from one observation (quadrat or Ekman grab) to the total number of samples collected in a given habitat. At each level of sampling effort, we performed 1,000 bootstrap runs and generated an estimate of variance for each habitat. To visualize how variance changes as a function of sampling effort at the habitat-specific level, we express variance as a percentage of the maximum observed variance for that habitat (i.e., a single observation), and fit a power curve between sampling effort and percent maximum variance.

## Results

### Subpopulation-level production estimates

Production was estimated for 239 subpopulations (taxon-habitat combinations) in Sparkling Lake using the four methods: SF,  $P/B$ , P&D, and B&M (See Table 1 in Appendix). Estimates from the four methods were strongly, positively correlated with each other (Fig. 2). For some comparisons, the difference between methods depended upon the magnitude of production, with closer

**Fig. 2** Comparison of four methods to estimate benthic invertebrate production ( $\text{g DM m}^{-2} \text{y}^{-1}$ ) using data from 239 subpopulations (taxa-habitat combinations) in Sparkling Lake, WI, USA. SF is the size-frequency method, B&M is the regression model of Banse and Mosher (1980), P&D is the regression model of Plante and Downing (1989), *P/B* is based on a compilation of literature *P/B* values. Circles are direct estimates, grey vertical dashes were not amenable to SF estimation, and were estimated indirectly using a regression of production and biomass (Eq. 4). 1:1 lines are indicated



correspondence for high production values (Fig. 2c–e). Across all 1,434 pairwise comparisons of production estimates, two estimates for the same subpopulation differed by an average of  $2.9\times$ .

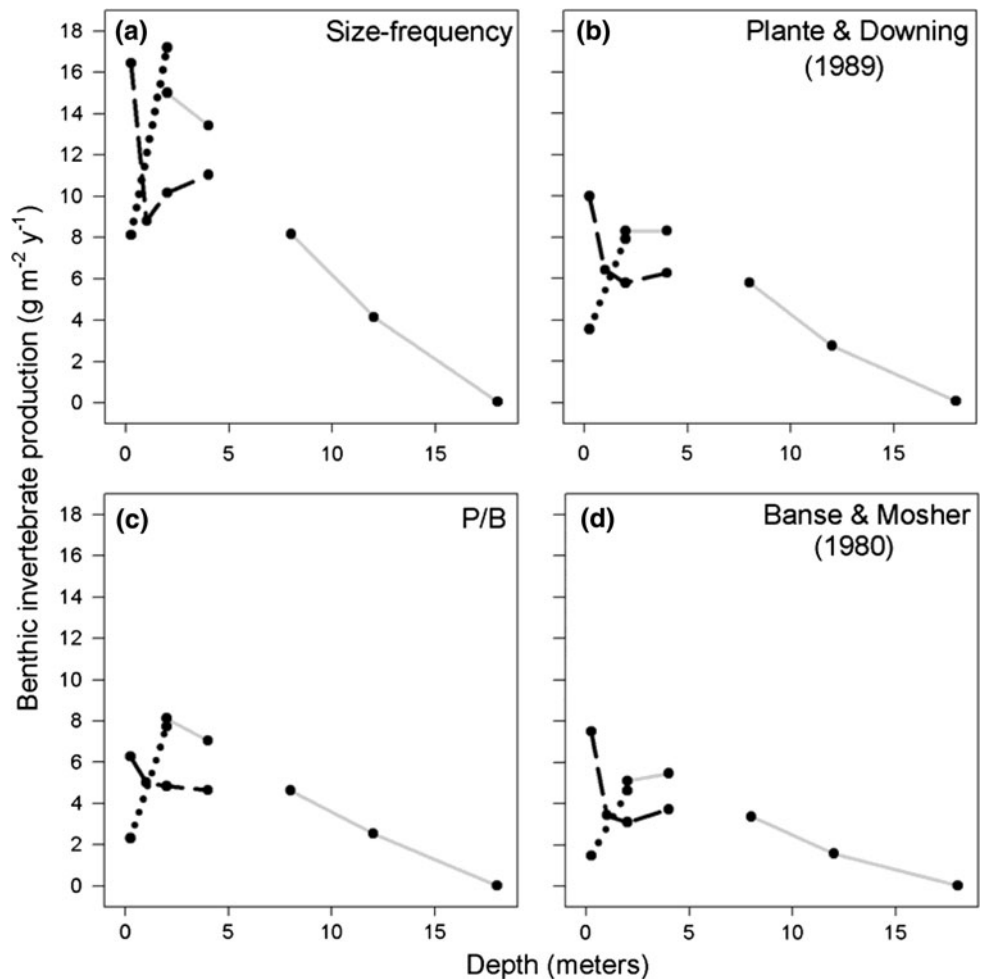
#### Habitat-specific production estimates

Habitat-specific production, defined here as the production of all taxa within a depth-substrate combination, was

estimated for the 11 habitats in Sparkling Lake using each of the four methods (Fig. 3). Benthic invertebrate production was highest in littoral habitats, averaging around  $5 \text{ g DM m}^{-2} \text{y}^{-1}$  (depending on habitat and method), and declined sharply with depth. Many qualitative trends were similar among methods. Production in sediments declined with depth. Production in macrophytes declined from 0.25 to 2 m and remained constant to 4 m. Production in cobble increased from 0.25 to 2 m (Fig. 3). Overall, SF



**Fig. 3** Depth- and habitat-specific patterns in benthic invertebrate production for Sparkling Lake, WI, USA as estimated using four methods. *Dashed line* macrophytes, *dotted line* cobble, *solid line* sediments

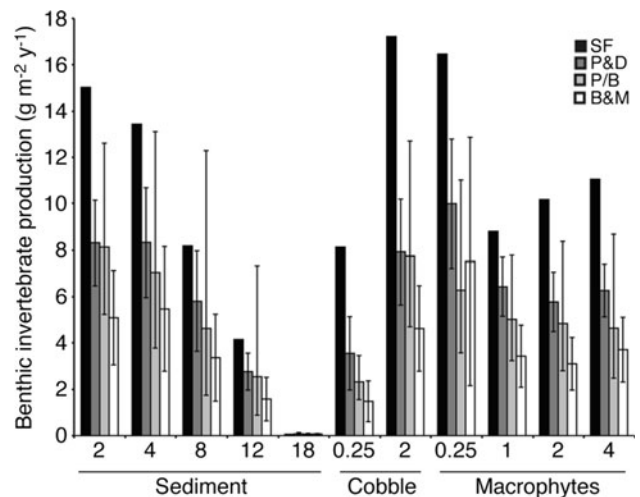


consistently gave the highest habitat-specific production, followed by P&D, *P/B*, and B&M. There were also some qualitative differences among methods. For example, the highest production was for macrophytes at 0.25 m for both P&D and B&M. For SF, the highest production was cobble at 2 m, while for *P/B* the highest production was sediment at 2 m (Fig. 3). The average difference between habitat-specific production estimates using different methods was a factor of 1.8 (range 1.0–5.4; Fig. 4).

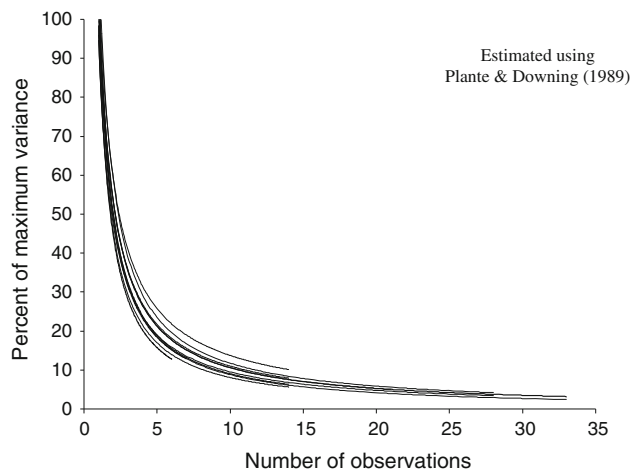
The average CV for habitat-specific production estimates was 0.45 for *P/B* (range 0.24–0.95), 0.17 for P&D (range 0.09–0.40), and 0.27 for B&M (range 0.19–0.46) (Fig. 4). For the regression models (P&D and B&M), variance in habitat-specific estimates was dominated by data uncertainty. Data uncertainty comprised an average of 88% of the total variance for P&D (range 81–96%) and 87% of the total for B&M (range 72–96%). For *P/B*s, uncertainty was dominated by model uncertainty (the uncertainty in the literature *P/B*s), which on average contributed 76% of the total uncertainty (range 60–94%).

Data uncertainty in P&D habitat-specific production estimates declined with sampling effort. The trend was

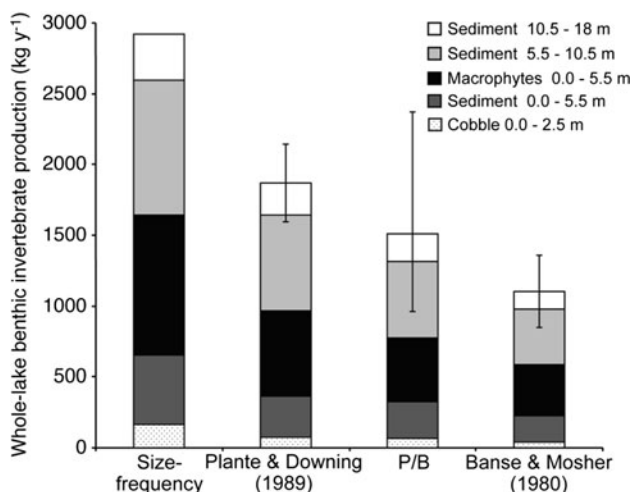
similar for all 11 habitats in Sparkling Lake (Fig. 5). Beyond approximately ten samples, there was little change in uncertainty with additional sampling effort.



**Fig. 4** Benthic invertebrate production for 11 habitats (substrate-depth combinations) in Sparkling Lake, WI, USA. *Error bars* represent 95% confidence intervals



**Fig. 5** The relationship between variance and sampling effort (number of observation) for habitat-level benthic invertebrate production in each of 11 habitats (depth-substrate combinations) in Sparkling Lake, WI, USA. Variance is derived from a nonparametric bootstrap procedure that considers data uncertainty, and is expressed as the percentage of the maximum variance (i.e.,  $n = 1$  observation) to allow comparison among habitats



**Fig. 6** Four estimates of whole-lake benthic invertebrate production for Sparkling Lake, WI, USA, divided into five general habitat categories. Error bars represent 95% confidence interval

#### Whole-lake production estimates

Habitat-level production estimates were scaled-up using lake bathymetry and habitat maps to estimate whole-lake benthic secondary production for each of the four methods. Whole-lake benthic invertebrate production estimates were in the 1,000–2,900 kg y<sup>-1</sup> range, depending on the method (Fig. 6). The highest estimate of whole-lake production (kg y<sup>-1</sup>) was generated using SF, followed by P&D, P/B and B&M. P&D and B&M estimates had relatively low errors (CV = 0.075 and 0.12, respectively), while the CV for the P/B estimate was 0.27 (Fig. 6).

#### Discussion

In this study, we estimated benthic invertebrate production in Sparkling Lake, WI at several levels of ecological organization. We were able to assess how a suite of alternative estimation methods and sampling effort affected production estimates and uncertainty at subpopulation (habitat–taxon combinations), habitat-specific, and whole-lake levels. At the habitat level, we examined the relative contributions of model versus data uncertainty for estimates derived from regression models and literature P/Bs. The four methods we considered are widely used in community and ecosystem studies of invertebrate production in a variety of ecosystem types (e.g., Lindegaard and Jonasson 1979; Strayer and Likens 1986; Lindegaard 1992; Huryn 1996; Carlisle and Clements 2003; Stead et al. 2005; Woodcock and Huryn 2007; Babler et al. 2008), though there is a paucity of studies that compare alternative methods and explicitly consider uncertainty associated with production estimates.

#### Benthic secondary production in Sparkling Lake

Our lakewide benthic secondary production rates for Sparkling Lake, in the range of 2–5 g m<sup>-2</sup> y<sup>-1</sup>, falls near the average from a recent global compilation (Gratton and Vander Zanden 2009). There was a sharp decline in benthic secondary production with depth, and a high degree of variability related to depth and substrate. Overall, the littoral zone supported a disproportionate fraction of whole-lake benthic secondary production (Fig. 6). Depth-specific patterns of benthic secondary production in Sparkling Lake are quite similar to patterns described for some lakes (Lake Mikolajskie, Lake Thingvallavatn), but not others (Lake Esrom, Turkey Lake, Little Turkey Lake), highlighting the high degree of among-lake variability in depth-specific benthic secondary production (Babler et al. 2008). Depth-specific patterns in Sparkling Lake differed notably from nearby Crampton Lake, though this may be because Babler et al. (2008) did not sample the typically unproductive profundal zone.

#### Effect of method on production estimates: subpopulations, habitats, and ecosystems

We used our field data from Sparkling Lake to compare alternative methods for estimating benthic invertebrate production in a situation that can be considered typical for north-temperate lakes. We found that any two estimates for an individual taxon differed, on average, by a factor of 2.9. Some of the largest differences among methods involved comparisons with the SF method, which we found to be problematic to apply in our study. The overall difference

among methods is comparable to that reported in other studies. Waters and Crawford (1973) found that Allen curve, removal-summation, instantaneous growth and SF estimates for a single stream mayfly population differed, at a maximum, by a factor of 1.3. Benke (1993) compared predictions from two regression models to cohort estimates for three stream taxa and found that, on average, estimates differed by a factor of 2.0 (range 1.0–4.1). Stockwell and Johannsson (1997) compared zooplankton production estimates from two regression equations to the egg ratio method for six taxa and found that, on average, estimates differed by a factor of 2.7 (range 1.0–13.0). Brey et al. (1996) compared artificial neural networks, multiple linear regressions, and instantaneous growth estimates for 32 marine benthic populations and found that on average any two estimates differed by a factor of 2.1 (range 1.0–6.2).

Two studies have considered how estimation methods affect habitat-level invertebrate production estimates. Brey et al. (1996) found that habitat-level production estimates for benthic marine taxa differed by a maximum of twofold, while a study of zooplankton community production (Stockwell and Johannsson 1997) found virtually no effect of method on production estimates. We found that, on average, habitat-level estimates generated using different methods differed by a factor of 1.8. The sometimes large among-method differences observed for individual populations are not reflected in habitat-level estimates, indicating an averaging effect, whereby differences between methods cancel out when scaling from subpopulation to habitat. Even where one method consistently provides higher estimate than another (e.g., Fig. 2a), the large among-method differences for some taxa are offset by more moderate differences for others.

We are not aware of any studies that have explicitly examined methodological and sampling issues involved with 'scaling up' population and habitat-level production estimates to the whole-lake level. Whole-lake benthic secondary production estimates for Sparkling Lake ranged by nearly threefold (Fig. 6), with the size-frequency method producing the highest production estimate. Use of this method for zoobenthos in Sparkling Lake was problematic: in addition to the need to estimate CPI, many taxa did not show a trend of decreasing frequency in larger size classes. Excluding SF estimates gives much better correspondence among methods, though this does not necessarily mean that SF was the least accurate, since we do not know actual production. Whole-lake production estimates tended to correspond more closely than habitat-specific estimates: larger differences among estimates for one habitat can be offset by differences in the opposite direction for others. Furthermore, taxa with the highest rates of production tend to fall on the 1:1 line for almost all

of the comparisons (Fig. 2), while the large deviations occur for organisms with low rates of production, which are minor contributors to total secondary production. The consequence is that when data are summed from subpopulations up to the whole-lake level, production estimates tend to converge.

#### Uncertainty in habitat and whole-lake production estimates

There are many challenges involved in generating ecosystem-level (in this case, whole-lake) estimates of benthic secondary production. Field sampling and sample processing are extremely laborious, particularly if efforts are made to sample the diverse habitats of a lake. This greatly limits the number of lakes that can be reasonably studied. Both *P/B* and regression models are generally based on the estimated annual average biomass (*B*). For logistic reasons, we sampled Sparkling Lake only during summer months, which may not be representative of the annual average condition. Like most other benthic production studies, we did not include meiofauna, which can comprise roughly half of total benthic production (Stead et al. 2005; Strayer and Likens 1986). In short, there are numerous sources of bias and uncertainty in benthic secondary production estimates that were not explicitly addressed here (Babler et al. 2008).

An increasing number of studies are explicitly considering at least some sources of uncertainty associated with production estimates. Woodcock and Huryn (2007) and Babler et al. (2008) used a bootstrap procedure to generate confidence intervals for community estimates generated using the SF method. Carlisle and Clements (2003) used a similar procedure to generate confidence intervals for community estimates derived from a combination of SF, *P/B*, and cohort methods. Our work expands upon these efforts to address uncertainty for estimates generated using regression models and literature *P/B* compilations.

Our CVs for regression model-derived habitat-specific estimates averaged 0.17–0.27, which corresponds with CVs reported in other studies. Babler et al. (2008) found that bootstrapping the measured variables for habitat-specific SF estimates produced community CVs ranging from 0.10 to 0.17. Carlisle and Clements (2003) bootstrapped measured variables and CPIs and reported CVs ranging from 0.20 to 0.27, while Woodcock and Huryn (2007) reported CVs ranging from 0.07 to 0.09. Huryn (1996) followed a similar procedure and obtained a CV of 0.28.

Though we included the SF method in our comparison, there were problems in applying this method to Sparkling Lake. For taxon–habitat combinations for which SF estimates could not be directly calculated, we used an empirical relationship between production (*P*) and biomass (*B*) to estimate production (Eq. 4). This equation was

applied to biomass values outside the range of values (lower) used to generate Eq. 4, which is not generally appropriate. We did this to enable comparison of the four methods at subpopulation, habitat, and whole-lake levels, though we would strongly advise against using an empirical relationship between a SF production estimate and biomass to estimate production in a research situation. Another challenge of the SF method is the need to estimate CPI. We approximated CPI values based on the literature (e.g., Stead et al. 2005; Babler et al. 2008). CPIs can be quite variable for a given taxon, depending on habitat and environmental factors, and may be difficult to accurately estimate in many cases. The SF method is best applied to populations for which there is firsthand knowledge of CPI.

Use of  $P/B$  values also involves sources of uncertainty that are difficult to quantify. We found that CVs for habitat-specific and whole-lake estimates using  $P/B$  methods are at least twice as high as CVs from regression model estimates. This uncertainty was due to the substantial variation in literature-derived  $P/B$  values for a given taxon. For example,  $P/B$  values for Tanypodinae ranged from 1.9 to 53.3. Including the full range of individual  $P/B$  estimates from north-temperate lakes, as we did, probably provides the upper bounds of the actual  $P/B$  uncertainty for a given taxon. Some of the high variability among literature  $P/B$  values may be due to the influence of biomass, temperature, and body size. Regression models explicitly control for the effect of these variables on production and thus, reduce model uncertainty in habitat and whole-lake production estimates (Fig. 6).

Published regression models rely on empirical relationships between population production and easily measured variables such as water temperature, biomass density, and individual body size (Banse and Mosher 1980; Plante and Downing 1989; Morin and Bourassa 1992; Benke 1993; Brey et al. 1996; Stockwell and Johannsson 1997; Shuter and Ing 1997). To estimate production, these variables are measured directly and production is estimated from the empirical model.

Whole-lake estimates derived from the two regression models differed (Fig. 6). There are fundamental differences between the two models used in this paper—Plante and Downing's (1989) Eq. 1 and Banse and Mosher's (1980) Eq. 1—that could cause estimates to differ. The datasets used in B&M and P&D differed in terms of the range of body mass ( $M_{\max}$  and  $M_{\text{mat}}$ ), biomass ( $B$ ), and production ( $P$ ) values. Banse and Mosher (1980) was based on limited data from lentic benthic invertebrates, terrestrial invertebrates, and marine benthic invertebrates. Plante and Downing (1989) use data from lentic benthic invertebrates and zooplankton. Plante and Downing (1989) used temperature and biomass density as predictors in their model while Banse and Mosher (1980) did not. Plante and

Downing (1989) used instantaneous growth, Allen curve, and SF estimates to build their model, while Banse and Mosher (1980) used cohort estimates only. These differences highlight the fact that the details of the empirical models often make a difference, and that these models ultimately reflect the underlying data used to build them. Nevertheless, in situations where cohort methods cannot be applied, we feel that regression models are an appropriate choice for community and ecosystem-scale production estimates. Unlike SF and cohort methods, they can be applied broadly, and only require estimates of body size, temperature, and mean annual biomass.

We characterized how uncertainty in habitat-level production varies as a function of sampling effort. For Sparkling Lake, we collected substantially more samples from a given habitat than was required to achieve a stable variance. Approximately 10–15 samples were needed to stabilize variance for habitat-level production estimates, and the general pattern was similar for all 11 communities (Fig. 5). Understanding how uncertainty changes with sampling effort is critical when planning and undertaking field sampling programs, and can help guide future field programs aimed at estimating whole-lake benthic invertebrate production.

#### Benthic invertebrate production in a broader context

Production is a fundamental ecological concept that provides the basis for much of ecosystem ecology (Begon et al. 1990). The concept of production has wide applicability in ecology and environmental sciences. It is a composite ecological measure that integrates mortality, reproduction, and individual growth (Benke 1993; Poff and Huryn 1998), and can be estimated at population, community, and ecosystem levels of organization. In an applied sense, production reflects the capacity for a population to sustain harvest or other sources of mortality, and thus has important resource management implications. There have also been numerous other applications. For example, Woodcock and Huryn (2007) and Carlisle and Clements (2003) used community-level production estimates to characterize effects of pollution on stream biota. Strecker and Arnott (2008) examined impact of an invasive zooplankton species on community zooplankton production, in effect, linking the spread of an invasive species to a basic ecosystem function. But perhaps most importantly, the study of production provides a foundation for understanding the structure and function of ecosystems—specifically the flow of energy through food webs and ecosystem energetics (Strayer and Likens 1986; Huryn 1996; Johannsson et al. 2000; Vander Zanden et al. 2006). Production can be estimated for all trophic groups (i.e., primary producers, secondary consumers, decomposers,



and predators), thereby allowing all taxa and energy transfers to be compared using a common currency of energy or carbon (Odum 1968).

In lakes, there is a growing understanding of the important contributions of benthic habitats to lake ecosystems (Reynolds 2008; Vadeboncoeur et al. 2002), both as a source of primary production, as well as an important trophic pathway supporting higher consumers. Benthic invertebrates are pivotal in linking benthic primary production to higher trophic levels such as fish, and large-scale studies of benthic invertebrate production are needed in order to expand our understanding of benthic-pelagic coupling, whole-ecosystem energy flow, and the trophic basis for fish production in lakes. Beyond this, recent work indicates that the presence of multiple trophic pathways in ecosystems may have profound implications for ecosystem stability and functioning (Post et al. 2000; Vadeboncoeur et al. 2005; Rooney et al. 2006).

In summary, measurements of benthic invertebrate production at the habitat and whole-lake level will comprise an important part of future efforts to characterize ecosystem function and the importance of benthic trophic

pathways in lakes. Our goal here was to address some fundamental methodological issues related to estimating benthic secondary production in lakes—specifically the comparison of alternative methods, the measurement of uncertainty, and the scaling up of production estimates from individual taxa to the whole-lake level.

**Acknowledgments** Laboratory and field assistance was provided by the following: Caitlin Kersten, Kate Abitz, Nicolas Coorough, Robyn Grayson, Katie Dosch, Lindsay Schaffner, James Tracey, Marcelle Richards, Maggie Lalor, Adam Schumaker, Nicole Hayes, Kelsey Peterson, Paul Schilke, Liz Gass, Nicole Hayes, and Shawn Devlin. Thanks to Jeff Maxted, Chris Solomon, Tony Ives, Bobbi Peckarsky, and Phil Townsend for providing comments and technical help with the manuscript. Bill Feeny assisted with figures. Special thanks to the staff of Trout Lake Station and the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) program (DEB-0217533). Funding was provided by NSF grant DEB-0449076 (M.J. Vander Zanden) and DEB-0448682 (Y. Vadeboncoeur).

## Appendix

See Table 1.

**Table 1** Mean biomass ( $\text{g m}^{-2}$ ) and production estimates ( $\text{g m}^{-2} \text{y}^{-1}$ ) using four different methods for the 239 taxa-habitat combinations sampled in Sparkling Lake

Taxa	Biomass (g dry mass/m <sup>2</sup> )	P&D	B&M	P/B	SF
Cobble, 0.25 m					
Amphipoda: Hyalella sp.	0.0196	0.1471	0.0516	0.0871	0.1413
Bivalvia: Sphaeriidae	0.0014	0.0298	0.0095	0.0066	0.0101
Bivalvia: Unionidae	0.1033	0.2120	0.0433	0.0127	0.7455
Coleoptera: Dysticidae	0.0011	0.0176	0.0039	0.0028	0.0077
Coleoptera: Ectopria sp.	0.0288	0.1979	0.0747	0.0757	0.2076
Decapoda: Orconectes rusticus	0.6925	0.8851	0.4737	0.9616	4.9956
Diptera (pupae)	0.0001	0.0046	0.0011	0.0006	0.0007
Diptera: Ceratopogonidae	0.000003	0.0005	0.0001	0.0000	0.0000
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0004	0.0169	0.0060	0.0016	0.0030
Diptera: Chironomidae (non-Tanytopodinae)	0.0156	0.1724	0.0792	0.0866	0.0985*
Diptera: Chironomidae: Tanytopodinae	0.0349	0.3283	0.1797	0.2683	0.1547*
Diptera: Tipulidae	0.00002	0.0015	0.0003	0.0001	0.0002
Ephemeroptera: Baetidae	0.0025	0.0459	0.0160	0.0100	0.0181
Ephemeroptera: Caenis sp.	0.0002	0.0059	0.0013	0.0006	0.0011
Ephemeroptera: Choroterpes sp.	0.0071	0.0927	0.0361	0.0284	0.0513
Ephemeroptera: Ephemera sp.	0.0324	0.2204	0.0864	0.1293	0.2339
Ephemeroptera: Eurylophella sp.	0.0001	0.0070	0.0019	0.0006	0.0011
Ephemeroptera: Stenonema sp.	0.0594	0.2897	0.1064	0.2370	0.4286
Gastropoda: Helisoma sp.	0.0002	0.0071	0.0015	0.0021	0.0016
Hydrachnidia	0.0098	0.1533	0.0805	0.0295	0.0709
Isopoda: Caecidotea sp.	0.0024	0.0331	0.0087	0.0070	0.0173
Megaloptera: Sialis sp.	0.0007	0.0153	0.0037	0.0016	0.0052
Odonata: Aeshnidae	0.0002	0.0054	0.0011	0.0007	0.0012
Odonata: Coenagrionidae	0.0007	0.0129	0.0028	0.0014	0.0048

Table 1 continued

Taxa	Biomass (g dry mass/m <sup>2</sup> )	P&D	B&M	P/B	SF
Odonata: Gomphidae	0.0417	0.1754	0.0486	0.1630	0.3005
Odonata: Gomphidae: Hagenius brevistylus	0.0398	0.1699	0.0468	0.1558	0.2871
Odonata: Libellulidae/Corduliidae	0.0018	0.0254	0.0061	0.0070	0.0129
Oligochaeta	0.0254	0.1747	0.0830	0.0458	0.1081
Trichoptera: Mystacides sp.	0.0012	0.0234	0.0064	0.0077	0.0087
Trichoptera: Nectopsyche sp.	0.0002	0.0055	0.0011	0.0011	0.0012
Trichoptera: Oecetis sp.	0.0033	0.0478	0.0151	0.0207	0.0235
Trichoptera: Polycentropodidae	0.0018	0.0253	0.0061	0.0114	0.0130
Turbellaria	0.0001	0.0039	0.0008	0.0003	0.0006
Cobble, 2 m					
Amphipoda: Hyalella sp.	0.0900	0.6510	0.4097	0.4002	0.4833*
Bivalvia: Sphaeriidae	0.0054	0.0864	0.0364	0.0254	0.0390
Decapoda: Orconectes rusticus	0.6925	0.8851	0.4737	0.9616	4.9956
Diptera (pupae)	0.0022	0.0447	0.0162	0.0137	0.0162
Diptera: Ceratopogonidae	0.0007	0.0208	0.0069	0.0026	0.0049
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0161	0.2699	0.1855	0.0627	0.1161
Diptera: Chironomidae (non-Tanypodinae)	0.2073	1.2001	0.8607	1.1531	1.5016*
Diptera: Chironomidae: Tanypodinae	0.1329	1.0158	0.7890	1.0201	0.9585
Ephemeroptera: Caenis sp.	0.0062	0.0729	0.0244	0.0247	0.0447
Ephemeroptera: Ephemera sp.	0.0220	0.1743	0.0673	0.0878	0.1588
Ephemeroptera: Stenonema sp.	0.0361	0.2205	0.0816	0.1441	0.2607
Gastropoda: Helisoma sp.	0.0195	0.1498	0.0535	0.1772	0.1406
Hydrachnidae	0.0113	0.1530	0.0745	0.0339	0.0816
Megaloptera: Sialis sp.	0.0146	0.1260	0.0446	0.0328	0.1055
Odonata: Gomphidae	0.8622	1.8211	0.9064	3.3741	6.2199
Odonata: Libellulidae/Corduliidae	0.0665	0.2773	0.0920	0.2604	0.4801
Oligochaeta	0.1868	0.7166	0.4952	0.2736	0.6450
Trichoptera: Mystacides sp.	0.0005	0.0137	0.0037	0.0031	0.0035
Trichoptera: Nectopsyche sp.	0.0001	0.0044	0.0011	0.0005	0.0006
Trichoptera: Oecetis sp.	0.0004	0.0114	0.0028	0.0027	0.0031
Macrophytes, 0.25 m					
Amphipoda: Crangonyx sp.	0.0001	0.0046	0.0009	0.0006	0.0009
Amphipoda: Hyalella sp.	0.0211	0.2185	0.1066	0.0940	0.1525
Bivalvia: Sphaeriidae	0.0594	0.5280	0.3404	0.2788	0.4284
Coleoptera: Dysticidae	0.0011	0.0181	0.0040	0.0030	0.0082
Coleoptera: Elmidae	0.0005	0.0101	0.0021	0.0012	0.0033
Diptera (miscellaneous)	0.0124	0.1510	0.0691	0.0759	0.0896
Diptera (pupae)	0.0071	0.1143	0.0542	0.0434	0.0512
Diptera: Ceratopogonidae	0.0156	0.1972	0.1025	0.0609	0.1128
Diptera: Ceratopogonidae: Dasyhelea sp.	0.1475	1.1725	0.9856	0.5749	1.1876*
Diptera: Chironomidae (non-Tanypodinae)	0.1041	0.5333	0.2577	0.5790	0.7509
Diptera: Chironomidae: Tanypodinae	0.0328	0.3258	0.1830	0.2522	0.2369
Ephemeroptera: Ephemera sp.	0.0021	0.0265	0.0061	0.0083	0.0150
Ephemeroptera: Eurylophella sp.	0.0008	0.0143	0.0031	0.0031	0.0057
Ephemeroptera: Hexagenia sp.	0.0029	0.0366	0.0096	0.0117	0.0211
Gastropoda: Helisoma sp.	0.0038	0.0476	0.0138	0.0349	0.0277
Gastropoda: Hydrobiidae	0.0064	0.0864	0.0332	0.0585	0.0464

Table 1 continued

Taxa	Biomass (g dry mass/m <sup>2</sup> )	P&D	B&M	P/B	SF
Gastropoda: Lymnaeidae	0.0153	0.1476	0.0592	0.1389	0.1102
Gastropoda: Physidae	0.0009	0.0167	0.0039	0.0082	0.0065
Gastropoda: Planorbidae (non-Helisoma)	0.0004	0.0129	0.0035	0.0038	0.0030
Hydrachnidae	0.5821	2.9093	2.7672	1.7462	4.1989
Megaloptera: Sialis sp.	0.0013	0.0193	0.0043	0.0028	0.0091
Odonata: Coenagrionidae	0.0037	0.0417	0.0109	0.0078	0.0264
Odonata: Gomphidae	0.3153	0.8653	0.3656	1.2341	2.2749
Odonata: Gomphidae: Hagenius brevistylus	0.0238	0.1382	0.0412	0.0930	0.1715
Odonata: Libellulidae/Corduliidae	0.0082	0.0684	0.0186	0.0319	0.0588
Oligochaeta	0.8583	2.1865	2.0325	1.1231	2.6475
Trichoptera: Homophylax sp.	0.0086	0.0647	0.0162	0.0544	0.0620
Trichoptera: Mystacides sp.	0.0017	0.0258	0.0065	0.0105	0.0120
Trichoptera: Oecetis sp.	0.0004	0.0088	0.0018	0.0023	0.0026
Trichoptera: Oxyethira sp.	0.0001	0.0045	0.0009	0.0008	0.0009
Macrophytes, 1 m					
Amphipoda: Hyalella sp.	0.0356	0.3108	0.1599	0.1585	0.1943*
Bivalvia: Sphaeriidae	0.0524	0.4618	0.2807	0.2461	0.2832*
Coleoptera: Dysticidae	0.0007	0.0122	0.0025	0.0018	0.0048
Coleoptera: Elmidae	0.0001	0.0035	0.0007	0.0002	0.0006
Diptera (miscellaneous)	0.0141	0.1572	0.0698	0.0862	0.1017
Diptera (pupae)	0.0095	0.1065	0.0405	0.0580	0.0684
Diptera: Ceratopogonidae	0.0040	0.0647	0.0245	0.0155	0.0286
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0453	0.4886	0.3383	0.1765	0.3266
Diptera: Chironomidae (non-Tanypodinae)	0.0692	0.5937	0.3940	0.3848	0.3519*
Diptera: Chironomidae: Tanypodinae	0.0521	0.4505	0.2682	0.4002	0.296*
Ephemeroptera: Baetidae	0.0007	0.0127	0.0026	0.0029	0.0052
Ephemeroptera: Caenis sp.	0.00001	0.0011	0.0002	0.0001	0.0001
Ephemeroptera: Hexagenia sp.	0.0040	0.0375	0.0085	0.0160	0.0289
Gastropoda: Helisoma sp.	0.0485	0.3160	0.1402	0.4411	0.3500
Gastropoda: Hydrobiidae	0.0070	0.0925	0.0362	0.0638	0.0506
Gastropoda: Lymnaeidae	0.0045	0.0563	0.0175	0.0408	0.0323
Gastropoda: Physidae	0.0100	0.0843	0.0250	0.0913	0.0724
Gastropoda: Planorbidae (non-Helisoma)	0.0001	0.0046	0.0009	0.0010	0.0008
Hydrachnidae	0.0863	0.5227	0.2738	0.2590	0.6227
Megaloptera: Sialis sp.	0.0001	0.0028	0.0005	0.0001	0.0005
Odonata: Coenagrionidae	0.0036	0.0445	0.0124	0.0078	0.0263
Odonata: Gomphidae	0.4871	1.2411	0.5838	1.9062	3.5139
Odonata: Gomphidae: Hagenius brevistylus	0.0115	0.0829	0.0225	0.0452	0.0832
Odonata: Libellulidae/Corduliidae	0.0533	0.2555	0.0884	0.2085	0.151*
Oligochaeta	0.2636	0.8236	0.5906	0.3263	0.7693
Trichoptera: Agrypnia sp.	0.0357	0.1497	0.0388	0.2261	0.2576
Trichoptera: Mystacides sp.	0.0030	0.0384	0.0104	0.0189	0.0216
Trichoptera: Oecetis sp.	0.0001	0.0042	0.0008	0.0008	0.0009
Trichoptera: Oxyethira sp.	0.00004	0.0021	0.0004	0.0003	0.0003
Turbellaria	0.00003	0.0017	0.0003	0.0001	0.0002
Macrophytes, 2 m					
Amphipoda: Hyalella sp.	0.0150	0.1538	0.0648	0.0666	0.0965*

Table 1 continued

Taxa	Biomass (g dry mass/m <sup>2</sup> )	P&D	B&M	P/B	SF
Bivalvia: Sphaeriidae	0.0394	0.3283	0.1685	0.1851	0.2844
Bivalvia: Unionidae	0.0420	0.1047	0.0178	0.0052	0.3030
Coleoptera: Dysticidae	0.0014	0.0178	0.0035	0.0036	0.0100
Diptera (miscellaneous)	0.0041	0.0660	0.0249	0.0253	0.0299
Diptera (pupae)	0.0043	0.0677	0.0257	0.0262	0.0309
Diptera: Ceratopogonidae	0.0025	0.0485	0.0180	0.0096	0.0178
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0148	0.2151	0.1249	0.0577	0.111*
Diptera: Chironomidae (non-Tanypodinae)	0.1161	0.7492	0.4700	0.6455	0.8568*
Diptera: Chironomidae: Tanypodinae	0.0814	0.5507	0.3125	0.6248	0.6298*
Ephemeroptera: Baetidae	0.00001	0.0009	0.0001	0.0000	0.0001
Ephemeroptera: Hexagenia sp.	0.0028	0.0301	0.0067	0.0112	0.0202
Gastropoda: Helisoma sp.	0.0493	0.3220	0.1442	0.4482	0.3556
Gastropoda: Hydrobiidae	0.0050	0.0696	0.0250	0.0456	0.0362
Gastropoda: Lymnaeidae	0.0026	0.0332	0.0085	0.0232	0.0184
Gastropoda: Physidae	0.0066	0.0614	0.0170	0.0597	0.0474
Gastropoda: Planorbidae (non-Helisoma)	0.0001	0.0033	0.0007	0.0006	0.0005
Hydrachnidiae	0.0254	0.2127	0.0918	0.0761	0.1829
Megaloptera: Sialis sp.	0.0027	0.0339	0.0086	0.0061	0.0196
Odonata: Coenagrionidae	0.0014	0.0238	0.0061	0.0030	0.0102
Odonata: Gomphidae	0.4857	1.1752	0.5260	1.9008	3.5041
Odonata: Libellulidae/Corduliidae	0.0390	0.1736	0.0493	0.1528	0.2816
Oligochaeta	0.4258	1.2083	0.9594	0.5301	1.2497
Trichoptera: Agrypnia sp.	0.0131	0.0734	0.0166	0.0827	0.0943
Trichoptera: Mystacides sp.	0.0023	0.0333	0.0090	0.0146	0.0167
Trichoptera: Nectopsyche sp.	0.0002	0.0059	0.0011	0.0015	0.0017
Trichoptera: Oecetis sp.	0.0002	0.0068	0.0014	0.0015	0.0017
Trichoptera: Oxyethira sp.	0.00001	0.0006	0.0001	0.00004	0.0001
Trichoptera: Polycentropodidae	0.0001	0.0026	0.0004	0.0004	0.0005
Turbellaria	0.00001	0.0009	0.0001	0.00005	0.0001
Macrophytes, 4 m					
Amphipoda: Hyalella sp.	0.0704	0.3981	0.1800	0.3131	0.3509*
Bivalvia: Sphaeriidae	0.0574	0.5058	0.3189	0.2696	0.324*
Bivalvia: Unionidae	0.0365	0.1076	0.0222	0.0045	0.2632
Coleoptera: Haliplidae	0.0029	0.0289	0.0061	0.0075	0.0206
Diptera (miscellaneous)	0.0016	0.0408	0.0160	0.0101	0.0119
Diptera (pupae)	0.0007	0.0188	0.0058	0.0040	0.0047
Diptera: Ceratopogonidae	0.0038	0.0645	0.0248	0.0149	0.0276
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0043	0.0930	0.0474	0.0168	0.023*
Diptera: Chironomidae (non-Tanypodinae)	0.0762	0.4357	0.2056	0.4237	0.5495
Diptera: Chironomidae: Tanypodinae	0.0595	0.4870	0.2908	0.4569	0.3591*
Ephemeroptera: Hexagenia sp.	0.0145	0.0888	0.0228	0.0577	0.1044
Gastropoda: Helisoma sp.	0.0666	0.4077	0.1941	0.6059	0.2417*
Gastropoda: Hydrobiidae	0.0170	0.1794	0.0816	0.1549	0.1229
Gastropoda: Lymnaeidae	0.0039	0.0475	0.0136	0.0354	0.0281
Gastropoda: Physidae	0.0014	0.0215	0.0050	0.0129	0.0102
Gastropoda: Planorbidae (non-Helisoma)	0.0009	0.0223	0.0067	0.0084	0.0067
Hydrachnidiae	0.0275	0.2360	0.1075	0.0826	0.1986



Table 1 continued

Taxa	Biomass (g dry mass/m <sup>2</sup> )	P&D	B&M	P/B	SF
Megaloptera: Sialis sp.	0.0072	0.0711	0.0214	0.0162	0.0315*
Odonata: Coenagrionidae	0.0007	0.0140	0.0031	0.0016	0.0053
Odonata: Gomphidae	0.3611	0.8913	0.3603	1.4131	2.6049
Odonata: Libellulidae/Corduliidae	0.0261	0.1258	0.0327	0.1020	0.1881
Oligochaeta	0.7635	1.9289	1.7343	0.9583	2.2591
Trichoptera: Mystacides sp.	0.0037	0.0376	0.0089	0.0232	0.0264
Trichoptera: Nectopsyche sp.	0.0002	0.0058	0.0011	0.0014	0.0016
Trichoptera: Oecetis sp.	0.0002	0.0062	0.0014	0.0011	0.0012
Sediment, 2 m					
Amphipoda: Hyalella sp.	0.1499	0.8667	0.5441	0.6667	0.9097*
Bivalvia: Sphaeriidae	0.0611	0.5176	0.3226	0.2870	0.3251*
Bivalvia: Unionidae	0.0344	0.1060	0.0203	0.0042	0.2482
Coleoptera: Dysticidae	0.0015	0.0212	0.0048	0.0038	0.0106
Diptera (pupae)	0.0071	0.0927	0.0361	0.0434	0.0512
Diptera: Ceratopogonidae	0.0050	0.0930	0.0439	0.0193	0.0358
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0255	0.3396	0.2265	0.0995	0.2004*
Diptera: Chironomidae (non-Tanypodinae)	0.1798	1.1226	0.8155	1.0003	1.4718*
Diptera: Chironomidae: Tanypodinae	0.1018	0.7337	0.4838	0.7816	0.6631*
Ephemeroptera: Ephemera sp.	0.0018	0.0243	0.0056	0.0073	0.0131
Gastropoda: Helisoma sp.	0.0371	0.2433	0.0973	0.3377	0.2679
Gastropoda: Hydrobiidae	0.0005	0.0131	0.0032	0.0048	0.0038
Gastropoda: Lymnaeidae	0.0077	0.0740	0.0224	0.0700	0.0556
Gastropoda: Physidae	0.0050	0.0549	0.0157	0.0459	0.0364
Hydrachnidiae	0.0808	0.7813	0.6176	0.2425	0.5832
Megaloptera: Sialis sp.	0.0002	0.0064	0.0014	0.0004	0.0014
Odonata: Coenagrionidae	0.0001	0.0038	0.0008	0.0002	0.0006
Odonata: Gomphidae	1.0934	2.2195	1.1723	4.2789	7.8879
Odonata: Libellulidae/Corduliidae	0.0016	0.0227	0.0052	0.0062	0.0114
Oligochaeta	0.2780	0.8590	0.6228	0.3442	0.8113
Trichoptera: Mystacides sp.	0.0076	0.0724	0.0215	0.0483	0.0550
Trichoptera: Oecetis sp.	0.0012	0.0188	0.0042	0.0076	0.0087
Trichoptera: Oxyethira sp.	0.0001	0.0036	0.0007	0.0006	0.0006
Trichoptera: Polycentropodidae	0.0007	0.0132	0.0028	0.0043	0.0049
Sediment, 4 m					
Amphipoda: Hyalella sp.	0.0878	0.6591	0.4252	0.3904	0.6333
Bivalvia: Sphaeriidae	0.0977	0.7779	0.5538	0.4588	0.5246*
Diptera (pupae)	0.0017	0.0405	0.0153	0.0106	0.0125
Diptera: Ceratopogonidae	0.0076	0.1211	0.0584	0.0297	0.0550
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0150	0.2592	0.1778	0.0586	0.0709*
Diptera: Chironomidae (non-Tanypodinae)	0.2523	1.4711	1.1506	1.4035	2.1636*
Diptera: Chironomidae: Tanypodinae	0.1736	1.0805	0.7717	1.3326	1.2739*
Ephemeroptera: Hexagenia sp.	0.0110	0.0867	0.0251	0.0440	0.0797
Gastropoda: Helisoma sp.	0.0409	0.2842	0.1249	0.3720	0.2952
Gastropoda: Hydrobiidae	0.0015	0.0322	0.0106	0.0137	0.0109
Gastropoda: Lymnaeidae	0.0083	0.0814	0.0259	0.0751	0.0596
Gastropoda: Physidae	0.0004	0.0102	0.0024	0.0034	0.0027
Gastropoda: Planorbidae (non-Helisoma)	0.0005	0.0127	0.0033	0.0042	0.0033

Table 1 continued

Taxa	Biomass (g dry mass/m <sup>2</sup> )	P&D	B&M	P/B	SF
Hydrachnidae	0.0321	0.3612	0.2262	0.0963	0.2315
Megaloptera: Sialis sp.	0.0087	0.0912	0.0315	0.0195	0.0625
Odonata: Gomphidae	0.6360	1.5791	0.8081	2.4887	4.5878
Oligochaeta	0.4550	1.2676	1.0194	0.5633	1.3278
Trichoptera: Mystacides sp.	0.0106	0.1022	0.0352	0.0674	0.0768
Sediment, 8 m					
Amphipoda: Hyalella sp.	0.0019	0.0336	0.0101	0.0085	0.0138
Bivalvia: Sphaeriidae	0.0264	0.2398	0.1135	0.1240	0.192*
Coleoptera: Dysticidae	0.0041	0.0493	0.0143	0.0107	0.0295
Diptera (miscellaneous)	0.0216	0.2218	0.1085	0.1321	0.1558
Diptera: Ceratopogonidae	0.0016	0.0361	0.0130	0.0061	0.0113
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0012	0.0297	0.0105	0.0045	0.0083
Diptera: Chironomidae (non-Tanypodinae)	0.3415	1.3166	0.7903	1.8996	2.4637
Diptera: Chironomidae: Tanypodinae	0.1775	1.0463	0.7166	1.3627	1.2804
Ephemeroptera: Ephemera sp.	0.0045	0.0566	0.0177	0.0179	0.0324
Ephemeroptera: Hexagenia sp.	0.2184	0.8146	0.3952	0.8710	1.5755
Gastropoda: Helisoma sp.	0.0140	0.1314	0.0495	0.1275	0.1012
Gastropoda: Lymnaeidae	0.0033	0.0531	0.0183	0.0304	0.0241
Hydrachnidae	0.0288	0.3226	0.1924	0.0864	0.2078
Isopoda: Caecidotea sp.	0.0010	0.0207	0.0057	0.0028	0.0070
Megaloptera: Sialis sp.	0.0422	0.2792	0.1188	0.0947	0.3045
Odonata: Gomphidae	0.0273	0.1692	0.0567	0.1070	0.1972
Oligochaeta	0.2142	0.9789	0.7349	0.4061	0.9572
Sediment, 12 m					
Amphipoda: Hyalella sp.	0.0003	0.0107	0.0031	0.0012	0.0020
Bivalvia: Sphaeriidae	0.0736	0.4574	0.2299	0.3458	0.5313
Diptera (miscellaneous)	0.0071	0.0903	0.0343	0.0435	0.0513
Diptera (pupae)	0.0001	0.0041	0.0009	0.0005	0.0006
Diptera: Ceratopogonidae	0.0011	0.0243	0.0074	0.0041	0.0077
Diptera: Ceratopogonidae: Dasyhelea sp.	0.0000	0.0009	0.0002	0.0000	0.0001
Diptera: Chironomidae (non-Tanypodinae)	0.3968	1.5428	0.9923	2.2071	2.8625
Diptera: Chironomidae: Tanypodinae	0.0372	0.2973	0.1435	0.2853	0.2681
Hydrachnidae	0.0043	0.0685	0.0261	0.0130	0.0313
Oligochaeta	0.0490	0.2676	0.1423	0.0787	0.1854
Sediment, 18 m					
Diptera: Chironomidae (non-Tanypodinae)	0.0021	0.0352	0.0107	0.0114	0.0148
Oligochaeta	0.0058	0.0403	0.0129	0.0071	0.0169

\* SF method was used to estimate production

## References

- Babler AL, Solomon CT, Schilke PR (2008) Depth-specific patterns of benthic secondary production in an oligotrophic lake. *J N Am Benthol Soc* 27:108–119
- Banase K, Mosher S (1980) Adult body-mass and annual production-biomass relationships of field populations. *Ecol Monogr* 50:355–379
- Baumgärtner D (2004) Principles of macroinvertebrate community structure in the littoral zone of Lake Constance. Ph. D. thesis. Universität Konstanz, Konstanz
- Begon M, Harper JL, Townsend CR (1990) Ecology: individuals, populations and communities, 2nd edn. Blackwell Publishers, Boston
- Benke AC (1979) A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol Oceanogr* 24:168–171

- Benke AC (1984) Secondary production of aquatic insects. In: Resh VH, Rosenberg DM (eds) *The ecology of aquatic insects*. Praeger Publishers, New York
- Benke AC (1993) Concepts and patterns of invertebrate production in running waters. *Verh Int Verein Limnol* 25:15–36
- 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
- Blukacz EA, Sprules WG, Brunner J (2005) Use of the bootstrap for error propagation in estimating zooplankton production. *Ecology* 86:2223–2231
- Brey T, Teichmann J, Borlich O (1996) Artificial neural network versus multiple linear regression: predicting P/B ratios from empirical data. *Mar Ecol Prog Ser* 140:251–256
- Carlisle DM, Clements WH (2003) Growth and secondary production of aquatic insects along a gradient of Zn contamination in Rocky Mountain streams. *J N Am Benthol Soc* 22:582–597
- Cummins KW, Wuycheck (1971) Caloric equivalents for investigations in ecological energetics. *Verh Int Verein Limnol* no 18. 158 p
- Dodson SI (2005) *Introduction to limnology*. McGraw-Hill, Boston
- Draper NR, Smith HS (1998) *Applied regression analysis*, 3rd edn. Wiley, New York
- Efron B, Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat Sci* 1:54–75
- Eleutheriadis N, Lazaridou-Dimitriadou M (2001) The life cycle, population dynamics, growth, and secondary production of *Bithynia graeca* (Westerlund, 1987) (Gastropoda) in Lake Kerkini, northern Greece. *J Mollus Stud* 67:319–328
- ESRI (Environmental Systems Research Institute) Inc. (2008) ArcGIS v. 9.2. Redlands, CA
- Gratton CG, Vander Zanden MJ (2009) Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. *Ecology* 90:2689–2699
- Huryn AD (1996) An appraisal of the Allen paradox in a New Zealand trout stream. *Limnol Oceanogr* 2:243–252
- Johannsson OE, Dermott R, Graham DM, Dahl JA, Millard ES, Myles DD, LeBlanc J (2000) Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. *J Great Lakes Res* 26:31–54
- Kalff J (2002) *Limnology*. Prentice-Hall, New Jersey
- Lafont M (1987) Production of Tubificidae in the littoral zone of Lake Leman near Thonon-les-Bains: a methodological approach. *Hydrobiologia* 155:179–187
- Lindgaard C (1992) Zoobenthos ecology of Thingvallavatn: vertical distribution, abundance, population dynamics and production. *Oikos* 64:257–304
- Lindgaard C (1994) The role of zoobenthos in energy flow in two shallow lakes. *Hydrobiologia* 275(276):313–322
- Lindgaard C, Jonasson PC (1979) Abundance, population dynamics, and production in Lake Myvatn, Iceland. *Oikos* 32:202–227
- Manly BFJ (1998) *Randomization, bootstrap, and Monte Carlo methods in biology*, 2nd edn. CRC Press, Boca Raton
- Momot WT, Gowing H (1977) Production and population dynamics of crayfish *Orconectes virilis* in 3 Michigan lakes. *J Fish Res Board Can* 34:2041–2055
- Morin A, Bourassa N (1992) Empirical models of annual production and productivity-biomass ratios of benthic invertebrates in running waters. *Can J Fish Aquat Sci* 49:532–539
- Neess J, Dugdale RC (1959) Computation of production for populations of aquatic midge larvae. *Ecology* 40:425–430
- Odum EP (1968) Energy flow in ecosystems—a historical review. *Am Zool* 8:11–18
- Phillips EC (1997) Life cycle, growth, survival, and production of *Macronychus glabratus* (Coleoptera: Elmidae) in northwest Arkansas and southeast Texas streams. *Invertebr Biol* 116:134–141
- Plante C (1987) Prediction de la production secondaire en milieu aquatique. Master's thesis. University of Montreal, Montreal
- Plante C, Downing JA (1989) Production of freshwater invertebrate populations in lakes. *Can J Fish Aquat Sci* 46:1489–1498
- Poff NL, Huryn AD (1998) Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Can J Fish Aquat Sci* 55:201–217
- Post DM, Conners ME, Goldberg DS (2000) Prey preference by a top predator and the stability of linked food chains. *Ecology* 81:8–14
- Potter DW, Learner MA (1974) A study of benthic macroinvertebrates of a shallow eutrophic reservoir in South Wales with emphasis on Chironomidae (Diptera); their life-histories and production. *Arch Hydrobiol* 74:186–226
- Reynolds CS (2008) A changing paradigm of pelagic food webs. *Int Rev Hydrobiol* 93:517–531
- Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. *Nature* 442:265–269
- Schindler DE, Scheuerell MD (2002) Habitat coupling in lake ecosystems. *Oikos* 98:177–189
- Shuter B, Ing KK (1997) Factors affecting the production of zooplankton in lakes. *Can J Fish Aquat Sci* 54:359–377
- Stead TK, Schmid-Araya JM, Hildrew AG (2005) Secondary production of a stream metazoan community: does meiofauna make a difference? *Limnol Oceanogr* 50:398–403
- Stockwell JD, Johannsson OE (1997) Temperature-dependent allometric models to estimate zooplankton production in temperate freshwater lakes. *Can J Fish Aquat Sci* 54:2350–2360
- Strayer DL, Likens GE (1986) An energy budget for the zoobenthos of Mirror Lake, New-Hampshire. *Ecology* 67:303–313
- Strayer DL, Cole JJ, Likens GE, Buso DC (1981) Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic softwater lake. *Freshw Biol* 11:435–440
- Strecker AL, Arnott SE (2008) Invasive predator, *Bythotrephes*, has varied effects on ecosystem function in freshwater lakes. *Ecosystems* 11:490–503
- Taylor RB, Blackburn RI, Evans JH (1995) A portable battery-powered suction device for quantitative sampling of small benthic invertebrates. *J Exp Mar Biol Ecol* 194:1–7
- Vadeboncoeur Y, Vander Zanden MJ, Lodge DM (2002) Putting the lake back together: reintegrating benthic pathways into lake food web models. *Bioscience* 52:44–54
- Vadeboncoeur Y, Jeppesen E, Vander Zanden MJ, Schierup HH, Christoffersen K, Lodge DM (2003) From Greenland to green lakes: cultural eutrophication and the loss of benthic energy pathways in lakes. *Limnol Oceanogr* 48:1408–1418
- Vadeboncoeur Y, McCann KS, Vander Zanden MJ, Rasmussen JB (2005) Effects of multi-chain omnivory on the strength of trophic control in lakes. *Ecosystems* 8:682–693
- Vander Zanden MJ, Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* 83:2152–2161
- Vander Zanden MJ, Chandra S, Park S, Vadeboncoeur Y, Goldman CR (2006) Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. *Can J Fish Aquat Sci* 63:2608–2620
- Waters TF (1977) Secondary production in inland waters. *Adv Ecol Res* 10:91–164
- Waters TF, Crawford GW (1973) Annual production of a stream mayfly population—comparison of methods. *Limnol Oceanogr* 18:286–296
- Weidel B, Carpenter S, Cole J, Hodgson J, Kitchell J, Pace M, Solomon C (2008) Carbon sources supporting fish growth in a north temperate lake. *Aquat Sci* 70:446–458
- Woodcock TS, Huryn AD (2007) The response of macroinvertebrate production to a pollution gradient in a headwater stream. *Freshw Biol* 52:177–196