LTER 2006 All Scientists Meeting – Working Group Report

Title: Metabolic Theory of Ecology and Stream Ecosystems

Organizers: Jennifer Follstad Shah, Chelsea Crenshaw, and Alex Huryn

Date: September 22, 2006 (Sessions 6 and 7, group 1)

Abstract: Metabolic rate is the most fundamental metric of living organisms. A Metabolic Theory of Ecology (MTE) has recently been developed that predicts how metabolic rate controls ecological processes at all scales; that is, from individuals to ecosystems. The theory is based on the premise that metabolic processes are some function of body mass, temperature, and the concentration of resources needed to fuel metabolism. The greatest strength of the MTE is that it describes the dependence of metabolic rate on organism size and temperature based on simple physical laws that govern reaction rates and resource distribution in networks. Temperature is a well-known correlate for whole stream metabolism. We will present a meta-analysis of published literature which shows that the slope of the relationship between whole stream metabolism and stream temperature is indistinguishable from that predicted by metabolic theory. We also will show that scaling exponents describing the relationship between production:biomass ratios and body mass for macroinvertebrates within three temperate stream communities are consistent with predicted quarter-power scaling relationships. Aquatic studies conducted through the LTER network provide datasets needed to more fully test the MTE. The MTE, in turn, provides a new framework for reassessing previous syntheses and inter-biome comparisons of whole stream metabolism, aquatic community structure, and rates of biomass turnover. The goals of this working group are: a) synthesize datasets on whole stream metabolism, stream temperature, organismal mass and metabolic rates, population densities, and rates of biomass turnover; b) test the MTE using these datasets; c) discuss directions for future research; and d) produce a manuscript for publication.

Participant List

| Farticipant List | | |
|------------------------|----------------------------------------|-------------------------------|
| Name | LTER/Other affiliation | E-mail address |
| Jennifer Follstad Shah | SEV/University of New Mexico | follstad@unm.edu |
| Chelsea Crenshaw | SEV/University of New Mexico | chelsea1@unm.edu |
| Alex Huryn | ARC/University of Alabama | huryn@bama.ua.edu |
| Robert Sinsabaugh | SEV/University of New Mexico | <u>rlsinsab@unm.edu</u> |
| Rafael J. Benítez | LUQ/ITES | rafjbenjoub@gmail.com |
| Debora Figueroa | LUQ/ITES & University of New Hampshire | dpv3@unh.edu |
| Joe Thoun | PIE/ University of New Hampshire | <u>jad28@unh.edu</u> |
| Lee Stanish | MCM/ University of Colorado | lee.stanish@colorado.edu |
| Henry Ruhl | CCE/Marine Bay Aquarium Research | hruhl@mbari.org |
| Ben Koch | University of Wyoming | bkoch@uwyo.edu |
| Jeanine McGann | LNO/University of New Mexico | jmcgann@unm.edu |
| Heidi Fuchs | CCE/Scripps & UC-San Diego | hfuchs@ucsd.edu |
| Steve Thomas | University of Nebraska | sthomas5@unl.edu |
| Bert Cushing | | |
| Pat Mulholland | Oak Ridge National Lab | mulhollandpj@ornl.gov |
| Dan Sobota | HJA/Oregon State University | daniel.sobota@oregonstate.edu |
| Jessica Eichmiller | Kansas State University | eich@ksu.edu |
| Justin Murdock | KNZ/Kansas State University | murdockj@ksu.edu |
| Katie Bertrand | KNZ/Kansas State University | <u>bertrand@ksu.edu</u> |
| Alyssa Standorf | KNZ/Kansas State University | standorf@ksu.edu |
| Maury Valett | CWT/Virginia Tech | mvalett@vt.edu |
| Sherri Johnson | HJA/USFS-PNW | johnsons@fsl.orst.edu |
| Todd Crowl | Utah State University | facrowl@cc.usu.edu |
| Dick Marzolf | KNZ/USGS | rmarzolf@shental.net |
| | | |

| Andrew Pike | University of Pennsylvania | apike@sas.upenn.edu |
|-----------------|-----------------------------------|-------------------------|
| Ryan Sponseller | Arizona State University | rspnonse@asu.edu |
| Bill McDowell | University of New Hampshire | bill.mcdowell@unh.edu |
| Roger Nisbet | UC-Santa Barbara | nisbet@lifesci.ucsb.edu |
| 28 participants | 9 LTER sites/20 research entities | |

The first session of the working group began with a presentation by Jennifer Follstad Shah that provided a brief background on the MTE, and an overview of published literature, primarily from terrestrial systems, testing the following predictions:

1. Rates of whole-organism metabolism (*B*) scale as the $\frac{3}{4}$ -power of body mass ($B \propto M^{\frac{3}{4}}$; [1]) and increase exponentially with temperature, as described by the Arrhenius equation

$$e^{-E/kT}$$

where E is the activation energy in electron volts [eV], k is Boltzmann's constant, and T is absolute temperature in K.

- 2. Mass-corrected whole-organism metabolism plotted as a function of the inverse of absolute temperature (1/kT), ranging from 0°-40°C, results in a linear relationship with a slope (*E*) that reflects the mean activation energy of biological metabolism (0.6-0.7 eV; [2]).
- 3. The density (*N*) of organisms, within a given body size category and area, scales as the - $\frac{3}{4}$ -power of body mass ($N \propto M^{-3/4}$; [3-5]).
- 4. Temperature-corrected individual biomass production (P) reflects the allocation of metabolic products to reproduction and growth, and is proportional to whole-organism metabolism ($P \propto M^{3/4}$; [6, 7]).
- 5. The product of the mass of individuals within a population and population density equals the standing stock of biomass (W), which scales as the ½-power of body mass ($W = M*M^{3/4} = M^{1/4}$; [3, 8]).
- 6. Temperature-corrected population-level biomass production (P_{tot}) is mass-invariant due to the interaction of scaling exponents for body mass with respect to whole-organism metabolism and population density ($P_{tot} = P*N \propto M^{3/4}*M^{-3/4} = M^0$; [3, 5, 6]).
- 7. Temperature-corrected population-level biomass turnover rate (P_{tot}/W) scales as the -1/4-power of body mass $(P_{tot}/W \propto M^0/M^{1/4} = M^{-1/4}; [3, 8])$.
- 8. The rate of energy flux per unit area (B_{tot}) is mass-invariant because it is the product of whole-organism metabolic rate and population density ($B_{tot} = B*N \propto M^{3/4}*M^{-3/4} = M^0$) [9]. However, energy flux per unit area, like the metabolic rate of individuals, increases exponentially with temperature at some constant rate of resource supply. Thus, the slope of the relationship between the rate of energy flux and the inverse of absolute temperature

(1/kT) is linear, and has a slope (E) that reflects the mean activation energy of metabolism (i.e., 0.6 eV; [9]).

Jennifer continued the presentation by showing that preliminary analyses of stream data showed mixed support for the MTE. Empirical patterns better fit predicted patterns (1) at the macroecological scale vs. that of an individual study, and (2) for annual mean data vs. individual sampling points. Temperature seemed to vary in terms of its dominance in driving ecological pattern. For example, resource supply in heterotrophic streams outweighed the effects of temperature for ecosystem-level rates of respiration. In contrast, predicted and empirical patterns pertaining to body mass showed strong similarity. Resource supply and its interaction with the feeding behavior of macroinvertebrates in the lowest trophic position also were singled out as possible reasons why stream community data from the Ogeechee River consistently resulted in departures from predicted patterns of production, biomass, and turnover. Working group participants found it interesting to note that the best fit between predicted and empirical patterns of production, biomass, and turnover in stream communities was found in a stream devoid of fish (Ball Creek, NC).

Session 2 began with another short presentation by Jennifer Follstad Shah. This presentation focused on the fact that the MTE lacks a quantitative expression for the effects of resources on metabolic rate. Thus, the discussion on resource supply from session 1 dovetailed nicely into session 2. Jennifer showed that trends in whole-stream respiration data collected during the LINX I and II experiments significantly departed from patterns predicted by the MTE. However, predicted and empirical patterns were similar once whole-stream respiration data was normalized by the quantity of benthic organic matter found in each stream. Jennifer then presented how Michaelis-Menten kinetics may be one approach for incorporating resources into the MTE. The discussion that ensued weighed the pros and cons of using the Michaelis-Menten approach. Working group participants also brainstormed alternative means for incorporating resources into the MTE.

Working group participants voiced strong interest in convening again to repeat these analyses with additional data from LTER sites, to determine how best to incorporate resources into the MTE, and to write manuscripts. Working group organizers agreed to submit a proposal to the LTER Network to facilitate these efforts.

Bibliography

- 1. Kleiber, M. 1932. Hilgardia 6:315-332.
- 2. Gillooly, J.F., J.H. Brown, G.B. West, et al. 2001. Science 293:2248-2251.
- 3. Huryn, A.D. and A.C. Benke. In Press. Advances in Ecological Research.
- 4. Damuth, J. 1981. Nature 290:699-700.
- 5. Enquist, B.J., J.H. Brown, and G.B. West. 1998. Nature 395:163-165.
- 6. Ernest, S.K.M., B.J. Enquist, J.H. Brown, et al. 2003. Ecology Letters 6:990-995.
- 7. Niklas, K.J. and B.J. Enquist. 2001. Proceedings of the National Academy of Sciences of the United States of America 98:2922-2927.
- 8. Allen, A.P., J.F. Gillooly, and J.H. Brown. 2005. Functional Ecology 19:202-213.
- 9. Enquist, B.J., E.P. Economo, T.E. Huxman, et al. 2003. Nature 423:639-642.