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Teaching Issues and Experiments in Ecology - Volume 7, March 2011

ISSUES : DATA SET

Metabolic ecology: How do body size and temperature affect nutrient cycling rates?

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THE ECOLOGICAL QUESTION:

Do nutrient cycling (excretion) rates of fish in lakes scale with body size and temperature as predicted by The Metabolic Theory of Ecology?

ECOLOGICAL CONTENT:

Animal metabolism, allometry, temperature dependence, nutrient cycling

WHAT STUDENTS DO:

Students use data on the nitrogen and phosphorus excretion rates of fish to test hypotheses related to metabolic ecology. Specifically, we examine predictions related to allometry and temperature dependences by asking how excretion rates are related to fish body size and temperature. The data are derived from fish in intact ecosystems (lakes), not from lab experiments. Therefore, the data can be used to ask how well predictions of metabolic ecology are borne out under field conditions.

SKILLS:

Using a spreadsheet to make graphs and do basic statistical analyses; working with a “large” data set; quantifying the simultaneous effects of two independent variables; working in groups; making presentations; evaluating the support for various hypotheses

STUDENT ACTIVE APPROACHES:

[Cooperative learning](#), [group work assessment](#), [guided inquiry](#)

ASSESSABLE OUTCOMES:

Graphs depicting patterns; estimates of slopes using simple linear regression; creativity in analyzing data; critical thinking; drawing conclusions about the validity of hypotheses

SOURCE:

Data are derived from these two papers:

Higgins, KA, MJ Vanni, and MJ González. 2006. Detritivory and the stoichiometry of nutrient cycling by a dominant fish species in lakes of varying productivity. *Oikos* **114**:419-430.

Schaus, M.H., M.J. Vanni, T.E. Wissing, M.T. Bremigan, J.E. Garvey and R.A. Stein. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology and Oceanography* **42**:1386-1397.

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

ACKNOWLEDGEMENTS:

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OVERVIEW OF THE ECOLOGICAL BACKGROUND

This activity explores two main concepts of “metabolic ecology.” One concept is **allometry**, the study of how biological rates (and other traits of organisms) vary with body size. The other is **temperature dependence**, i.e., how biological rates vary with temperature. Specifically, this exercise examines how body size and temperature control an important metabolic and ecological rate, the excretion of nutrients. To accomplish this exercise, we use field data on the nutrient excretion rates of fish. This exercise is also designed to enhance students’ data analysis skills, such as searching for patterns, deriving calculations that summarize a relatively large data set, constructing graphs that best portray patterns, and using some simple statistical techniques to analyze the data.

Why study the effects of body size and temperature on metabolic rates?

The metabolic rates of organisms – plants, microbes and animals – are strongly influenced by the organism’s body size and body temperature (Gillooly et al. 2001, Brown et al. 2004, Anderson-Teixeira et al. 2009, [Martinez del Rio and Karasov 2010](#)). Many biological rates vary with body size; larger organisms obviously have higher metabolic rates than smaller organisms, when these rates are expressed on a *per individual* basis (sometimes called *per capita* basis). In addition, because the rates of most biochemical reactions are temperature dependent, most metabolic rates also increase with body temperature, at least up to the upper tolerance limit for that organism.

It is important to study how biological rates vary with body size, for several reasons. There is great variation in body size among the life forms on earth, ranging from tiny bacteria to great whales and giant sequoia trees. Even within a species, body size can vary greatly. Knowledge of how biological rates vary with size can therefore provide critical information about how individuals of difference size use resources, how they process materials such as nutrients and energy, and therefore how they interact with other species. Similarly, it is important to study how temperature affects biological rates. Organisms experience a wide range of temperatures, both due to natural variation as well as humans’ effects on temperature. Knowledge of how biological rates respond to temperature can therefore inform us as to how organisms, and ultimately ecosystems, may be affected by changes in temperature.

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

The importance of body size

At a constant temperature, the effect of body size on metabolic rate can be described with the following simple equation (see [Martinez del Rio and Karasov \(2010\)](#) for more information):

$$B = B_0 M^b \quad (\text{eq. 1})$$

where B is an organism's metabolic rate (e.g., grams of oxygen consumed, or nitrogen excreted, per day); B_0 is a constant that is fitted to the data; b is the “**allometric scaling exponent**”; and M is the organism's body mass (Fig. 1). By taking the logarithm of both sides of equation 1, we can express this relationship as a straight line:

$$\log B = \log B_0 + b \log M \quad (\text{eq. 2})$$

where $\log B_0$ is the intercept and b is the slope (Fig. 1). Allometry theory and empirical data show that for many biological rates, the increase in metabolic rate is less than proportional to the increase in body mass. Mathematically, this is equivalent to saying that b (i.e., the exponent in equation 1, or the slope in equation 2) is less than 1. When b is less than 1, this is sometimes referred to as **negative allometry**.

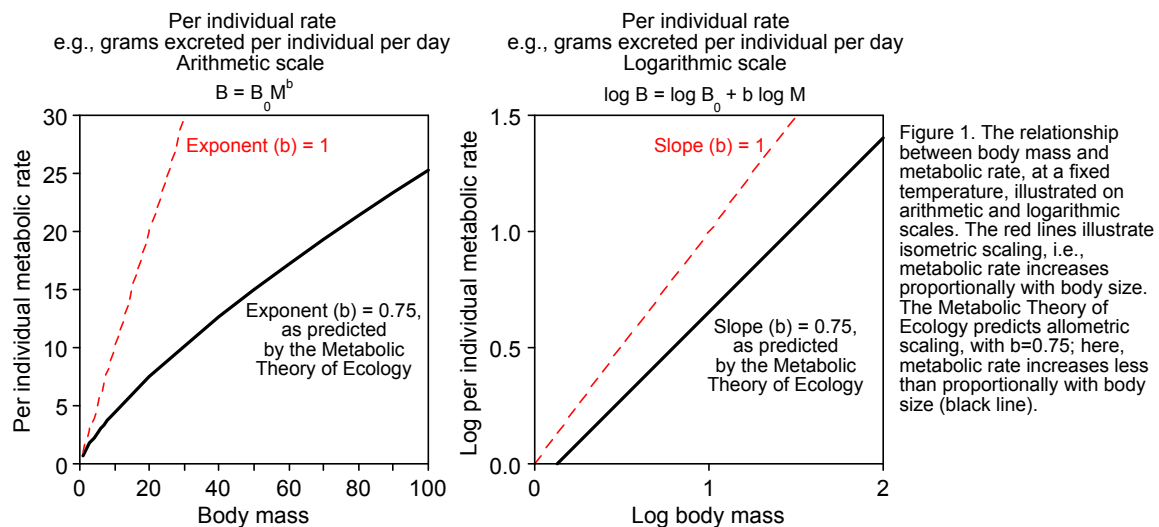


Figure 1. The relationship between body mass and metabolic rate, at a fixed temperature, illustrated on arithmetic and logarithmic scales. The red lines illustrate isometric scaling, i.e., metabolic rate increases proportionally with body size. The Metabolic Theory of Ecology predicts allometric scaling, with $b=0.75$; here, metabolic rate increases less than proportionally with body size (black line).

By measuring metabolic rates of different-sized organisms, the allometric scaling exponent (b) has been estimated for many species, including plants, animals and microbes. The **Metabolic Theory of Ecology (MTE)** predicts that $b = 0.75$ (Fig. 1). This specific prediction is based on the way in which an organism's system for transporting resources within its body (e.g., the circulatory system of animals or the

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

vascular system of plants) scales with body size (West et al. 1997, 1999). There is considerable support for this prediction (Gillooly et al. 2001, Brown et al. 2004), although many studies have found allometric scaling coefficients different than 0.75 (as discussed below).

The importance of body temperature

MTE also incorporates the effects of temperature on metabolic rates. Gillooly et al. (2001) showed that an organism's metabolic rate can be predicted from both its body mass and its body temperature, by expanding on equation 1:

$$B = B_0 M^b e^{-(E/kT)} \quad (\text{eq. 3})$$

where e is the base of the natural logarithm (2.718...); E is the activation energy of enzymes regulating metabolism; k is Boltzmann's constant, which relates energy to temperature; and T is temperature in degrees K.

An important concept regarding the temperature dependence of metabolic rates is Q_{10} , which is defined as the factor by which a rate increases when temperature is increased 10°C. For example, suppose an organism's metabolic rate (e.g., nitrogen excretion per unit time) doubles (i.e., increases by a factor of 2) when we increase temperature by 10°C. In this case, Q_{10} is equal to 2. Q_{10} varies among species and among different physiological and ecological rates, but most Q_{10} values are between 1.5 and 3. If Q_{10} is known for a particular rate, then it can be used to estimate that rate at a fixed temperature (e.g., 20°C). Standardizing the rate to a common temperature facilitates comparisons of different studies conducted at different temperatures (Gillooly et al. 2001).

Note that the relevant temperature for determining metabolic rates is the organism's body temperature. For most plants, microbes and ectothermic ("cold-blooded") animals, body temperature is equal to (or very similar to) environmental temperature. Therefore, environmental temperature can be used in equation 3. In contrast, endothermic ("warm-blooded") animals generally maintain a fairly constant body temperature that is independent of environmental temperature, except at extreme temperatures. Therefore, for endotherms, body temperature (not environmental temperature) must be used in equation 3.

Are the predictions of Metabolic Theory of Ecology generally supported?

The dependence of metabolism on body size and temperature has been studied for many decades (see [Martinez del Rio and Karasov \(2010\)](#) for a review), and there is no doubt that both body size and temperature exert strong controls on metabolic rates. However, the specific predictions of The Metabolic Theory of Ecology (Gillooly et al. 2001, Brown et al. 2004) are somewhat controversial. In particular, some ecologists have disputed the notion that the allometric scaling exponent (b in the

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

equations above) is universally 0.75. Rather, some data suggest that it is often closer to 1 (e.g., for many plants; Reich et al. 2006). Other studies argue that the exponent tends to be ~0.75 only when averaged over many species, but that it varies considerably among species and other phylogenetic categories (Isaac and Carbone 2010). Similarly, while it is beyond questioning that temperature strongly affects metabolic rates, the magnitude of the temperature effect, and how much this effect varies among species, is subject to debate (Irlich et al. 2009).

Basal metabolism, active metabolism, and nutrient excretion rates

Most tests of the effects of temperature and body size measure **basal metabolic rate**, defined as the metabolic rate of an organism when it is inactive, experiences a “neutrally thermal” temperature, and has not eaten for some time (i.e., has fasted). Use of such controlled and restrictive conditions allows researchers to minimize external influences that might increase variability in metabolic rate. However, organisms in nature are often active, experience a wide range of temperatures, and must spend some time feeding; therefore, they often display **active metabolic rates**. Activity generally increases metabolic rates because more energy is needed, and this requires an increase in the speed of biochemical reactions. Endotherms (“warm-blooded” animals) that experience environmental temperatures that are very different from optimum body temperature often show increased metabolic rates. At cold temperatures, they shiver to generate heat and at very warm temperatures they may sweat or pant to dissipate heat; both require energy and thus increase metabolic rates. Feeding can also increase metabolic rate, because it takes energy to capture, consume and digest food.

Nutrient excretion rate, which we will study in this exercise, is a type of metabolic rate – organisms consume and release nutrients as part of their metabolism. For example, some of the protein consumed by an animal is catabolized. This process converts some of the nitrogen (N) in the protein to waste products that are released by the animal (e.g., freshwater animals release N primarily as ammonia, while terrestrial animals release mostly urea). The rates at which organisms excrete nutrients, and how these rates are affected by body size and temperature, are important because nutrients are necessary for plant growth, and therefore for ecosystem productivity. Feeding may have a strong effect on nutrient excretion rates, because an animal will release (via excretion as well as defecation) any nutrients it does not need for growth and reproduction. Thus, all else being equal, when an animal consumes more nutrients, it also excretes more nutrients. The study of how animals and microbes vary in their excretion of nutrients is a very active area of ecology; to learn more about this area, see Sterner and Elser (2002).

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

Nutrient excretion by fish

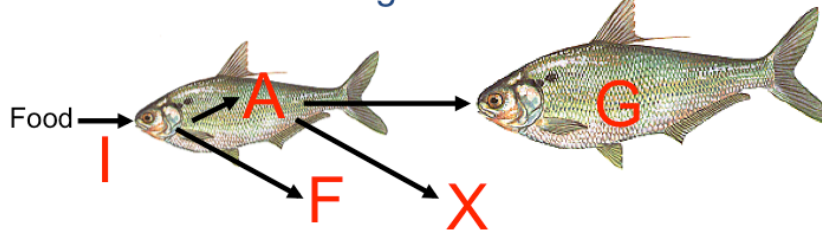
Relatively few studies have examined the effect of temperature and body size on metabolic rates in the field, where variation in activity, diet and other factors can potentially obscure the effects of body size and temperature. This study investigates nutrient excretion rates under field conditions, where other factors can come into play. Specifically, the exercise explores how body size and temperature mediate nutrient excretion rates of a particular fish species, the gizzard shad *Dorosoma cepedianum*. Published excretion rates on 200 fish, measured in three lakes (Schaus et al. 1997, Higgins et al. 2006), are used in this exercise.

The rate at which consumers excrete nutrients is important not only for understanding metabolic ecology, but also for understanding ecosystem-scale nutrient cycling (Sterner and Elser 2002). Gizzard shad is probably the most abundant fish species (based on species biomass) in lakes of the southern and lower Midwest USA (Vanni et al. 2005). This species is omnivorous but mostly consumes sediment detritus from the bottom of lakes, i.e., these fish eat mud. Thus, they consume nitrogen (N) and phosphorus (P) contained in sediment detritus, use some of the N and P for growth and reproduction, and release the leftovers (Fig. 2). Because they are so abundant and consume large amounts of sediment detritus (it's not easy to make a living eating mud!), gizzard shad consume and later excrete (recycle) large quantities of N and P, which are the elements most likely to limit the growth of algae (Vanni et al. 2005). Note that excretion refers to release of nutrients that have previously been assimilated into the bloodstream and then processed by kidneys (i.e., nutrients are excreted as urine). Excreted nutrients are thus released in dissolved form, and are easily taken up by algae. (In contrast, nutrients released in feces have not been assimilated and are released in particulate forms, which are not easily taken up by algae). By excreting N and P in bioavailable forms, gizzard shad provide nutrients for algae (Fig. 3). In some lakes, the flux of nutrients from sediments to water mediated by gizzard shad, is quantitatively important compared to other nutrient fluxes, and can fuel a significant percentage (>25%) of algae primary production (Vanni et al. 2006). Thus, although this exercise focuses on excretion by individual fish, it is important to keep in mind the ecosystem-scale consequences (Fig. 3).

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

Nutrient budget of an animal



- I = Ingestion (consumption) of nutrients (e.g., nitrogen or phosphorus)
 F = Nutrients released as feces (egestion or defecation)
 A = Assimilation of nutrients, i.e., absorption of nutrients across gut wall, into the bloodstream; assimilation equals ingestion minus egestion
 G = Nutrients allocated to growth (and reproduction, if applicable)
 X = Nutrients released as excretion (e.g., as urine); these nutrients were previously assimilated (unlike those released as feces)

$$X = I - F - G \quad \text{or} \quad X = A - G$$

Figure 2. A nutrient budget for an animal. This exercise focuses on X, the excretion of nutrients.

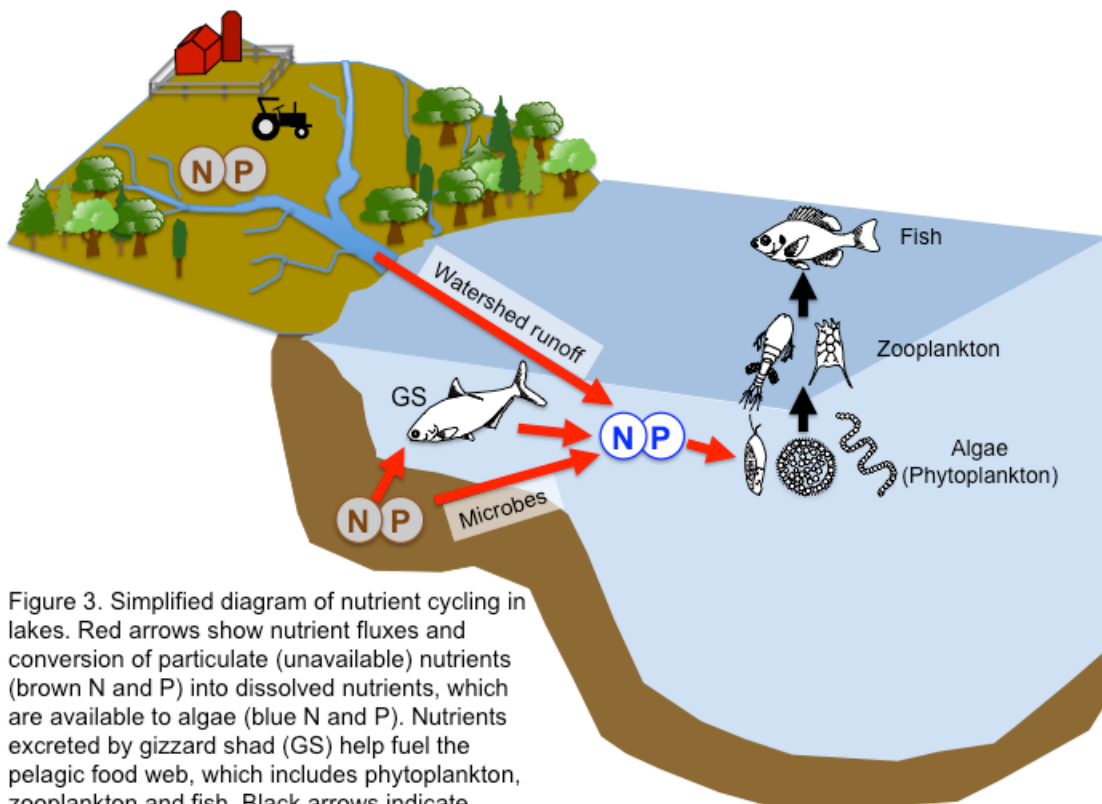


Figure 3. Simplified diagram of nutrient cycling in lakes. Red arrows show nutrient fluxes and conversion of particulate (unavailable) nutrients (brown N and P) into dissolved nutrients (blue N and P), which are available to algae (blue N and P). Nutrients excreted by gizzard shad (GS) help fuel the pelagic food web, which includes phytoplankton, zooplankton and fish. Black arrows indicate feeding interactions in the pelagic food web.

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

STUDENT INSTRUCTIONS:

Overview

In this exercise, we will explore how body size and temperature control an important metabolic and ecological rate, the excretion of nutrients. There are two main concepts we will study. One concept is **allometry**, the study of how biological rates (e.g., metabolic rate) vary with body size. The other is **temperature dependence**, i.e., how metabolic rates vary with temperature. We will analyze real data, produced from field experiments designed to quantify nutrient cycling (excretion) rates of fish of various size and living at a range of temperatures. This exercise is also designed to enhance your data analysis skills, including searching for patterns in data, deriving calculations that summarize a relatively large data set, constructing graphs that best portray patterns, and using some simple statistical techniques to analyze the data.

Background

Allometry and temperature dependence have been studied for decades by physiological ecologists. Recent papers by [Shingleton \(2010\)](#) on allometry and [Martinez del Rio and Karasov \(2010\)](#) provide nice overviews of these concepts, including historical developments. The **Metabolic Theory of Ecology** predicts that the metabolic rates of organisms – plants, microbes and animals – can be predicted by the organism's body size and body temperature (Gillooly et al. 2001, Brown et al. 2004, Anderson-Texeira et al. 2009). Because increasing temperature increases the rate of biochemical reactions, many biological rates also increase with temperature, at least up to the upper tolerance limit for that organism. For organisms whose body temperature varies with environmental temperature (ectotherms, or “cold blooded” organisms), this means that many rates vary directly with environmental temperature. We can express the temperature sensitivity of biological rates using Q_{10} , which is defined as the factor by which a rate increases when temperature is increased 10°C. For example, suppose an organism's metabolic rate (e.g., oxygen consumption per unit time) doubles (i.e., increases by a factor of 2) when we increase temperature by 10°C. In this case, Q_{10} is equal to 2. Q_{10} varies among species and among different physiological and ecological rates, but most Q_{10} values are between 1.5 and 3.

Many biological rates also vary with body size (Gillooly et al. 2001). Large organisms have a higher metabolic rate than small organisms, when the rate is expressed on a *per individual* basis, e.g., oxygen consumed per individual per hour. However, the increase in metabolic rate is often not proportional to the increase in body mass. The study of how metabolic rate (or any other rate) varies with body size is called **allometry**. Precisely how biological rates change with body size is referred to as **allometric scaling**. Allometric scaling has been studied in many organisms and for many biological rates, and some general patterns have emerged. The Metabolic Theory of Ecology (MTE) predicts that we can relate body size and metabolic rate

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

with this simple equation:

$$B = B_0M^{0.75} \quad (\text{eq. 1})$$

where B is an organism's metabolic rate (e.g., grams of oxygen consumed, or nitrogen excreted, per day); B_0 is a constant that is fitted to the data; and M is the organism's body mass. The exponent 0.75 is the “**allometric scaling exponent**” predicted by MTE. By taking the logarithm of both sides of equation 1, we can express this relationship as:

$$\log B = \log B_0 + 0.75 \log M \quad (\text{eq. 2})$$

Equation 2 describes a linear relationship in which $\log B_0$ is the intercept and 0.75 is the slope. If metabolic rate increased in proportion to body mass, the exponent in Equation 1 (slope in Equation 2) would be 1.

There are profound consequences of an allometric scaling exponent that is substantially less than 1. For example, an elephant (5×10^6 g) weighs about 500,000 times more than a mouse (10 g). However, if their metabolic rates vary with body size with an allometric scaling exponent of 0.75, the elephant's metabolic rate will be only about 19,000 times greater than that of the mouse – proportionally much less than the difference in body mass.

In addition to body mass, MTE incorporates the effect of temperature on metabolic rate, as shown in the next equation (Gillooly et al. 2001):

$$B = B_0M^{0.75}e^{-(E/kT)} \quad (\text{eq. 3})$$

where e is the base of the natural logarithm (2.718...); E is the activation energy of enzymes regulating metabolism; k is Boltzmann's constant (8.617×10^{-5} eV K^{-1}), which relates energy to temperature; and T is temperature (K). E tends to vary from 0.2 to 1.2 eV, depending on the reaction, and MTE predicts it to be close to ~0.6 (Gillooly et al. 2001).

Although MTE makes some specific predictions about the allometric scaling exponent (0.75) and assumes that E is close to 0.6, in nature there is considerable variability in these values. For example, the scaling exponent may be closer to 1 than 0.75 (e.g., for many plants; Reich et al. 2006). Or, the exponent may average out to be ~0.75 when many species are considered, but it can vary considerably among species and other phylogenetic groups (Isaac and Carbone 2010). Similarly, while it is beyond questioning that temperature strongly affects metabolic rates, the magnitude of the temperature effect (which depends directly on E) can also vary greatly among species (Irlich et al. 2009).

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

In this exercise, we will explore how nutrient excretion rates vary with body size and temperature. We will use a particular fish species, the gizzard shad *Dorosoma cepedianum*, as a model organism for this study. Published excretion rates on 200 fish, measured in three lakes (Schaus et al. 1997, Higgins et al. 2006), are used in this exercise. The rate at which an animal excretes nutrients is an example of a metabolic rate, in the sense that this rate represents the quantity of nutrient released after metabolic and structural needs are met. For example, the catabolism of proteins produces nitrogen-rich waste products, which animals then release as urine (or other excretory product).

The rate at which consumers excrete nutrients is important not only for understanding metabolic ecology, but also for understanding ecosystem-scale nutrient fluxes (Sterner and Elser 2002). Gizzard shad is probably the most abundant fish species (based on species biomass) in lakes of the southern and lower Midwest USA (Vanni et al. 2005). This species is omnivorous but mostly consumes



Gizzard shad, *Dorosoma cepedianum*

sediment detritus from the bottom of lakes, i.e., these fish eat mud. Thus, they consume nitrogen (N) and phosphorus (P) contained in sediment detritus, use some of the N and P for growth and reproduction, and release the leftovers. Because they are so abundant and consume large amounts of sediment detritus (it's not easy to make a living eating mud!), gizzard shad consume and later excrete large quantities of N and P, which are the elements most likely to limit the growth of algae (Vanni et al. 2005). By excreting N and P in bioavailable forms, gizzard shad provide nutrients for algae to use. In some lakes, the flux of nutrients from sediments to water mediated by gizzard shad is quantitatively important compared to other nutrient fluxes, and can fuel a significant percentage (>25%) of algae primary production (Vanni et al. 2006). Thus, although this exercise focuses on excretion by individual fish, it is important to keep in mind the ecosystem-scale consequences (e.g., Schaus et al. 2010).

Most tests of the effects of temperature and body size on metabolic rates have been done in the lab, where activity, temperature and diets can be controlled, and where metabolism is measured as the **basal metabolic rate**. This is the metabolic rate of an organism that is inactive, experiences a "neutrally thermal" temperature, and has not eaten for some time (i.e., has fasted). Use of such controlled and restrictive conditions allows researchers to minimize external influences (activity, extreme temperatures, feeding) that might increase variability in metabolic rate. However, organisms in nature are often active, experience a wide range of temperatures, and

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

spend some time feeding; therefore, they would display **active metabolic rates**. Activity generally increases metabolic rates because more energy (and in aerobic organisms, oxygen) is needed under active conditions, and the speed of many biochemical reactions increases to deliver energy and oxygen to cells. Feeding can also increase metabolic rate, because it takes energy to capture, consume and digest food. Also, an animal will release (via excretion as well as defecation) any nutrients it does not need for growth and reproduction. Thus, all else being equal, when an animal consumes more nutrients, it also excretes more nutrients.

Our study investigates whether temperature and body size effects are also observed under field conditions, where other factors such as diet, feeding rate and activity level, can come into play. Such field-based studies of allometric scaling and temperature dependence are somewhat rare.

Specific goals and hypotheses

You will be given a dataset containing 200 observations on excretion of nutrients (N and P) by gizzard shad. These data have been used in publications by Schaus et al. (1997) and Higgins et al. (2006), which also describe how excretion rates were measured in the field. You will use these data to test the following hypotheses:

1. N excretion rate of gizzard shad scales with body size as predicted by the Metabolic Theory of Ecology, i.e. the slope of the log N excretion rate vs. log body mass is ~ 0.75 .
2. P excretion rate of gizzard shad scales with body size as predicted by the Metabolic Theory of Ecology, i.e. the slope of the log P excretion rate vs. log body mass is ~ 0.75 .
3. N excretion rate increases with temperature with a Q_{10} near 2.
4. P excretion rate increases with temperature with a Q_{10} near 2.

We can offer alternatives to hypotheses 1 and 2, because some theory as well as data suggest that the allometric scaling exponent (slope on a log-scale) is closer to 1 than 0.75. Therefore, our alternative hypotheses are:

- 1_{alt.} N excretion rate of gizzard shad scales isometrically with body size, i.e. the slope of the log N excretion rate vs. log body mass is ~ 1 .
- 2_{alt.} P excretion rate of gizzard shad scales isometrically with body size, i.e. the slope of the log P excretion rate vs. log body mass is ~ 1 .

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

Data

The dataset consists of an Excel file with 4 data columns, each with 200 rows. Each row (observation) represents a different fish, whose excretion rate was measured in one of three lakes in Ohio (Acton, Burr Oak and Pleasant Hill lakes). Column 1 has the temperature experienced by the fish (i.e., water temperature where gizzard shad live at the time of the experiment). Column 2 gives the mass of each fish, in grams



Aerial view of Acton Lake, Ohio. Some of the excretion rates in the data set were measured on fish living in this lake. Photo by WH Renwick, Department of Geography, Miami University.

(wet mass). Columns 3 and 4 have the *per individual* nitrogen and phosphorus excretion rates of each fish, in units of μmol of N or P excreted per fish per hour. Excretion rates were measured in the field, using a relatively simple method. Fish are captured and placed in a known volume of filtered lake water (1-4 liters depending on fish size) for a known period of time (usually an hour). Water samples are taken before and after fish are incubated, to estimate nutrient concentrations. Excretion rate is quantified simply as the change in nutrients over time, during the incubation. The lake water is filtered before experiments to remove particles such as algae and bacteria, which would otherwise take up nutrients released by fish. These methods are described in detail in Schaus et al. (1997).

Student activities

General approach

For some of the hypotheses, there is potentially more than one way to analyze the data. In other words, there might not be one single “correct” answer. For many scientific questions, data can be analyzed in more than one way, and deciding which way to analyze data is part of the learning process. For example, we are considering how two variables (body size and temperature) affect excretion rates. If we want to understand how body size affects excretion rate, how do we deal with measurements made at various temperatures? Similarly, when trying to quantify the effect of temperature, how do we deal with rates measured on fish of varying size?

Hypotheses 1 and 2 (and 1_{alt} and 2_{alt})

For these hypotheses, you need to calculate the \log_{10} of excretion rates. Then, on

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

separate graphs, plot log body mass vs. both log N excretion rate and log P excretion rate. Here is a place where you have to make a decision about how to analyze the data. Remember that excretion rates were measured at several temperatures, and at each temperature rates were measured on several fish of varying size. So, to examine the relationship between size and excretion rate, should you make a graph using all the data (i.e., all temperatures)? Or a separate graph for each temperature? Or some other approach?

Once you've made these plots, you can analyze them using **linear regression**. Linear regression is a technique whereby a straight line is "fit" to the data. Imagine an x-y scatterplot (e.g., log body mass vs. log N excretion rate) with many data points. Linear regression can be used to determine whether the two variables are associated, and the strength of the association. For example, suppose the plot suggests that the two variables are associated, but there is "scatter" among the data, i.e., the points do not all fit along a straight line. Linear regression produces the straight line that best fits the data (basically, it produces the line that minimizes the cumulative distances between the data points and the line itself). We can evaluate the strength of the association by examining the " R^2 " value, which ranges from 0 to 1. An R^2 of 0 means that there is no statistically detectable relationship between x and y, whereas an R^2 of 1.0 means that the fit is perfect, i.e., all points fall exactly on the line. Another way to view R^2 is that it represents the amount of variance in y that is explained by variance in x. If R^2 is 1 (an extremely rare occurrence in biology!), that means that we can explain all the variance in y with one single variable, x. If R^2 is 0.5 (a relatively high value in field ecology), that means that 50% of the variance in y can be explained by x – which also means that half the variance in y is due to some other, unknown, factor(s).

Another feature of linear regression, which is very important for this exercise, is that it allows you to estimate the slope (and intercept) of the regression line. The slope, of course, is of great interest because MTE predicts a slope of 0.75 for the log body mass vs. log excretion rate relationship, whereas our alternative hypothesis predicts a slope of 1. You can easily obtain the slope (and the intercept and r^2) in Excel, using the "Add Trendline" feature once a graph is made (your instructor can provide more details about using Excel).

Once you make the plots, and analyze them with regression, you can address our hypotheses. Are the slopes near 0.75, as predicted by MTE? Or are they closer to 1, as predicted by the alternative hypotheses? Or are the slopes substantially different from both 0.75 and 1? Is the relationship between body size and excretion rate better when separate plots are made for different temperatures, compared to when all the data are pooled together?

To address these hypotheses, you may need to take an iterative approach; that is,

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

you may want to make several plots. First plot what you feel is an appropriate the set of data points to address a hypothesis. Then evaluate the correlation. After this first step, you may want to try different plots (e.g., with different subsets of data) to evaluate the hypotheses. As mentioned above, there is often not a singular “right” approach to analyzing data, and you should feel comfortable trying and evaluating different approaches.

Hypotheses 3 and 4

The first thing to do here is estimate a Q_{10} value for N excretion and P excretion. Remember that Q_{10} is the factor by which a rate increases with an increase of 10°C . So, if a rate is $12 \mu\text{mol fish}^{-1}\text{hour}^{-1}$ at 10° and $26 \mu\text{mol fish}^{-1}\text{hour}^{-1}$ at 20° , then Q_{10} is 2.17 ($26/12=2.17$). How might you estimate Q_{10} with our data? Specifically, what is the best way to calculate Q_{10} when both fish body size and temperature vary? Also, the temperatures in our data set do not sort out at evenly spaced, 10° increments, because we could not control the temperature of the lake. However, the Q_{10} estimate can be done using any temperature range interval (but its value may depend on the range used) as shown in equation (4) in Gillooly et al. (2001). There is more than one approach you can take here – so think about it, and be creative! As mentioned above for Hypotheses 1 and 2, you may want to try different approaches, evaluating each relative to the other.

Interpreting the results

Familiarity with some published papers on allometry and temperature dependence will help you interpret your results. Several papers describe the general concepts of allometry and temperature dependence, including [Martinez del Rio and Karasov \(2010\)](#) and [Shingleton \(2010\)](#). Papers that illustrate the Metabolic Theory of Ecology’s prediction that the allometric scaling exponent should be 0.75 include Gillooly et al. (2001), Brown et al. (2004), and Anderson-Texeira et al. (2009); the latter two papers also discuss how MTE can be extended beyond individuals to populations, communities and ecosystems. As mentioned, MTE’s specific predictions are controversial. Good discussions of this controversy include Martinez del Rio (2008), which offers a philosophy of science perspective, and Isaac and Carbone (2010) from a statistical perspective. Papers that directly challenge MTE, and offer some alternative hypotheses, include Reich et al. (2006), O’Connor et al. (2007), Irlich et al. (2009), and Glazier (2010).

What to hand in and present

You should make graphs of the relationships between $\log(\text{mass})$ and $\log(\text{excretion rate})$. Also, include the calculations you made to estimate Q_{10} (calculations can be done in Excel); you may also make a graph or table showing the Q_{10} values. Place all of the information you plan to present (graphs, tables, text) into a Powerpoint file. Each group should email its Powerpoint file to the instructor ahead of time. During the class period when presentations are made, the instructor will load all the files on

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

the computer in the classroom so that the entire class can view them. All group members are expected to understand the material, how calculations and graphs were made, and to contribute to discussion. During class, groups will be selected randomly to present different parts of the assignment. You will be graded on the material you hand in as well as participation during the exercise.

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TIEE

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NOTES TO FACULTY

Data sets

Two data sets are included for this exercise:

- Fish nutrient excretion (Faculty) [[xls](#)]
- Fish nutrient excretion (Students) [[xls](#)]

Data are taken from two papers coauthored by one of us (MJV):

- Higgins, KA, MJ Vanni, and MJ González. 2006. Detritivory and the stoichiometry of nutrient cycling by a dominant fish species in lakes of varying productivity. *Oikos* 114:419-430.
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Collection of these data, and associated research, was supported by NSF grants DEB 9318452 and 9726877 to MJV and collaborators.

Assessment forms

- Fish nutrient excretion rubric [[doc](#)]
- Fish nutrient excretion peer evaluation [[doc](#)]
- Fish nutrient excretion student assessment [[doc](#)]

Images

- Gizzard shad [[jpg](#)]
- Acton Lake aerial view [[jpg](#)]
- Animal nutrient budget [[tif](#)]
- Lake nutrient cycling diagram [[tif](#)]
- Allometry graphs [[tif](#)]

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

Objectives and audience

This exercise is designed to teach students about the concepts of metabolic ecology, specifically how biological rates are related to body size and temperature. Students are introduced to the concepts of allometry and temperature dependence, including the Metabolic Theory of Ecology (MTE), which makes some very specific predictions about allometric scaling exponents. They are also introduced to some of the controversy surrounding MTE – several papers have criticized both the mechanistic basis of the theory (fractal-like scaling of resource distribution networks with plants and animals) as well as its predictions about the value of the allometric scaling exponent and the way that temperature regulates metabolism.

We use field data on nutrient (nitrogen and phosphorus) excretion rates of fish to test hypotheses about these concepts. The use of field data (rather than lab data) is deliberate, as one goal is to see if the predictions of allometry and temperature dependence are evident in animals living in real ecosystems, where other factors (e.g., diet, behavior, prior physiological conditions) can mediate these relationships. Students are asked to quantify allometric scaling of nitrogen (N) and phosphorus (P) excretion rates, and how rates change with temperature. Students work with real data that have been used in publications.

Detailed background information and key references are provided in the Overview and Student Instructions sections. Depending on their familiarity with these concepts and the controversy surrounding MTE, instructors may want to read (or review) some or all of these papers. For example, instructors unfamiliar with the concepts of allometry and temperature dependence may want to read, and assign to students, the excellent overviews provided by [Shingleton \(2010\)](#) on allometry, [Martinez del Rio and Karasov \(2010\)](#) on the general importance of temperature and body size in mediating an metabolic rates, and Anderson-Teixeira et al. (2009) on MTE in particular. These can provide an excellent starting point, before discussing more advanced papers or conducting the exercise.

Students also gain valuable experience using Excel and how to manage “large” datasets. There are 200 observations in this data set, one for each fish. While this is not a huge amount of data for trained ecologists, for beginning students it’s probably much larger than any other data set they have used. Excel skills used in this exercise include using formulas, making graphs, and using basic statistics (linear regression).

The exercise was first developed for use in an honors section of a general ecology class. In order to take this class, students must be in the university honors program, so they are generally very good students. However, the

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

exercise should be appropriate for any general ecology or physiological ecology class, and with some additional activities could be used in an advanced ecology class.

Suggestions for implementing this exercise

Before students conduct this exercise, they must be introduced to the general concepts of allometry and temperature dependence (including the “Metabolic Theory of Ecology”). Prior to taking a general ecology course, most students have not been exposed to these concepts, even if they took an ecology or environmental science class in high school. Nor are they likely to be exposed to these concepts in their general biology course. Many students with biomedical interests and whose biology training has been from a human-centered perspective have never thought about ectotherms and how their metabolic rates change with temperature. Thus, it's important to start with basic concepts.

Students can be introduced to the concepts of allometry and temperature dependence in lecture (e.g., during a unit on physiological ecology), and they can be assigned some background readings. Depending on students' (and instructors') backgrounds, the background reading may start with very general papers such as those by [Shingleton \(2010\)](#) and [Martinez del Rio and Karasov \(2010\)](#). In trial runs of this exercise, after being given the appropriate background but before doing the actual exercise, our students have read Gillooly et al. (2001) and then discussed it in class with the instructor. Before the in-class discussion, each student is asked to submit a thoughtful question or comment on the paper, using an on-line discussion board. The Gillooly et al. paper is difficult for students, even honors students, because it contains a fair number of equations. Thus, the discussion is used not only to clarify concepts but also to help students overcome their fear of equations. The papers by Anderson-Teixeira et al. (2009), [Shingleton \(2010\)](#), and [Martinez del Rio and Karasov \(2010\)](#) do a nice job explaining the general equations of allometry and temperature dependence, and the specific prediction of MTE that the value of the allometric scaling exponent should be 0.75. These two papers also will help students visualize and interpret relationships on arithmetic and logarithmic scales, which is critical in this field. Thus, these papers can be used to prepare students for the more advanced equations of Gillooly et al. (2001) (or an alternative advanced paper).

Once students have a familiarity with metabolic ecology concepts, they are placed in groups of 3-5 students (depending on class size, time available, etc.). Because the exercise relies on the use of Excel and some basic statistics, students are first given a survey in which they are asked to self-rank their skills in statistics (e.g., whether they've had no course in statistics, a basic course, or an advanced course) and in the use of Excel (e.g., their familiarity with using formulas and making graphs). Then, groups are constituted such that each has

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

at least one person with some familiarity of statistics and one person with some level of competence in Excel. In the Student Instructions section, we have provided a basic description of linear regression and how it is used to evaluate the strength and slope of a relationship. However, instructors may want to provide more training in these areas for students prior to the exercise.

Students are given the assignment one week prior to the class period in which they will present their answers. They are told they must meet as a group to formulate and discuss their answers. As a group, they then compile a powerpoint presentation, which has all of their graphs, tables and text, and which they email to the instructor prior to class. The instructor then loads all the presentations on the classroom computer, and groups are called randomly and asked to address whether the data support the hypotheses. Each group is called on at least once, and they present their answers using the powerpoint files. During the presentations and especially after all groups have presented, students are asked to discuss the various answers and approaches of the different groups. Sometimes different groups obtain somewhat different answers, and the groups are then asked to discuss why this was the case.

Potential pitfalls and challenges

There are several places in this exercise where students can become confused or feel like they don't have the background to optimally answer the questions. Also, the exercise is designed so that students have to think about how to analyze the data, and there is not one specific "correct" answer for each hypothesis. As a consequence, answers from the different student groups can vary quite a bit. This presents a challenge in terms of how to grade students' work. At least part of the grade should be based on the thoughtfulness and creativity of students in analyzing the data.

Many biology students, including very talented students, struggle with equations and generally exhibit "math anxiety." In particular they find it difficult to interpret the implications of log-transforming data (which is necessary to test some of the hypotheses). Thus, it may be useful to show students, step-by-step, how x-y plots can be viewed using raw data and log-transformed data. The review papers of Anderson-Teixeira et al. (2009) and [Martinez del Rio and Karasov \(2010\)](#) are very useful in this regard. Still, instructors may want to spend some time with this concept.

One of the biggest challenges for students is dealing simultaneously with two independent variables (body size and temperature). Many of them do not have the statistical training to analyze the data in an optimal way. Specifically, students are confronted with nutrient excretion rates of fish (the dependent variable) that vary with both temperature and body size (independent variables), and then are

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

asked to examine how each independent variable affects the dependent variable. A trained ecologist or physiologist would probably use multiple regression, with log body size and temperature as independent variables and log excretion rate as the dependent variable. One could then obtain the allometric scaling coefficient and Q_{10} from the multiple regression parameters. Of course, very few (if any) general ecology students will have the statistical background to do such calculations. So they often take more intuitive approaches, which can vary quite a bit. In the [Faculty Excel file](#), we illustrate the multiple regression approach that a trained ecologist might take, as well as some sample approaches typically taken by students.

The “Multiple regressions” worksheet in the Faculty Excel file shows statistics that can be used to obtain allometric scaling coefficients and Q_{10} . These multiple regressions revealed no interactions between the independent variables (temperature and log body size), so regressions without interaction terms are shown. For both N and P, the slope associated with the log body size effect was close to 0.75 (both were ~ 0.79), and based on their standard errors, both slopes’ 95% confidence intervals overlapped 0.75. Thus, there is support for the first two hypotheses (and thus for MTE), i.e., that allometric scaling coefficients are close to 0.75. Q_{10} can also be obtained from the slope of the temperature vs. log excretion rate relationship. This slope was 0.0214 for N excretion, meaning that log N excretion rate increases by 0.0214 for each 1°C increase in temperature, or by 0.214 with a 10°C increase. Converting from log units reveals a Q_{10} of $10^{0.214} = 1.637$. Similarly, for P excretion, this method yields a slope of 0.0290 and a Q_{10} of 1.95. Thus, as hypothesized the Q_{10} for P excretion is clearly very close to 2 (based on the standard errors from the multiple regression, it is not significantly different from 2). However, the Q_{10} for N appears to be significantly less than 2, counter to the hypothesis.

As mentioned, because beginning students don’t have the background to do such analyses, they often take a more intuitive approach. For example, most students make separate plots of log body size vs. log excretion rate for each temperature and obtain a slope (allometric scaling exponent) for each temperature. They often then take the average of these slopes to obtain an overall mean slope. An example of such an approach is provided in the Faculty Excel file (see the worksheets entitled “Graphs – by temperature” and “Summary – slopes table”). This is a perfectly reasonable approach to estimating allometric scaling coefficients. Calculating Q_{10} seems to pose more of a challenge for students, and the approaches that students take vary greatly among groups. Most students seem to think that Q_{10} can only be calculated when rates are measured at 10°C intervals. (In reality, any temperature range can be used, and if students are clever they can see how this is done in one of the equations in Gillooly et al. (2001) and other papers). Therefore, students often search for fish

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

similar in size, whose excretion rates were measured at temperatures that differ by approximately 10°. They do this for several fish pairs, or sometimes groups of fish, and calculate Q_{10} for each pair of fish (or pair of groups). An example of this is also provided in the Faculty excel file, in the “ Q_{10} example” worksheet.

Suggested additional or alternative activities

Alternative discussion papers. The Gillooly et al. (2001) paper, which we have used in a class discussion, is short but dense with equations. Many students struggle with it. Depending on the class and the concepts the instructor wishes to emphasize, there are a number of alternative discussion papers. Brown et al. (2004) includes a more general and probably more accessible introduction to the subject; it also applies MTE to several levels of organization, including individuals, populations, communities and ecosystems. Thus, if one goal is to show the generality of metabolic ecology across levels of organization, Brown et al. (2004) might be more applicable. If the focus is on physiological ecology, Gillooly et al. (2001) might be preferred.

Instructors might also want to delve more into the controversy surrounding MTE. For example, students could read and discuss a paper that presents MTE’s predictions (e.g., Gillooly et al. 2001; Brown et al. 2004; Anderson-Teixeira et al. 2009) as well as a paper (or papers) that present alternative hypotheses or conclusions (e.g., Reich et al. 2006; Irlich et al. 2009; Isaac and Carbone 2010; Glazier 2010). This discussion could include the back-and-forth comments and responses that have sometimes characterized this controversy (e.g., Enquist et al.’s (2007) comment on Reich et al. (2006), and Reich et al.’s (2007) counter-response). This would give students a sense of the give-and-take nature of science.

Incorporate more theory. Inquisitive students ask *why* MTE predicts that allometric scaling exponents should be 0.75. There is a body of theory for this (and a lot of controversy behind it), and it may be appropriate for some classes to delve into this more deeply. The papers by West et al. (1997, 1999) serve as a useful starting point. The theory postulated by West et al. is controversial and has been questioned in several papers (e.g., O’Connor et al. 2007; Glazier 2010; and reviewed by Martinez 2008). Once again, proponents of MTE have responded to some of these challenges (e.g., Allen and Gillooly’s (2007) response to O’Connor et al. (2007)). Thus, additional activities might delve into this controversy; this seems most appropriate for an advanced class.

Extend the analysis to several species. This exercise uses data from a single fish species, whose body mass varies over 2 orders of magnitude (~2 to 200 g). However, metabolic ecology “works” best when body size varies over several orders of magnitude. Thus, an alternative or additional approach is to use data

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

from many species. Hall et al. (2007) present N and P excretion rate data from a variety of aquatic species in field settings (including the gizzard shad excretion data used in this exercise), which could be used in a multi-species analysis. In analyses using many taxa of greatly varying body size, species means rather than individual data are often used as the observations, i.e., each point represents mean body size and mean metabolic rate for a particular species, rather than data for an individual (e.g., Gillooly et al. 2001). This presents another possible thought exercise for students: if a species varies by in body size by 2 orders of magnitude (as for gizzard shad in this exercise), how can we obtain a mean for this species, and what are the implications of lumping all individuals together?

Explanation of Excel file

The [Faculty Excel file](#) contains several worksheets, which are described here.

Worksheet 1: Data. This sheet contains all the raw data, as well as columns that are calculated from the raw data. The first 6 columns (A-F) are also provided to the students (students are provided with *only* these 6 columns). The first column (A) explains the data and the next 5 represent the actual data including a fish identification number (B), water temperature (C), fish body mass (D) and excretion rates for nitrogen (E) and phosphorus (F). The next three columns (G-I) contain log-transformed data that the students must calculate to do the exercise.

Worksheet 2: Graphs - all fish. This sheet contains two graphs: 1) log body size vs. log N excretion rate and 2) log body size vs. log P excretion rate. Linear regressions are also provided, including slopes (allometric scaling exponents) and r^2 values. Students are very likely to produce graphs similar to these.

Worksheet 3: Graphs – by temperature. This sheet contains log(body size)-log(excretion rate) plots for each temperature. Students are likely to include such plots in their answers.

Worksheet 4: Summary – slopes table. This sheet has the slopes (and r^2 values) from all of the regressions plotted in the preceding sheet. In addition, the mean slope, standard error of this mean and approximate 95% confidence interval is given for N and P excretion rates. This table allows one to test whether the mean slope is significantly different from 0.75.

Worksheet 5: Q_{10} example. This contains an example of how some student groups have estimated Q_{10} . The number of fish in each size class (10 mm bins) and at each temperature are provided in a table. From this, one can see that there are several fish between 40-50 mm and 50-60 mm for which excretion rates were measured at 16.4 and 26.6°, basically a 10° difference. The mean

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

excretion rate is then calculated for each group at each temperature and Q_{10} is estimated with these means. This approach is not ideal because it uses only a small fraction of the data; however, it is commonly used by students.

Worksheet 6: Multiple regressions. This sheet contains results of multiple regressions using log body mass and temperature to predict log excretion rates, which are then used to get estimates of allometric scaling exponents and Q_{10} . Regressions were done using JMP and the results copied into the file. Students in general ecology classes will generally not have the background to conduct this kind of analysis. Nevertheless, it is presented because a) it could be done by an advanced ecology class; b) it could be used, after the exercise is completed, to show students how a trained ecologist might analyze the data; and c) it probably represents the best way to estimate these parameters and therefore provides “true” values to which other estimates can be compared. This sheet also contains 3-D response surfaces (also done in JMP) that show graphically how excretion rates depend on body size and temperature. These may help students grasp the meaning of multiple regressions, and more generally, how two independent variables affect a dependent variable.

Grading and assessment

Students should be graded using at least these three criteria: 1) data analysis; 2) presentation of results; and 3) participation. The data analysis grade should consider how much thought and creativity students put into the assignment, and of course must be scaled to the level of the students’ background. The presentation grade may include criteria such as how clearly results were presented, how well graphics conveyed the results, and how well students justified whether or not hypotheses were supported. The participation grade should include performance in the preparatory group meetings and during the in-class presentation. A [rubric](#) is included that may be of use in assessing students’ performances.

As with any group activity, it is sometimes difficult to assess each group member’s contributions. To assist with this aspect of grading, students can be asked to rate each group members’ participation. (Note: this type of survey cannot be done anonymously). A [form](#) is included for assistance with this assessment activity.

The effectiveness of the exercise, as a learning tool, can be assessed in many ways. Students can be asked to write a short paper on their findings, immediately after the exercise is completed or the next class period. Students can also be asked to apply the knowledge they gained in this exercise to new situations; for example, on an exam they could be given some simple data or graphs and asked if the patterns support the predictions of metabolic ecology. In addition, it is often

TIEE

Teaching Issues and Experiments in Ecology - Volume 7, March 2011

desirable to survey the students on their perceptions on the effectiveness of the exercise. An [assessment form](#) for this purpose is also included here. If several group exercises are done during a semester, this tool can be used to compare them in terms of effectiveness.

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TIEE

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