**A global database of nitrogen and phosphorus excretion rates of aquatic animals**

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**INTRODUCTION**

The recycling of nutrients by animals is important at many levels of ecological organization. At the level of the individual, the rates at which animals recycle nutrients (egestion of solids and excretion of dissolved molecules) are important because they can be used to explore theories related to Metabolic Ecology (Gillooly et al. 2001; Brown et al. 2004) and Ecological Stoichiometry (ES, Sterner and Elser 2002). Metabolic Ecology predicts that biological rates of individuals (for example, nutrient excretion rates) are power functions of body size (Gillooly et al. 2001). Body size dependence is usually captured in the formula $B = B_0M^b$, where $B$ is individual metabolic rate (e.g., oxygen consumed, or nitrogen excreted, per individual per unit time), $B_0$ is a 'normalization constant,' $M$ is organism body mass, and $b$ is the 'scaling coefficient.' A prominent version of ME, the Metabolic Theory Ecology (MTE), predicts that $b$ is ~0.75 for most biological rates (West et al. 1997; Gillooly et al. 2001), although there is controversy regarding the theory and empirical evidence for this value (White and Seymour 2005; Glazier 2010; Isaac and Carbone 2010). The MTE framework also recognizes the importance of temperature; most biological rates increase exponentially with temperature over most of the thermal tolerance range of an organism (Gillooly et al. 2001, Clarke 2004). MTE has focused mostly on the allometry and temperature dependence of metabolic rates (e.g., oxygen consumption). However, the theoryis applicable to other biological rates, including excretion rates (Allen and Gillooly 2009). Several studies have examined the allometry of excretion rates, and scaling coefficients vary greatly among taxa and studies (e.g., Hall et al. 2007; Sereda et al. 2010).

Ecological Stoichiometry theory (ES) predicts that nutrient excretion rates and ratios of consumers are functions of the imbalance between the nutrient content of the organism's body versus that of its food source.  ES usually focuses on nitrogen (N) and phosphorus (P), and their ratio (N:P; Sterner and Elser 2002). For example, ES predicts that an animal with a high concentration of P in its body (i.e., low body N:P) will sequester more dietary P to grow, compared to a counterpart with low body P (high body N:P). As a consequence, the animal with low body N:P will release wastes at a higher N:P than its counterpart with high body N:P. More generally, across individuals or species, body N:P and waste N:P should be negative correlated (Sterner 1990; Sterner and Elser 2002). Differences among animals in body N:P are often driven by differences in the allocation of P-rich structures such as RNA and bone (Elser et al. 1996; Vanni et al. 2002). ES also recognizes the importance of dietary nutrients in driving nutrient excretion rates and ratios; specifically, consumers whose diet is rich in a particular element should release that element at higher rates than a counterpart consuming a diet that is deficient in that element, given similar body elemental compositions (Sterner 1990; Sterner and Elser 2002). Thus, ES also predicts that food N:P will be positively correlated with the N:P of wastes.

Animals can be important agents of nutrient cycling at the ecosystem level. In some ecosystems, the release of potentially limiting nutrients by animals can sustain a substantial proportion of primary production (McNaughton et al. 1997; Vanni 2002; McIntyre et al. 2008). However, the importance of animals in nutrient cycling varies greatly among species and ecosystems (Vanni 2002), in part because in most ecosystems, animal excretion is but one of many fluxes and transformations of nutrients mediated by animals, microbes and physical processes (e.g. Wood et al. 2016). For example, across aquatic ecosystems, nutrient excretion by animal assemblages can support anywhere from <5% to >80% of algal primary production, depending on the ecosystem. Furthermore, the relative importance of different animal groups (e.g., zooplankton, benthic invertebrates, fish) varies greatly among ecosystems (Taylor et al. 2015).

Given the potential ecosystem-level importance of animal-mediated nutrient cycling, and the potential value of data on animal nutrient recycling rates for testing predictions of Metabolic Ecology and Ecological Stoichiometry, a comprehensive compilation of animal nutrient excretion rates can be of great use to the ecological community. The number of studies of animal mediated nutrient cycling has increased greatly in recent decades (Taylor et al. 2015). However, a comprehensive compilation of excretion rates has not been available. Here, we combine published and unpublished data to create a dataset that includes 10,534 observations of N or P excretion rates of animals from freshwater and marine ecosystems worldwide.

This data set was used recently to test predictions of MTE and ES, as described in Vanni and McIntyre (2016). The main findings of that paper are that body size is by far the best predictor of excretion rates, followed by temperature. Whether an animal was a vertebrate or invertebrate was also a significant predictor, with vertebrates excreting both N and P at higher rates than invertebrates, after accounting for body size and temperature. Other predictors based on ecological stoichiometry, such as theN:P ratio of animal bodies or their food resources, explained very little variance in excretion rates or N:P excreted, once body size, temperature, and the vertebrate/invertebrate classification were accounted for. The

temperature dependence of excretion was stronger for N than P, and thus N:P excreted increased with temperature. Allometric scaling coefficients differed for N and P, were significantly less than 0.75 for both elements, and varied greatly among species. While these findings shed light on the variation in excretion rates among animal taxa, the data set should be useful for additional analyses.

## METADATA

Note: Metadata follows the format in Table 1 of Michener et al. (1997). Although we exclude Fields that are not applicable, we maintained their numbering system.

### Class I. Data set descriptors

**A. Data set identity:** A global database of nitrogen and phosphorus excretion rates of aquatic animals

**B. Data set identification code**:

***1. Excretion rates and ancillary data:*** Aquatic_animal_excretion_data.csv

***2. Variable descriptors:*** Aquatic_animal_excretion_variable_descriptions.csv

**C. Data set description**

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## *2. Abstract*

Animals can be important in modulating ecosystem-level nutrient cycling, although their importance varies greatly among species and ecosystems. Nutrient cycling rates of individual animals represent valuable data for testing the predictions of important frameworks such as the Metabolic Theory of Ecology (MTE) and ecological stoichiometry (ES). They also represent an important set of functional traits that may reflect both environmental and phylogenetic influences. Over the past two decades, studies of animal-mediated nutrient cycling have increased dramatically, especially in aquatic ecosystems. Here we present a global compilation of aquatic animal nutrient excretion rates. The dataset includes 10,534 observations from freshwater and marine animals of N and/or P excretion rates. These observations represent 491 species, including most aquatic phyla. Coverage varies greatly among phyla and other taxonomic levels. The dataset includes information on animal body size, ambient temperature, taxonomic affiliations, and animal body N:P. This data set was used to test predictions of MTE and ES, as described in Vanni and McIntyre (2016; Ecology).

**D. Key words:** *Freshwater and marine ecosystems (lakes, rivers and oceans); invertebrates; vertebrates; body size; ecological stoichiometry; metabolic ecology; nitrogen excretion; nutrient cycling; phosphorus excretion; temperature*

## Class II. Research origin descriptors

### A. Project description

*6. Sources of funding*

The primary sources of funding used to compile and synthesize these data were an US National Science Foundation (NSF) OPUS (Opportunities for Promoting Understanding through Synthesis) award to M.J.V. (DEB 0918993) and NSF award DEB-1030242 to P.B.M. This data set contains observations from many studies, and therefore many funding sources, information on which is provided in the acknowledgments sections of the individual papers. In addition, some authors wished to further acknowledge the following sources (funding sources, authors of this paper), and/or to clarify the role of their employer in supporting the research:

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## B. "Specific subproject" description

### *1. Site description*

a. Site type

Sites include freshwater and marine ecosystems from across the globe.

b. Geography

Marine sites include all five oceans: Atlantic, Arctic, Indian, Pacific and Southern. Freshwater sites included every continent except Antarctica (Africa, Asia, Australia, North America and South America). In aggregate, coverage includes those in polar, temperate and tropical ecosystems.

c. Habitat

Freshwater sites include lakes, rivers and streams, as well as a small amount of data from wetlands. Marine sites include estuaries, coastal ecosystems, and open ocean.

d. Geology

Sites include oceans and freshwater sites scattered across the globe and hence associated with various geological formations.

e. Watersheds, hydrology

Sites include dozens of watersheds spread across the world, ranging from essentially no flow (many lakes) to large rivers.

f. Site history
Sites range from pristine (e.g., lakes in Alaska, the Antarctic Ocean) to highly managed (e.g., reservoirs).

g. Climate
Climate range greatly from polar to tropical. For example, the temperature ranged across observations from -1.9 to 33.5°C.

## ***2. Experimental design***

a. Design characteristics
In general, the design includes measuring excretion rates of field caught animals, which are assumed to have been feeding at 'natural' rates typical for that species in that particular ecosystem. These are 'mensurative' experiments (Hurlbert 1984) in which rates are measured but no experimental treatments are imposed on the animals. Our data set does not include any 'basal rate' data from starved animals.

To find appropriate data, we attempted to do comprehensive searches on Web of Science and Google Scholar, using terms such as "nutrient cycling," "nitrogen excretion," "phosphorus excretion," and related search strings. However, these searches returned several thousands of sources, of which only a tiny proportion included excretion rates measured in the field (the majority of excretion rate measurements obtained in this way were lab studies, with animals provided with controlled diets). Searches using more specific terms such as "animal-mediated nutrient*" or "ecological stoichiometry" returned many fewer sources, but these searches missed many earlier papers published before such terms were commonplace. Therefore, to generate our database we started with keyreview/synthesis papers (Andersson et al. 1988, Sterner 1990, Vanni 2002, Hall et al. 2007, Sereda and Hudson 2011), and scoured these for papers they cited and papers that cited them. We repeated this process for each new paper found, until we were confident we had compiled the vast majority of sources. Our search process was completed in early 2014, and newer papers have been incorporated opportunistically.

Once a potential data source was identified, the two first authors (MJV and PBM) contacted its authors to ask for the original data. In nearly every case, this request was accepted. All individuals providing raw data in this manner, and all 'co-owners' of these data are listed as authors of this data paper. In addition, MJV and PBM contacted other scientists who were likely to have unpublished nutrient excretion data, and contributed unpublished data of their own. Approximately 5% of data were obtained from unpublished sources. Finally, in cases where the author of a paper could not be reached or provide data, but individual-level data were depicted explicitly, we digitized data from published graphics using the free software Digitizeit (http://www.digitizeit.de/). All data providers and source papers (when applicable) are identified in the data file.

## ***3. Research methods***

a. Field/laboratory
Investigators obtained excretion rates in the field by collecting animals and incubating them in a fixed volume of water for a measured period of time. The incubation water is usually pre-filtered to remove particles that could take up or release nutrients. For example, $NH_4$ excreted by animals could be rapidly converted to $NO_3$ via nitrification (e.g., Moulton et al. 2016), so removal of microbes is essential for accurate estimates of animal excretion rates. Nevertheless, some microbial transformations could have occurred in some experiments, which would result in an underestimation of actual excretion rates. Usually incubation containers were placed in the body of water to maintain ambient temperature but in some experiments incubations are done on shore or on a ship (but most these studies also maintained ambient temperature). For most observations in our dataset, an individual animal was incubated by itself in a container. However, it is sometimes not possible to measure rates on single individuals of small species, because they do not excrete enough N or P for accurate measurements. Thus for the smallest animals, a single rate was often measured on several animals (similar in size) incubated together.

Following incubations, animals were weighed to determine their mass. Vertebrates generally were weighed live to determine their wet mass (WM), and in some cases dry mass (DM) was also provided. Most invertebrates were euthanized and dried before weighing for dry mass (DM), and wet mass was not estimated. Weplaced all measurements in the same mass units by converting to WM to DM whenever necessary (this was necessary only for some vertebrates). In cases where DM was not measured directly, we estimated it by multiplying WM by a conversion factor of 0.25 (i.e. DM = 0.25WM). This conversion factor reflects our own measurements of both WM and DM on hundreds of fish, and is in keeping with the literature. For mollusks and turtles, mass measurements represent only soft tissue because structural materials are unlikely to be metabolically active. For all other taxa, the mass of all body tissues was used.

In the lab, water samples from the incubation containers were analyzed for nitrogen (N) and phosphorus (P). N was usually measured as ammonium (NH4, >98% of observations) and rarely as total N. P was usually measured as soluble reactive P (SRP, 87% of observations), but sometimes as total dissolved P or total P. Excretion rates are calculated as the difference in element mass (N or P) over time from the beginning to the end of the incubations. Nutrient mass at the beginning of an incubation was generally inferred from either incubations with no animal, or samples from a common water source before it was aliquoted into incubation containers. Incubation times typically lasted from 15 minutes to 24 hours, but most incubations were relatively short (median 1.3 h). Thus, the unit of observation in the dataset is considered to be individual excretion of nitrogen (N) or phosphorus (P) per unit time (µg N or P excreted per capita per hour).

Some studies reported only mean excretion rates (i.e., the average of what we refer to as observations) rather than data from individual animals. If we could not obtain data on individual observations from the authors, these studies were not included in our dataset.

Our dataset includes a total of 10,534 records (lines of data). However, studies vary in whether they report N excretion rate, P excretion rate, and/or excreted N:P. Thus, the data set contains includes 9822, 8245 and 7513 observations for N excretion rate, P excretion rate, and excreted N:P, respectively. Excreted N:P was sometimes reported by the authors (if both rates were measured) but otherwise we calculated it by dividing N excretion rate by P excretion rate and converting this value to molar units.

b. Instrumentation

N and P were usually measured using standard colorimetric techniques, though $NH_4$-N was sometimes measured by fluorometry.

c. Taxonomy and systematics

The dataset includes both invertebrate and vertebrate animals. Most aquatic invertebrate phyla are represented, as well as numerous fishes and some amphibians and turtles.

**4. *Project personnel***

Many individuals were involved in collection of original data, as shown in the data file "Aquatic_animal_excretion_data.csv." The data were compiled, standardized, and organized by the two lead authors, M.J. Vanni and P.B. McIntyre.

## Class III. Data set status and accessibility

### A. Status

**1. *Latest update***

27 November 2016

**2. *Latest archive data***

27 November 2016

**3. *Metadata status***

27 November 2016

**4. *Data verification***

Data were checked in several ways by the two first authors (MJV and PBM). For each variable (e.g., body mass, temperature, excretion rates, etc.), we sorted the data, examined distributions, and looked for outliers or suspicious data points. In a very small proportion of cases, P excretion rates were reported as negative values (this occurs when P excretion rates are very low, such that the change in concentration in incubation chambers is within the range of analytical precision, and concentrations may appear to decline due solely to measurement error). These observations were deleted, precluding us from calculating excreted N:P for these observations.

### B. Accessibility

**1. *Storage location and medium***

The metadata and data files have been submitted to Ecology.

**2. *Contact person***

Michael J. Vanni, Department of Biology, Miami University. vannimj@miamioh.edu; 513-529-3192

***3. Copyright restrictions***



***4. Proprietary restrictions***

a. Release date: n/a

b. Citation: n/a

c. Disclaimer: n/a

***5. Costs***

There are no costs associated with using these data.

## Class IV. Data structural descriptors

### A. Data set file

***1. Identity***

Aquatic_animal_excretion_data.csv
Aquatic_animal_excretion_variable_descriptions.csv

***2. Size***

Aquatic_animal_excretion_data.csv: 10,534 observations, 3.4 MB
Aquatic_animal_excretion_variable_descriptions.csv: List of 35 variables, 5 KB

***3. Format and storage mode***

The data are contained in a .csv file downloadable from Ecology or Ecological Archives.

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