Exploring the role of bottom-up provisioning by consumers across ecosystems

Carla L. Atkinson

Ocean Carbon and Biogeochemistry Workshop
28 June 2017

http://atkinsonlab.ua.edu
Acknowledgements

Caryn Vaughn
Stephen Golladay
Lora Smith
Woodstoich 2014

Mike Vanni
Amanda Rugenski
Alan Covich
Ken Forshay

Krista Capps
Lab Group at UA

NSF
U.S. Fish & Wildlife Service
Environmental Protection Agency
Alabama Wildlife & Freshwater Fisheries
“A major future challenge is to determine how biodiversity dynamics, ecosystem processes, and abiotic factors interact.”
Biodiversity-Ecosystem Function

Abiotic environment
Temperature, nutrient supply, geology,…

Ecosystem functioning
Productivity, biomass, nutrient cycling,…

Biodiversity
Species richness, composition, interactions,…
Conducting ecological research across scales

- Change in Temperature, Precipitation, Habitat
  - Physicochemical Structure (Discharge, nutrients, etc.)
  - Tolerance/Vulnerability (thermal, sedimentation, etc.)
  - Species Traits (stoichiometry, trophic status, etc.)

- Community Structure & Ecosystem Function (Population Growth, Nutrient Recycling, Primary Production)

- Environmental Monitoring, Land use Analysis, and Forecasting
- Organismal and Population Level
- Community and Ecosystem Level
Excretion and egestion of nutrients are proportional to the ingestion of an element.

Animals are considered stoichiometrically homeostatic and are storing nutrients.

Excretion rates scale with mass and temperature.
Consumer-driven nutrient dynamics

Resources

Consumption

C:N:P

Excretion

C:N:P

C:N:P

N:P

Excretion rates and stoichiometry also varies across taxa
Consumer-Driven Nutrient Dynamics

**Direct Effects**

- Consumption
- C:N:P
- Resources
- Excretion
- N:P

**Indirect Effects**

- Hawlena & Schmitz 2010 (Am. Nat)
- Costello and Michel 2013 (Ecology)
How do we examine if consumer effects are important for higher trophic levels and ecosystem function?
Consumer-Driven Nutrient Dynamics

Organismal Traits
- Body size, Tissue composition
- Temperature preference and tolerance
- Degree of homeostasis
- Growth rate, Reproductive strategy, Lifespan

Population Effects
- Population size
- Biomass, Age/size structure
- Feeding guild, Migration, Distribution

Ecosystem Processes
- Biogeochemical cycling, nutrient limitation
- Reciprocal inter-ecosystem flows of nutrients
- Energy flow to top consumers
- Source–sink dynamics
- Net ecosystem productivity
- Leaf-litter decomposition

External Drivers
- Temperature
- Hydrodynamics
- Light, Canopy Cover
- Allochthonous subsidies

Evolutionary history

Atkinson et al. In press, Biological Reviews
Organismal Traits

Tissue composition, Body size, Feeding guild, Temperature preference, Growth rate, Reproductive strategy, Lifespan, Evolutionary history
Rates vary due to body mass, temperature, and vertebrates vs invertebrate (Vanni and McIntyre 2016)
Excretion N:P most strongly driven by body size in this data set (Vanni and McIntyre 2016)
Stoichiometric Traits

Alabama, Atkinson, *unpublished*

Also, variation in N:P due to age and phylogenetic grouping
Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems

Jacob E. Allgeier,1,3 Lauren A. Yeager,2 and Craig A. Layman2

Variation in N:P with feeding guild

Allgeier et al. 2013 (Ecology)
Population Effects

Population size, Age/size structure, Distribution, Migration, Biomass
N Areal Excretion

Capps and Flecker 2013

SW Georgia Anurans

Panama

Rugenski et al. *In review*
Allgeier et al. 2013 (Ecology)

Allgeier et al. 2014 (Global Change Biology)
Mussel Sampling:
Quantitatively sampled 12 sites with georeferencing.

Transects selected and abiotic variables measured at each quadrat.

A GPS coordinate was taken at each quadrat.

Quadrats were dug with all material going into a mesh bag.

All bags were sorted using a series of sieves and mussels measured.

Excretion and egestion rates measured for 12 species.
30 species encountered
Excretion Rates

N Excretion Rates

P Excretion Rates
Average = 369 µg NH₄-N m⁻² h⁻¹
Areal N Excretion
Average = 44.9 µg P m⁻² h⁻¹
Areal P Excretion
Densities
Average = 35 indiv m⁻²
Average = 35 indiv m\(^{-2}\)  
Average = 369 µg NH\(_4\)-N m\(^{-2}\) h\(^{-1}\)

Biomass-corrected average N:P of Excretion = 18.2;  
Background water column N:P ~8.9

Some species doing more than what their biomass would suggest

- Big contributors:
  - *Pleurobema decisum*
  - *Obovaria unicolor*
**Do species matter?**

Applying an Average Excretion value versus the Species-Weighted

<table>
<thead>
<tr>
<th>Accuracy</th>
<th>Percent Coverage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Underestimate</td>
<td>2.6</td>
</tr>
<tr>
<td>Good</td>
<td>43.2</td>
</tr>
<tr>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>Overestimate</td>
<td>46.5</td>
</tr>
<tr>
<td>High</td>
<td>7.7</td>
</tr>
</tbody>
</table>

**N Excretion Difference**

- Quadrates

<table>
<thead>
<tr>
<th>Estimated Minus Real N Excretion Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>-321 to -50</td>
</tr>
<tr>
<td>-49.9 to 50</td>
</tr>
<tr>
<td>50 to 400</td>
</tr>
<tr>
<td>400 to 1,500</td>
</tr>
</tbody>
</table>

Source: soil, land use, vegetation, etc. (Real Averaged N Excretion Estimate - Actual N Excretion)
# Do species matter?

Applying a Average Excretion value versus the Species-Weighted

## P Excretion

<table>
<thead>
<tr>
<th>Accuracy</th>
<th>Percentage Coverage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Underestimate</td>
<td>4.6</td>
</tr>
<tr>
<td>Good</td>
<td>90.7</td>
</tr>
<tr>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>Overestimate</td>
<td>2.4</td>
</tr>
<tr>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Overestimate</td>
<td>2.3</td>
</tr>
</tbody>
</table>

---

**P Excretion Difference**

- Quadrats
- Mania_Pdiff.tif

**Value**

-50 to -20
-19.9 to 20
20 to 40
50.1 to 100
Do species matter? Applying a Average Excretion value versus the Species-Weighted

N:P Excretion

<table>
<thead>
<tr>
<th>Accuracy</th>
<th>Percent Coverage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Underestimate</td>
<td>2.0</td>
</tr>
<tr>
<td>Good</td>
<td>64.7</td>
</tr>
<tr>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>Overestimate</td>
<td>23.4</td>
</tr>
<tr>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Overestimate</td>
<td>10.0</td>
</tr>
</tbody>
</table>

Source: Raw, modified by: [Author/Contributor]. Cite underlying figures, datasets, and materials as needed. See citation file.
Effects on Ecosystem Processes

Nutrient limitation, Biogeochemical cycling, Production, Decomposition, Energy flow within food webs, Sink-subsidy dynamics
Organism effects are often temporally and spatially variable.

Roman and McCarthy 2010 (PLoS One)
Biogeochemical hotspots

patches that show disproportionately high reaction rates relative to the surrounding matrix (McClain et al. 2003)
Invasive Fishes Generate Biogeochemical Hotspots in a Nutrient-Limited System

Krista A. Capps¹,²*, Alexander S. Flecker¹

¹ Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, United States of America, ² Sustainability Solutions Initiative, University of Maine, Orono, Maine, United States of America

Abstract

Fishes can play important functional roles in the nutrient dynamics of freshwater systems. Aggregating fishes have the potential to generate areas of increased biogeochemical activity, or hotspots, in streams and rivers. Many of the studies documenting the functional role of fishes in nutrient dynamics have focused on native fish species; however, introduced fishes may restructure nutrient storage and cycling freshwater systems as they can attain high population densities in novel environments. The purpose of this study was to examine the impact of a non-native catfish (Loricariidae: Pterygoplichthys) on nitrogen and phosphorus remineralization and estimate whether large aggregations of these fish generate measurable biogeochemical hotspots within nutrient-limited ecosystems. Loricariids formed large aggregations during daylight hours and dispersed throughout the stream during evening hours to graze benthic habitats. Excretion rates of phosphorus were twice as great during nighttime hours when fishes were actively feeding; however, there was no diel pattern in nitrogen excretion rates. Our results indicate that spatially heterogeneous aggregations of loricariids can significantly elevate dissolved nutrient concentrations via excretion relative to ambient nitrogen and phosphorus concentrations during daylight hours, creating biogeochemical hotspots and potentially altering nutrient dynamics in invaded systems.
Patchy Distribution Mussel beds can be separated by a stream distance of 800m – 2500 meters in "undisturbed" systems. Atkinson and Vaughn 2015, Freshwater Biology Special Issue
Mussel Nutrient Recycling

Hotspots of nutrient regeneration – densest beds

$>600 \text{ mol N d}^{-1} = \frac{8.5 \text{ kg N d}^{-1} =}{3 \text{ metric tons N yr}^{-1}}$

Atkinson and Vaughn 2015, *Freshwater Biology* Special Issue
Stoichiometry and Species Traits

Meets the expectations of ecological stoichiometry

Higher excretion N:P = beds dominated by *Actinonaias ligamentina*

*A. ligamentina* classified as a thermally sensitive species*

*Spooner & Vaughn 2008 (Oecologia)*
Mussels live 5 to >50 years (Shell = long term store, “nutrient sink”*)

Across the Kiamichi (47 reaches) ~ Storing:
- 14 tons C
- 5 tons N
- 0.5 tons P

*Vanni et al. 2013 (Ecology)
Atkinson et al. 2015 (FWB)
Atkinson et al. Accepted, Ecosystems
Mussels are acting as sequestration and cycling hotspots

Higher gross primary productivity in reaches with mussels
Alleviation of Nitrogen Limitation by Mussels

Atkinson et al. 2013 (Ecology)

Difference in benthic algae community composition
Nutrient recycling by mussels: comparing to uptake rates and tracing N in the food web

Tracing Consumer-Derived Nitrogen in Riverine Food Webs

Carla L. Atkinson,* Jeffrey F. Kelly, and Caryn C. Vaughn
Tracing $\delta^{15}\text{N}$ into the Food Web

**Food web $\delta^{15}\text{N}$ sampled** = periphyton, *Justicia americana*, mayflies, and stoneflies

-10 m  -5 m  5 m  10 m  25 m  50 m  100 m

Created mussel bed

Little River, Oklahoma

Enriched mussels – grew for ~1 year
Nutrient Uptake Measurements

Excretion Rate Measurements

Atkinson et al. 2014 (Ecosystems)
Mussel Derived N moved into the food web

Mussels meet up to 40% of N demand; could be up to 98% in natural mussel beds

Up to 70% of N in the tissue of organisms near mussels beds from N remineralized by mussels

Atkinson et al. 2014 (Ecosystems)
*Sansom et al. In prep
Under increased human impact - implications

Climate change, Fishing pressure, Nutrient loading, etc.
Over-fishing & Habitat Fragmentation

Areal excretion $\mu g \cdot m^{-2} \cdot h^{-1}$ for NH$_4$-N and TDP-P

Layman et al. 2011
(Ecological Applications)
Consumers lead to greater nutrient heterogeneity, but enhanced nutrient loading dampens this.
What are the ecological consequences for the continued loss of species?

Atkinson et al. 2014, *Biological Conservation*
Reduction of Thermally Sensitive Species

Between 1992 and 2003

Galbraith et al. 2010 (*Biological Cons.*)

Between 2010 and 2012 (severe drought 2011)

Atkinson et al. 2014 (*Biological Cons.*)
Loss in ecosystem function

Remineralization

- 30% N loss = 40 µmol N m$^{-2}$ h$^{-1}$
- 20% P loss = 5 µmol P m$^{-2}$ h$^{-1}$

Storage Average

- 29% Loss = >15 g N m$^{-2}$
- 30% P Loss = 5 g P m$^{-2}$

Atkinson et al. 2014 (Biological Conservation)
Alteration of N:P

Excretion N:P increased with increasing numbers of thermally sensitive species, but not significantly ($p = 0.10$)

N:P declined significantly due to drought conditions ($W = -45.0, p = 0.004$)

Excretion N:P was predicted by tissue N:P

Atkinson et al. 2014 (*Biological Conservation*)
Stoichiometric traits may vary as a function of tolerance.

Vulnerability to extreme events can lead to different species responses, with tolerant and sensitive species showing distinct body stoichiometry. Changes in nutrient recycling and a shift in N:P ratios can have community effects, impacting overall species dynamics.
Can we link stoichiometric traits and physiological traits (i.e. thermal traits) to understand ecosystem vulnerability and predict species losses and consequential declines in ecosystem function?

Modified from Diaz et al. 2013 (Ecology and Evolution)
Can we link stoichiometric traits and physiological traits (i.e. thermal traits) to understand ecosystem vulnerability and predict species losses and consequential declines in ecosystem function?
Can we link stoichiometric traits and physiological traits (i.e. thermal traits) to understand ecosystem vulnerability and predict species losses and consequential declines in ecosystem function?
Can we link stoichiometric traits and physiological traits (i.e. thermal traits) to understand ecosystem vulnerability and predict species losses and consequential declines in ecosystem function?

If we understand the traits and functions that may be lost, we can better predict the ramifications of ecological change.
Can we link traits to species responses to abiotic conditions to understand ecosystem vulnerability and predict species losses and consequential declines in ecosystem function?

If we understand the traits and functions that may be lost, we can better predict the ramifications of ecological change.
Ecological Stoichiometry as framework

Physicochemical —structure
(Temp, nutrient limitation, geology)

Community Structure
(Density, biomass, body size of species)

Species traits

Ecosystem Processes

Body size & stoichiometric relationships

Areal excretion & storage N & P

Homeostasis

Primary production
Leaf decomposition

Net effects of nutrient remineralization and uptake and turnover of N and P
ANY QUESTIONS?

More info
Email: clatkinson@ua.edu
Website: https://atkinsonlab.ua.edu

“Mussels are not dismissible, even by those who have little interest in the natural world. Their presence is a signature of healthy aquatic ecosystems, to which they contribute as living water filters.”

- E.O. Wilson
Tadpole chamber experiment

What are the effects of tadpoles & invertebrate shredders on leaf decomposition processes?

4 Treatments: 32 day incubation
Control
Tadpoles (Grazer on algae)
Tadpoles + Shredders
Shredders

* Natural stream densities used for each chamber

Rugenski et al. 2012

Smilisca
Anchytaurus
Phylloicus
### Chamber experiment

↑ Respiration in Tadpole & Tadpole+INV

↑ Leaf area loss in Tadpole+INV

Facilitation between tadpoles & shredding macroinvertebrates

F_{3,15} = 5.82, P = 0.004

**Leaf respiration (mg O\textsubscript{2} DM\textsuperscript{-1} h\textsuperscript{-1})**

**Leaf area loss (%)**

**Rugenski et al. 2012**

TP

TP+INV

INV
Stoichiometric Traits, Age, and Phylogeny

Some phylogenetic signal

Decline in N:P with age