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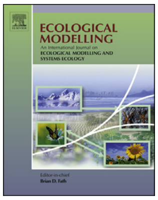

A class exercise for Systems Ecology: Synthesis of stream energetics and testing Allen's paradox

Charles A.S. Hall[a,*], Frances Knickmeyer[b], Adrian Wiegman[c], Andrew Brainard[a], Avriel Rose Diaz[a], Carolyn Huynh[b], Jerry Mead[d]

[a] Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, United States
[b] Division of Environmental Science, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, United States
[c] Department of Environmental Studies, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, United States
[d] New York City Department of Environmental Protection, 7870 State Route 42, Grahamsville, NY 12740, United States

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ABSTRACT

We report energy stocks and flows, as well as other ecosystem properties, measured in Little Sandy Creek in Upstate New York as part of an intensive class project in a graduate-level Systems Ecology course at the SUNY College of Environmental Science and Forestry. Our study synthesizes information on Little Sandy Creek both as a whole system and through examination of key individual trophic components. We also test Allen's paradox in Little Sandy Creek – whether there is enough biomass produced by the invertebrate community to support the energetic needs of the fish community. Students collected data in the field over the course of a weekend in September 2012. During the ensuing semester, we synthesized all of these data (often utilizing relatively simple quantitative models) to generate a spatial synthesis populated with trophic levels for a one kilometer reach of stream. We utilized two synthesizing procedures during our trophic flow analysis: first, we sampled organisms along a depth gradient, and modeled trophic levels and size class with depth to give more precise estimates of biomass. Second, we used models for the relation between production and also respiration (energy requirements) and organism size to estimate production and energy use of trophic levels and functional feeding groups. We synthesized and extrapolated upon our data with a numerical model that simulated the stocks and flows in Little Sandy Creek using abiotic forcing functions and functional responses derived from our field measurements. The mean values indicate the benthic macroinvertebrate production (11 kJ m^{-2} day^{-1}) is insufficient to support the fish energy requirements (13 kJ m^{-2} day^{-1}) within our uncertainty estimates; given an 80% assimilation efficiency for fish, the macroinvertebrate production is enough to supply only 68% of the fish needs. Our primary hypothesis was supported: students were able to thoroughly collect and organize data from Little Sandy Creek in a single weekend. Further, over the course of a semester, students successfully analyzed their data. We were then able to take that data and build a realistic model of the Little Sandy Creek system. Based on our model outputs, we fail to reject our secondary hypothesis that Allen's paradox is present in Little Sandy Creek.

1. Introduction

Ecology, as a discipline, had been unified by Eugene Odum's textbook (Odum, 1953) when one of us (C. Hall) took the course in 1963. In recent years, there has been a compartmentalization of Ecology into sub disciplines (e.g. population ecology and community ecology), that from our perspective has diluted the impact of the Odum brother's (Eugene and Howard) teachings of systems thinking that ecology was once founded upon despite its continuation in some quarters. There is a need to bring back systems thinking more generally to the field because of the increasing complexity, scope, and urgency of environmental issues. Specifically due to the proliferation of compartmentalized approaches to ecology and the death or

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* Corresponding author.
E-mail addresses: chall@esf.edu (C.A.S. Hall), fbknickm@syr.edu (F. Knickmeyer), awiegman@syr.edu (A. Wiegman), abrainar@syr.edu (A. Brainard), ardiaz@syr.edu (A.R. Diaz), ckhuynh@syr.edu (C. Huynh), jmead@dep.nyc.gov (J. Mead).

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retirement of most of the second generation of systems ecologists, it is imperative that we formally document successful approaches to teaching systems ecology. While there are a number of Systems Ecology textbooks available (e.g., Odum, 1994; Jørgensen, 2012), in our opinion, none of them capture the essence of what we perceive as a true systems ecology teaching experience. We believe systems perspectives and ideas should first be introduced by having students study nature conceptually and quantitatively from a systems approach, including physical and biotic elements and the interactions among them. Thus, in our opinion, modeling should be complementary to the conceptual and quantitative studies in the field. With this in mind, we present here the methods and results of our experience with developing such an approach (including conceptualization, field data collection, and modeling) in a graduate class called Systems Ecology.

The concepts and methodology described here were formalized over the span of 30 years as part of the Systems Ecology course taught at Cornell University in Ithaca N.Y. and the State University of New York College of Environmental Science and Forestry (SUNY ESF), in Syracuse, NY. The concepts taught in the Systems Ecology course are derived from the teachings and writings of Howard Odum (see Hall and Day, 1977; Odum, 1994) modified by sampling developments in stream ecology. The objective of this class was to teach students how to understand, measure, synthesize, and ultimately model general properties and principles of natural and human-dominated systems, not from books or equations but from nature herself. The Systems Ecology course included a field trip wherein the students measured and analyzed different elements of the biotic, physical, and chemical characteristics of a stream ecosystem. The field trip and successive analyses are based on Odum's Silver Springs study (Odum, 1957) and Hall's stream ecosystem analysis (Hall, 1972). The students were given a series of assignments, which use their own data as a primary tool for learning a systems approach to ecology by building, parameterizing, and analyzing models. Over the years we have found that for our students, the lessons taken from investigating and quantifying the stream system are broadly applicable to many other systems. This experience has prepared our students very well for applying a systems approach to later careers in ecology, resource management, health and many other disciplines.

This publication is meant to give others an introduction to this teaching approach within the context of generating a scientific paper, as suggested by the editor of this Journal. It is based on giving the summary and synthesis of data gathered principally on one weekend in 2012, although we compare these students' results to the much more extensive database on Little Sandy Creek of Mead (2007) and that of other years. As such, it is one of the relatively few recent papers to summarize the complete physical and trophic energy structure and flow for any ecosystem (but see Gaichas et al., 2009).

Energy in an ecosystem can be quantified as stocks (e.g., biomass) and flows (e.g., trophic energy fluxes). Stocks, known as *state variables* or *endogenous variables,* are influenced by the dynamics of other internal stocks. Stocks and flows are also influenced by the *forcing functions or exogenous variables* – external factors (e.g., solar input) that affect the ecosystem but are themselves not affected by the dynamics of the ecosystem. In a single field trip, we measured key stocks and flows for our ecosystem "Little Sandy Creek", a small creek in upstate New York. The exercise allowed us to trace energy flow from the sun through the various trophic levels in the stream community. We found that a group of 15–25 highly motivated students could indeed quantify the essential features of a stream ecosystem in one demanding weekend. We would not expect others using this paper as a guide for a class exercise would necessarily go to such detailed assessment as we did (e.g., correcting organism density and metabolism for specific depths vs. just using riffles and pools) so that the sampling and calculations can be undertaken much more easily than presented here.

We hope to formalize and promulgate a very successful teaching experience with the anticipation that others might find it useful. We have included considerable information and analyses here in an effort to address the entire ecosystem, and used the data generated by the students to address a specific research question (Allen's paradox). Instructors and/or students may find certain sections to be more relevant than others, depending on the context of instruction. Nevertheless, the information presented here provides an example of the extent, types of data, and analyses that can be generated in a graduate-level Systems Ecology course. Given the fragmentation and non-quantitative nature of much environmental education, we hope this will help to make a systems perspective more accessible to ambitious teachers of ecology and environmental science. Once the general principles of systems are identified, modeled, and understood, scientists (as well as managers, policy makers, economists, etc.) are better prepared to ask questions and solve problems objectively and quantitatively.

1.1. *Streams as excellent laboratories for systems studies*

Small streams are superb ecosystems for this exercise because they have clear boundaries (banks, bottom, and water surface) and are a manageable size. Additionally, it is possible for a group of students to sample individual components and total ecosystem metabolism with modest equipment. The biotic community of a stream can be classified into trophic levels by which energy captured by the primary producers (notably benthic algae) flows in the form of measureable food webs. These ecological food webs reflect energy transformation among trophic levels (Odum, 1994). We measured physical, chemical, and biotic properties of the Little Sandy Creek ecosystem both as a whole system ("Gestalt") and by examining its principal sub-systems.

1.2. *Allen's paradox revisited*

Allen (1951) studied the Horokiwi Stream in New Zealand, and found that the secondary production of the prey (benthic invertebrates) community was insufficient to support trout biomass and production in the same section of stream (utilizing 40–150 the benthic invertebrate production), even though macroinvertebrate communities remained present in the system over time. While production did not appear sufficient to support the energy needs of the fish community, the benthic invertebrate community persisted and therefore must not have all been consumed (Waters, 1988). If organisms are to reproduce, they must acquire a large enough net energy gain to overcome environmental stress, procure food, and mate, all while maintaining a basic rate of maintenance metabolism; for populations to persist, enough individuals must acquire energy surpluses to compensate for the majority that do not reproduce (Hall et al., 1992). Huryn (1996) reassessed Allen's paradox by analyzing the production budgets for a different stream (Sutton Stream) in New Zealand. Huryn expanded the boundaries of his study to include terrestrial and hyporheic sources of invertebrate production and found that these sources were roughly equal to the trout's respiration requirements, and perhaps enough surplus production occurred to support the continued abundance of invertebrates (Huryn, 1996). Allen's paradox has served as a troubling issue in ecology for some 60 years for systems that appear to be food-limited.

In this paper, we test the hypothesis that Allen's paradox exists in Little Sandy Creek by measuring and quantifying stocks (e.g., biomass) and flows (e.g., respiration and production) of invertebrates and fish. As this was a simple class exercise constrained