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

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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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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

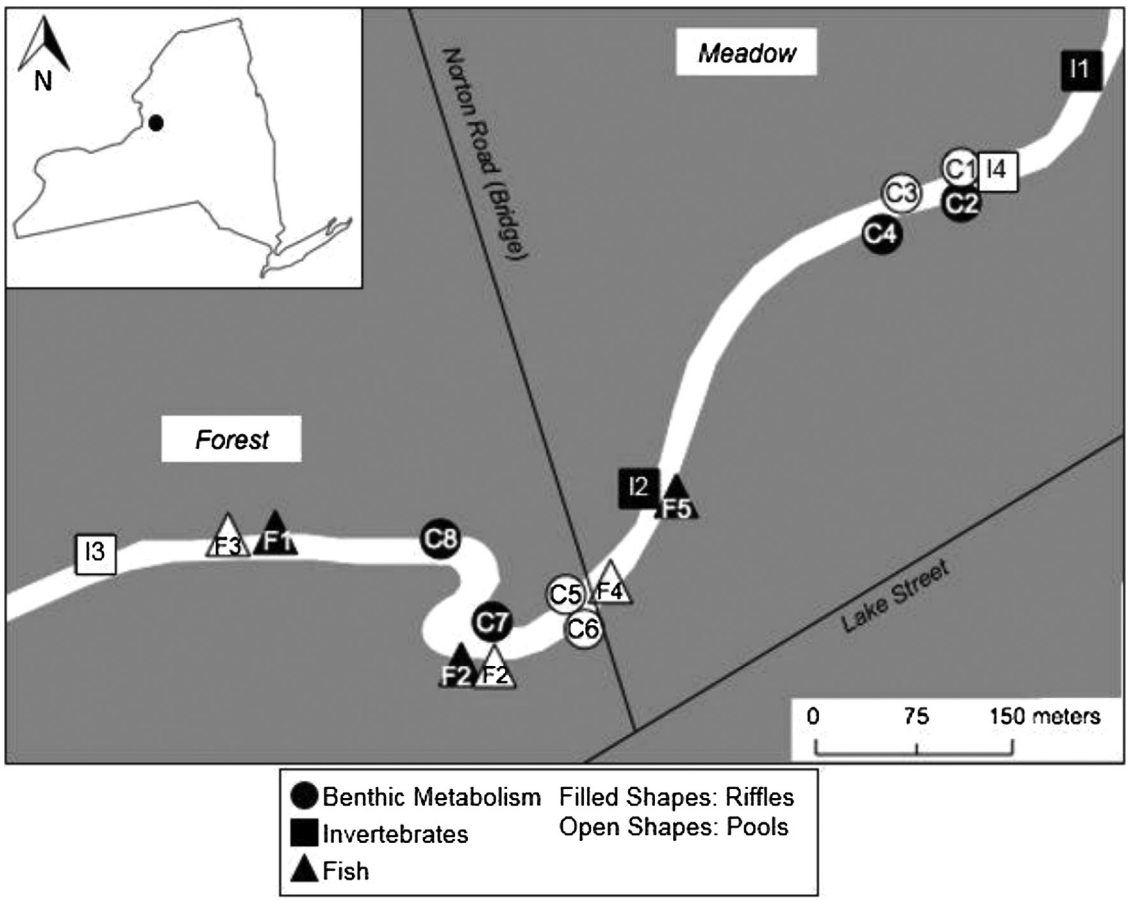

Fig. 1. The study reach of Little Sandy Creek, approximately 5 km west of the Sandy Creek, NY. The stream emerges through forests from the northeast, passes through a meadow for 550 m above Norton Road, and then enters a 425 m forested section for a total length of approximately 1 km. Lake Ontario is approximately 5 km to the west. The various symbols represent sampling sites: benthic metabolism (circles), invertebrate community sample locations (squares), and fish community sample locations (triangles).

by equipment, funding and sampling time, we do not contribute any novel sampling techniques that might improve quantitative approaches to detecting Allen's paradox in the field. However, by developing a size class and trophic level based respiration-production model that can be used with a small amount of non-destructive sampling techniques, we believe we have made a small but noteworthy contribution to the methodology of the Allen's paradox literature.

1.3. Site description

The study site is a 975 m stretch of Little Sandy Creek, a tributary to Lake Ontario, located in Upstate New York (Fig. 1). Little Sandy Creek is known as a good fishing stream for migratory Chinook salmon, coho salmon, and steelhead trout and provides particularly productive nursery habitat for these species. The water level in Little Sandy Creek fluctuates seasonally, and is characterized by low water levels in early September. On September 8, 2012, the principal day of our study, the area sampled had a mean width of 8.8 m, a mean depth of 20 cm, and a mean discharge of 0.49 $m^3\ s^{-1}$. The average stream temperature for September 7–9 was 19.5 °C.

The stream section that we studied emerges from dense mixed hardwood forest, flows through a meadow and then, below Norton Road, re-enters a heavily forested area. Little Sandy Creek is generally a clear stream with relatively clean and well-oxygenated waters. It contains a variety of substrate types ranging from silt to bedrock but most common are various sizes of stones and cobble. It has a golden-brown hue due to the growth of diatoms and other algae on the rock surfaces. During our study, the depth in our section varied from 1 to 102 centimeters, with relatively well-defined pools and riffles. We considered pools to have a water depth greater than or equal to 0.40 m. Any depth less than 0.40 m was considered a riffle. Most of the area, about 90 percent, consists of relatively shallow riffles.

The stream is populated with a wide variety of invertebrates including the larvae of caddisflies, stoneflies, blackflies, and mayflies, and a variety of fish species including brown and rainbow trout, juvenile silver (coho) and Chinook salmon, various minnow species, suckers, darters, and a few centrarchids. The benthic community consists of various species of bacteria, diatomic algae, macroinvertebrates, arthropods and some fish that live on and within the substrate (Bott et al., 1985). Although the stream appears to have the characteristics of a biological system relatively untouched by human activities, there is some treated sewage input approximately 5 km upstream and anglers frequent the creek seasonally. Of importance to its role in teaching the stream is clear and lovely and just the right size, and we had excellent relations with the land owners.

2. Methods

2.1. Overview

We estimated biomass stocks and energy flows of Little Sandy Creek using representative locations sampled with standard stream sampling gear and methods for each entity, described below. Because the stream itself had considerable heterogeneity (pools, riffles and runs) most of the samples were taken along gradients of

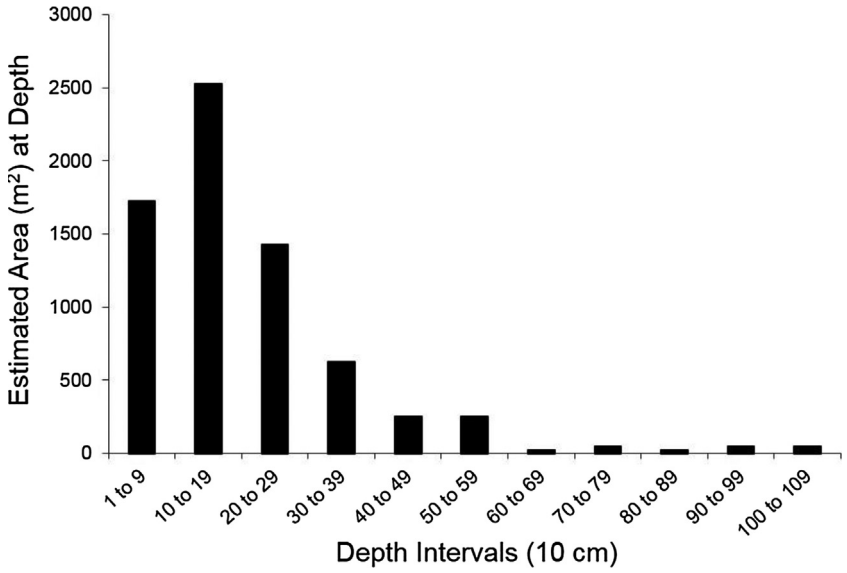

Fig. 2. Area distribution of depths in Little Sandy Creek across the study reach (approximately 1 km). Total wetted area was estimated to be 7000 m^2.

depth and velocity. From these data, we established relations for biomass and metabolism, subdivided by trophic level, as a function of depth/water velocity (the principle determinants). We developed a model using these relations along with extensive physical measurements to populate the entire one-kilometer stream section with fish and invertebrate biomass and metabolism. From this data we derived estimates of the stocks and flows of energy in the biotic community of the stream ecosystem and hence the production of invertebrates and energy requirements of fish to test Allen's paradox.

We divided our Systems Ecology class into five groups: physical, stream metabolism, benthic metabolism, benthic invertebrates and fish. Each group was responsible for measuring stocks and flows for their respective component using conventional stream sampling techniques (e.g., Hall and Moll, 1975; Hauer and Hill, 2006; Hall, 2012). The frequency and accuracy of our measurements were slightly compromised by an unexpected thunderstorm that occurred mid-day on September 8th. To compensate for this we took additional measurements the next morning, on a relatively sunny September 9th. In addition, we used summary data from other studies conducted in Little Sandy Creek to check for the general validity of our results. This included data from Mead (2007) as well as data from the 2011 and 2013 Systems Ecology classes. We also measured the metabolism of representative species through oxygen consumption during incubations in various metabolic chambers.

We measured or estimated the principal abiotic (physical dimensions, sunlight and dissolved oxygen) and biotic properties (biomass, respiration and production of aquatic macroinvertebrates, fishes, and the entire benthic community). Our characterization of the stream ecosystem was done in four steps: first, observation and systematic collection of data from the study site under the assumption that depth (and its inverse relation with water velocity) was the principal determinant of community structure for different organisms. Second, we analyzed the collected data to derive functional relations with depth that characterized the component systems. Third, we used these functional relations to populate stocks and flows in energy units for the one kilometer stretch of stream that was the focus of our research. In a few cases (as noted), we had to eliminate some outliers; we assume these to be due to student inexperience or equipment difficulties. Instead, we use interpolations based on decades of field experience and common sense. Finally, we simulated the behavior of the ecosystem over that day with a computer model. Thus we were able to do an entire systems analysis of a complete ecosystem in one semester (including additional analysis and write-up time) while exploring a fundamental issue in ecology. We have done more or less this same exercise for some 30 years, on several ecosystem types, always with at least moderate success. Details of all procedures follow.

2.2. Field data collection

As a general rule we attempted to organize our sampling not so much by "habitat type" but by "functional response", such as biomass of a taxon as a function of depth. This was done in order to interpolate our point samples (necessary given the impossibility of sampling every square meter of the entire stream) so that we could extrapolate our point data to the entire stream and to facilitate later modeling. We also did this as a means of exposing the students to thinking in terms of deriving and using "functional responses" for their later modeling and professional lives.

2.2.1. Physical measurements

We divided the study area of Little Sandy Creek longitudinally into 39 transects (each 25 m in length) from upstream to downstream, with Norton Road as the midpoint (Fig. 1). The upstream sections (transects 1–22) were classified as "meadow" and the downstream sections (transects 23–39) were classified as "forested"; each section had varied geomorphology (Table A in the Appendix). We categorized each transect as riffle or pool depending on depth (Fig. 2 and Table 4). In the middle of each transect, we estimated the canopy cover over the banks and the center of the stream. We then measured the width of the stream as well as the depth at 1 m intervals across the width at each transect. We also measured the velocity of the stream at each transect point and for the entire length of both the meadow and the forested areas by following six neutrally buoyant objects (lemons) downstream. We took measurements of solar flux (photosynthetically active radiation (PAR)) using a LI-COR LI-190 quantum sensor ($\mu mol\ m^{-2}\ s^{-1}$) at five-minute intervals from an unobstructed location. In addition, we took seven measurements of the solar intensity at each benthic chamber.

2.2.2. Metabolism of whole stream

Our objective here was to measure whole stream metabolism (net ecosystem production, respiration, and gross primary production) using the diel curve method (summarized below and described in detail in Hall and Moll, 1975). We achieved this by measuring the change in the concentration of dissolved oxygen (DO) during the time taken for a unit volume of water to travel between sites as measured by the physical team (i.e., the free water method). The advantage of the diel curve method is that it does not use bottle incubation, which might interfere with the natural processes one is trying to measure. The disadvantage is that one has to correct for the diffusion of oxygen across the stream's surface, which is likely to be an issue with a shallow turbulent stream such as Little Sandy Creek.

We define net ecosystem production (NEP) as the diffusion-adjusted DO change during the day. We define respiration of the entire stream ecosystem as the diffusion-adjusted DO change measured at night and interpolated during the day. We discarded positive DO changes at night and inserted the average respiration value. We estimate gross primary production (GPP) as NEP minus respiration.

We sampled stream temperature and DO, using the Winkler method (Hall and Moll, 1975; Hall, 2012), at transects 1 (beginning of top meadow), 22 (Norton Road), and 39 (below the second forested area) at three hour intervals over a 24-h period. Fundamentally, a triplicate oxygen and temperature sample was taken at the top, middle, and bottom of our one km river stretch. We sampled each location approximately one half hour apart; this interval was determined by the time it took neutrally buoyant objects (lemons) to travel from one section to another. Thus, in principle, we are following a "parcel" of water as it flows through first the meadow and then the forested section of our ecosystem.

2.2.3. Metabolism of benthic community

We set up eight benthic chambers in the streambed to measure metabolism of the benthic community. We assume that the benthic community lives within the stream substrate and is comprised of invertebrates, microbes, and primary producers. We did not attempt to quantify the respiration of sub-communities within the benthic substrate, therefore respiration was estimated as the average of negative DO changes observed at night (positive DO changes recorded at night were disregarded and replaced with the average). It is very difficult to gain an estimate of primary producer respiration in the benthos, so we do not report any values for net primary productivity (NPP) of the periphyton alone. Rather we measured net benthic primary productivity (NBP), as the DO changes measured during the day, the net change in oxygen from photosynthesis including that which compensates for respiration of the entire benthic community in the chambers. We calculated GPP as the difference between NBP and benthic community respiration (see Fig. B2 in Appendix). Since there was insignificant metabolism of the water column organisms, as determined by light and dark bottle studies, we would expect the values measured by free water and benthic community techniques to be somewhat similar.

We installed the chambers in two riffles and two pools in both the meadow and the forest sections of our study area a week before the field trip on September 1, 2012. When installing the chambers, we removed the stream substrate layer by layer and then reconstructed the strata as they occurred in the stream within the chamber. We submerged the chambers at the spot from which we dug out the substrate. We measured depth from the top of the substrate to the surface of the stream, making sure that each chamber had sufficient depth so that it would not breach the surface if water levels decreased. We left the chambers open to the stream for one week, which allowed the resident biota to recolonize and establish within each chamber before measurement. For the chambers, we used Rubbermaid® "Roughneck" bins with dimensions of ~48 by ~35 cm (width) x 31.0 cm or 22.1 cm (height) (Fig. A in the Appendix). We put the 22.1 cm tall bins in the riffles and the 31.0 cm tall bins in the pools to reduce the risk of the water level falling below the chamber.

On September 7th, 2012, the night before measurements, we sealed the chambers with Plexiglas lids held in place by a series of clamps and foam rubber seals. There was a small electric bilge pump installed on the inside of each lid to simulate stream water flow. Each lid also contained a circular hole, which could be sealed by a removable rubber stopper, which allowed us to take DO measurements using a YSI 550 probe (Fig. A in the Appendix).

We took measurements of air temperature, DO of the stream and DO inside the chamber approximately every hour for 24 h, starting from 01:00 on September 7th. On September 9th, at 18:00 we flushed the forest chambers with stream water to avoid critically low oxygen concentrations, and on September 9th from 10:00–13:30, a sunnier day, we recorded additional measurements for all chambers at half hour intervals to get DO response in the chambers at higher solar flux. After the study period, we removed the benthic chambers from the streambed and measured the volume of water present above the substrate and within the interstitial space (Table 4).

2.2.4. Stocks of benthic invertebrates and fish

Based on past experience, we assumed that biomass of different taxa and sizes within taxa were principally a function of water depth (or velocity, as they were inversely related), so we deliberately chose representative shallow riffles and deep pools as areas to sample (Table 4). We classified all organisms captured into trophic levels (to examine energy flow pathways and to test Allen's paradox and size class, as respiration and production are a function of organism size (Brown et al. in press).

We sampled aquatic macroinvertebrates quantitatively using a Portable Invertebrate Box Sampler (PIBS), with an area of 0.1 m^2, in duplicate at four sites. At each site we recorded water depth (cm), took samples, sorted the macroinvertebrate samples and recorded the dry weight biomass of each taxon (dried at 60 °C for 24 h in the laboratory, see Table 4). Taxa were classified to genus (where possible) and assigned to a trophic level (Merritt et al., 2008) (Table B in the Appendix).

We determined the number, biomass, and trophic levels of each species within the fish community at five locations (Table 4). We used two fine meshed seines to block off each section and an electro-shocker to stun and collect the fish. We measured temperature, length, and average width and depth of the area sampled at each location. Sampling efficiency was assessed using duplicate samples. Additionally, using the Seber-Le Cren equation (Seber and Le Cren, 1967), we estimated the total biomass and abundance that were present (Table C in the Appendix). We identified fish to species, and measured the length and weight for each fish caught (Werner 2004).

2.2.5. Other stocks

We measured allochthonous input over a 24-h period at eight forested and four meadow locations. Tops of the benthic chamber Rubbermaid® bins (dimensions of 60.7 cm (length) x 40.4 cm (width)) were placed in the riparian zone approximately 1 m from the water line at a given location. After 24-h, all terrestrial material that had fallen on the bin tops was collected and stored in Ziploc bags for transport back to the laboratory. All material was dried at 60 °C for at least 24-h, weighed to obtain dry biomass (g), and converted to area (g m^{-2}) then to energy units (MJ).

The occurrence of top predators such as kingfishers and great blue herons were noted when observed, but their biomass or

metabolism per hour per square meter was trivial and hence ignored. We did not directly measure the abundance of terrestrial predators, viruses, bacteria, fungi etc., but assume they are abundant if not weighty (see Odum 1957). Likewise, we did not quantify terrestrial invertebrate inputs (although we measured leaf inputs), or measure the meiofauna of the stream hyporheic zone, plus upstream detrital or macroinvertebrate inputs into our study reach, explicitly.

2.2.6. Energy flows of invertebrates and fish

We measured the oxygen consumed (mg O_2 g^{-1} h^{-1}) for small and large individuals of the dominant taxa (stoneflies and caddisflies) using the Winkler method at 3 °C, 12 °C, and 20 °C. We used Winkler bottles as incubation chambers and found that we could get detectable oxygen changes with several grams of insects in several hours.

We measured the oxygen consumption (mg O_2 g^{-1} h^{-1}) of several characteristic species of fish: brown trout (*Salmo trutta*), fallfish (*Semotilus corporalis*), northern hogsucker (*Hypentelium nigricans*), rock bass (*Ambloplites rupestris*), and yellow perch (*Perca flavescens*) at the ambient stream temperature (20 °C) using the Winkler method and Winkler bottles or gallon jars depending on the size of the fish. We also used the Wisconsin bioenergetics model (Kitchell et al., 1977) to calculate the size- and temperature-specific metabolism of all sampled fish.

2.3. Data analysis

We adjusted sunlight data collected at the hill over the entire day to values at the water surface in the meadow and the forest (i.e., corrected for shading) by examining the relation between PAR measurements taken at each chamber relative to the open hill location (i.e. estimating% of available PAR that was transmitted to the stream surface (ESTPAR)). We measured the metabolism of the primary producers in the open water and in the benthic chambers directly with oxygen changes in the water and plotted the results as a function of sunlight and depth. Additionally, we compared our metabolism results with the much more extensive record for the same stream in Mead (2007). For higher trophic levels, we took our biotic samples and derived the total number and biomass of each trophic level as a function of depth, then populated the entire one-kilometer stream by multiplying the relation between the number of individuals in size classes by trophic level to depth for the area of each depth of our section (see Table 1). This allowed us to derive values for the total biomass (and metabolism) of each trophic level for our entire one kilometer stream section.

2.3.1. Summary of conversion processes

Table 1 provides examples of the calculations used to convert number and biomass for macroinvertebrates and fish. Table 2 gives the standard conversion factors used in Tables 1, 3a, and 3b. Tables 3a and 3b summarize the various conversions by which we went from raw data to kilojoules (kJ) per square meter for each metabolic process. In general, we went from volume changes of dissolved oxygen (such as measured with a Winkler titration or oxygen meter) to area values, and then converted from dissolved oxygen changes to its equivalent in kJ. We derived daily values by summing hourly values; in some cases, these values were derived from functional relations.

2.3.2. Extrapolation to entire reach: model construction

We generated quantitative summaries of stocks and flows of the various trophic levels of Little Sandy Creek for September 8, 2012, first in tabular form, then in functional relations with depth. This was followed by multiplying the value for each depth by the area of that depth interval within the one-kilometer section, thus

Table 1
Example calculation (for one size class and one trophic level at one location) of abundance and biomass for macroinvertebrate and fish. Expansion factor for fish is to correct for sampling efficiency of electro-shocker (Seber and Le Cren, 1967).

Organism	Raw Data					Conversion Process for Population Expansion			Calculating Mass		Converting Biomass ($g\,m^{-2}$) to $kJ\,m^{-2}$	
	Location	Trophic Level	Location Area (m^2)	Size Class	Abundance	Expansion Factor	Total Population	Total Mass	Biomass ($g\,m^{-2}$)	Dry Biomass ($g\,m^{-2}$)	Biomass ($cal\,m^{-2}$)	Biomass ($kJ\,m^{-2}$)
Macro-invertebrate	I1	Detriti-vore	0.1[a]	3	6	N/A	N/A	N/A	N/A	0.007	33.8	0.14
Notes and Sources	–	–	–	–	–	–	–	–	–		[a]	[b]
Fish	F1	Insecti-vore	227	1	21	3.1	65.1	65.1	0.29	0.06	315	1.32
Notes and Sources	–	–	–	–	–	Table C in Appendix	abundance * expansion factor	total pop. *midpoint mass (Table F in Appendix)	total mass/location area	biomass * 0.2	[b]	[c]

[a] This is the actual sampling area. See Table 4 for the transect area.
[b] Multiply the dry biomass by the average gram to calorie conversion for each trophic level (from Cummins and Wuycheck, 1971); see Tables 3a and 3b for conversion factors.
[c] Multiply the caloric biomass by 4.184, the calorie to Joule conversion factor.

Table 2
Standard conversion factors used.

Taxon	Average mass (g) to calorie conversion factor (Cummins and Wuycheck, 1971)	O_2 (mg) to calorie conversion factor (Hall and Moll, 1975)	Calorie to joule conversion factor
Allochthonous material	4371 cal g^1	–	4.184 J cal^{-1}
Benthic Community	–	3.5 cal mg $O_2{}^{-1}$	4.184 J cal^{-1}
Macroinvertebrate	4823 cal g^{-1}	"	"
Fish: Insectivore	5493 cal g^{-1}	"	"
Fish: Piscivore	4512 cal g^{-1}	"	"
Fish: Mixotroph	4853 cal g^{-1}	"	"

giving us an estimate for the entire reach of the stream. These values were summarized in a quantitative Odum flow diagram, and in a FORTRAN computer model (see model code in Appendix).

Our computer model calculated stocks and flows in Little Sandy Creek using depth as an abiotic forcing function. The program read in depth values measured at 1 m increments across the stream every 25 m for the 1 km transect (each grid cell had an area of 25 m^2). We used functional responses derived from our field measurements of abundance with depth for each size class and trophic level to populate the stream. The abundance estimates were multiplied by the average mass of size classes to obtain biomass estimates (J m^{-2}). Respiration was modeled as a function of size class and trophic level (and temperature, which changed only 3 ° during the study). Productivity was modeled as a function of respiration (Eqs. (16)–(19); Humphreys 1979; see also Brown et al. in press). We did not measure production as part of our initial data collection, or collect data on the many variables normally used to calculate production. Therefore, we used the Humphreys equations, which were derived from multiple data sets of various animals, to estimate production. Stocks and flows for the 1 km transect (7000 m^2 of wetted area) were obtained by multiplying the model outputs by the area of each grid cell, 25 m^2; to convert stocks and flows to mean per m^2 over the entire stretch (to facilitate comparison with other studies) the total stream estimate was divided by 7000 m^2. The total invertebrate production was then compared to total fish respiration (energy availability versus energy need) to test whether Allen's paradox existed on September 8, 2012 in Little Sandy Creek. Specific procedures for field data and model calculations follow (listed as numbered steps in ascending order by trophic level or energy hierarchy, for stocks then flows).

2.3.3. Sunlight

We used two steps to obtain hourly estimates of PAR corrected for shading (see Tables $D_{1\text{-}2}$ in the Appendix). To estimate the percent of sunlight transmission at each chamber, we took the mean PAR measured at a benthic chamber over the course of the day and divided by mean PAR observed at the unshaded hill at corresponding times (Step 1). Subsequently, to estimate the amount of light reaching each benthic chamber at every hour of the day, we multiplied the percent transmission calculated for each chamber by the observed values measured at the hill over the course of the day (Step 2).

STEP 1: Estimate percent transmission of sunlight at each benthic chamber.

$$Trans_{bc} = MPAR_{bc}/\mathrm{MPAR_{hill}} \quad (1)$$

Where *MPAR* is mean photosysnthetically active radiation observed at benthic chambers (*bc*) or hill.

STEP 2: Estimate shade adjusted PAR values for each benthic chamber at each time period.

$$Est.PAR_{bc,t}(\mathrm{kJ}\,m^{-2}\,s^{-1}) = Trans_{bc} * \mathrm{MPAR_{Hill,t}}(\mu\mathrm{mol}\,m^{-2}\,s^{-1}) * 4.78 * 10^{-4}(\mathrm{kJ}\,\mu\mathrm{mol}^{-1}) \quad (2)$$

Where $Est.\ PAR_{bc,t}$ is the estimated sunlight flow at a benthic chamber (*bc*) during time period t, $Trans_{bc}$ is the percent transmission of sunlight at a given benthic chamber (from Eq. (1), see Appendix Table D), $PAR_{Hill,t}$ is the mean sunlight flow observed at the hill during time period t (See Appendix Table J). $4.78{*}10^{-4}$ is a conversion factor from *μmol to kJ*, taken as the ratio of J s^{-1} (Watts) per μmol, 4.78 divided by the number of Joules per kJ, 1000. The ratio of Watts per μmol was obtained through light measurements taken simultaneously at Little Sandy Creek using a Pyranometer (W m^{-2}) and a Quantum (μmol m^{-2} s^{-1}) light sensor.

2.3.4. Whole stream metabolism

We calculated whole stream metabolism using the 2-station "diel curve" method described in Hall and Moll (1975). We adjusted our open water dissolved oxygen measurements for diffusion of oxygen from or to the atmosphere as a function of the O_2 saturation deficit at the ambient water temperature of a measurement interval (Step 1) and calculated the diffused quantity of oxygen per volume of stream (Step 2). The average travel time between sites was roughly 30 min. We calculated the rate of DO change between sites based on travel time and then adjusted for an estimate of the oxygen that had been lost or gained by diffusion (Step 3). We converted the diffusion-corrected rates of oxygen changes to kJ per square meter (Table 3a) and summed hourly values to get estimated daily production and respiration (Step 4). We took interpolated respiration (ideally just before sunrise and just after sunset (Hall and Moll, 1975)), and calculated daytime gross photosynthesis (GPP) from daytime NEP measurements. The sum of respiration and GPP values for each hour were adjusted for the measurement interval to obtain a daily total. We then multiplied values by average stream depth to convert from volume to area (Step 4).

STEP 1: Calculate saturation values at water temperature of each measurement:

$$S(mgO_2\mathrm{L}^{-1}) = 14.652 - (0.41001 * T) + (0.0079910 * T^2) - 0.000077774 * \mathrm{T}^3 \quad (3)$$

Where *S* represents saturation value for oxygen in water, and *T* represents temperature (Mead 2007).

STEP 2: Calculate the saturation deficit and change in oxygen per hour via diffusion:

$$Sat\% = DO/S \quad (4)$$

$$Dvol = k * (1 - Sat\%)/Depth \quad (5)$$

Where *Sat%* is the saturation percent (where 1.0 is equal to 100% saturation) and *DO* is the measured dissolved oxygen (mg L^{-1}). *Dvol* is diffused oxygen (g) per volume of stream (m^3) per hour (negative values represent oxygen leaving the stream when the stream is supersaturated, positive values represent oxygen entering the stream), *k* is the diffusion coefficient assumed to be 1.0 g m^{-2} h^{-1} at 100% saturation (Hall 1972), and *Depth* is the median depth of the reach between sample sites (see Hall and Moll 1975).

Table 3a
Examples of conversion processes to go from raw values to kJ m^{-2} h^{-1} for light, benthic chambers and free water using typical example values from September 8, 2012. Hourly values were derived from field observations; daily values are derived by summing hourly values. See Table 2 for standard conversion factors.

Trophic Groups	Raw Data[a]	Conversion Process to J m^{-2} h^{-1}						Final Daily Values	
	Representative Energy Value (Various Units)	Conversion Factor[b]	Converted to Area	Conversion Factor	Converted to Joules	Conversion Factor	Converted to Hours	Integration Method	Daily Values
SUNLIGHT (units →)	µmol m^{-2} s^{-1}	–	–	kJ µmol^{-1}	kJ m^{-2} s^{-1}	s $hour^{-1}$	kJ m^{-2} h^{-1}	–	kJ m^{-2} day^{-1}
PAR	203	–	–	$4.87*10^{-4}$	0.969	3600	349	Add Hourly	1300
Notes/Sources	–	–	–	Measured in Field (see Eq. (2))	–	60 s min^{-1} * 60 min h^{-1}	–	See Table J in Appendix	–
METABOLISM (units→)[c]	g O_2 m^{-3}[d]	m^3 m^{-2}[e]	g O_2 m^{-2}	kJ g^{-1} O_2	kJ m^{-2}	hr	kJ m^{-2} h^{-1}	–	kJ m^{-2} day^{-1}
Free Water (Two Station)	1	0.2	0.2	14.644	2.93	0.5	5.88	Add Hourly	76
Notes/Sources	ΔOpenDO value, (see Eq. (6))	Multiply by Mean Stream Depth (0.2m)	–	4.184 kJ $kcal^{-1}$ * 3.5 kcal g^{-1} O_2 (Table 2)	–	Travel time between sites (see Eq. (2))	–	NEP = GPP − Resp (see equations 7–9)	NEP
Benthic Chamber	0.5	0.075	0.0375	14.644	0.55	0.95	0.58	Add Hourly Values	−3.2
Notes & Sources	ΔDO (see Eq. (10))	Multiply Chamber Water Volume/Chamber Area	(See Eq. (11) and Table 4)	4.184 kJ $kcal^{-1}$ * 3.5 kcal g^{-1} O_2 (Table 2)	–	Divide by Time Between Measurem-ents	–	See Eq. (12)	NBP was Highly Variable

[a] For PAR an actual data point, measured at Hill 9:00 am in 2012 as shown in Fig. 4, was selected. For Free Water and Benthic Metabolism arbitrary raw data values were chosen.
[b] The contents in the conversion factor columns are multiplied by the column to the left to obtain the new value in the column to the right. However, when converting to time, divide the column to the left (data in joules) by the "time" column.
[c] Metabolism measured as changes in dissolved oxygen concentration of water for free water (two station), and benthic chamber DO (see steps in methods below).
[d] 1 mg L^{-1} = 1 g m^{-3}.
[e] Volume to Area ratio of benthic chambers (m^3 m^{-2}) (see Table 4).

STEP 3: Calculate the DO rate of change between stations at each measurement interval, adjusted for diffusion of oxygen into (and occasionally out of during afternoon supersaturation) the water:

$$\Delta OpenDO(g\,m^{-3}\,hr^{-1}) = (DO_{site2} - DO_{site1})/\mathrm{Dt} - \mathrm{Dvol} \quad (6)$$

Where $\Delta OpenDO$ is the rate of change in dissolved oxygen adjusted for diffusion (an estimate of net stream metabolism and respiration – see Step 4), $DO_{site\,1}$ is dissolved oxygen concentration at upstream site 1, DO_{site2} is the dissolved oxygen at site 2 (also 2 vs 3). *Dt* is the amount of time (hours) it takes for a stream parcel to travel between sample sites (30 min), and *Dvol* is diffused oxygen (grams) per volume of stream (cubic meters) per hour.

STEP 4: Calculate of the hourly change in open water DO ($\Delta OpenDO$) over time to estimate daytime net metabolism and nighttime respiration:

$$GPP(g\,m^{-2}\,hr^{-1}) = (NEP_{day} - \mathrm{Resp}) * \mathrm{Depth} \quad (7)$$

$$TotGPP(g\,m^{-2}\,day^{-1}) = \sum_{hr=1,n}(\mathrm{GPP_{hr}}) \quad (8)$$

$$TotResp(g\,m^{-2}\,day^{-1}) = \sum_{hr=1,n}(\mathrm{Resp_{hr}}) \quad (9)$$

Where *GPP* is gross photosynthesis (g m^{-2} h^{-1}), NEP_{day} (g O_2 m^{-3} h^{-1}) is equal to daytime (sunny) $\Delta OpenDO$ values, and *Resp* (a negative value) is the average nighttime respiration $\Delta OpenDO$. *Depth* is the median depth between sample sites. *TotGPP* and *TotResp* are the summed daily total gross photosynthesis and respiration, respectively (see Fig. 5a and b).

2.3.5. Benthic community metabolism

We derived a rate of metabolic flow for each measurement interval at each benthic chamber and converted this rate from g O_2 m^{-3} to kJ m^{-2}. Metabolism was converted from g O_2 to joules by multiplying by a conversion factor of 3.5 kcal g^{-1} O_2 from Hall and Moll (1975) and by 4.184 kilojoules $kcal^{-1}$ (Table 3a). The conversion from volume to area is adapted from Mead (2007) and Hall et al. (1979) (Table 3a), this was done by multiplying by the volume of water between the substrate and the lid of the benthic chamber and dividing by the area of the chamber – effectively, this is the same as multiplying by height of water between the substrate and the lid of the benthic chamber. We plotted data to test functional relations between benthic metabolism, depth, and sunlight. Metabolism was plotted as a function of sunlight (*ESTPAR)* for each chamber (Fig. $B_{1\text{-}2}$ in the Appendix). We fit a Michaelis-Menten regression for NBP as a function of solar intensity (Step 3).

STEP 1: Calculate the rate of change of DO for each benthic chamber (*bc)* for each measurement interval.

$$\Delta DO(g\,m^{-3}\,hr^{-1}) = (DO_{int} - \mathrm{DO_{int\text{-}1}})_{bc}/(\mathrm{time_{int}} - \mathrm{time_{int\text{-}1}}) \quad (10)$$

Where ΔDO is change in dissolved oxygen over change in time, $DO_{int\text{-}1}$is dissolved oxygen concentration of the measurement interval preceding DO_{int}, and $time_{\ int\text{-}1}$ is the decimal time interval preceding $time_{int}$.

STEP 2: Convert the metabolic flow per volume to joules per square meter.

$$NBP(kJ\,m^{-2}\,hr^{-1}) = \Delta DO * OxToE * V_{bc}/\mathrm{A_{bc}} \quad (11)$$

Where *NBP* is benthic metabolism rate in joules per meter squared per hour, ΔO_{2int} is the rate of DO change from Step 1 and *OxToE* is a conversion factor from mg O_2 to joules (14.65 kilojoules per gram O_2). V_{bc} equals volume (L) of water in the benthic chamber (between 50 and 90 liters) and A_{bc} is area (m^2) of benthic chamber (0.17 m^2) measured from the top (Table 3a).

STEP 3: Fit Michaelis-Menten (half saturation) curve for benthic NBP versus sunlight at pool and riffle locations.

$$NBP(kJ\,m^{-2}\,hr^{-1}) = GPP_{max}*(PAR/(K_s + PAR) + Resp \quad (12)$$

Table 3b
Examples of conversion processes to convert respiration from mg O_2 g^{-1} day^{-1} or g O_2 g^{-1} day^{-1} into kilojoules m^{-2} day^{-1} for macroinvertebrates and fish, using representative values from September 8, 2013. See Table 2 for standard conversion factors.

Taxon	Raw Data	Conversion Process to J m^{-2} day^{-1}					FINAL Values
	Representative Value (Measured Units)	Conversion Factor	Converted to Area[c]	Conversion Factor	Converted to cal	Conversion Factor	Daily Values in kilojoules
Macroinvertebrates (units →)	mg O_2 g^{-1} day^{-1}	g m^{-2}	mg O_2 m^{-2} day^{-1}	cal mg^{-1} O_2	cal m^{-2} day^{-1}	joules cal^{-1}	kJ m^{-2} day^{-1}
RESPIRATION	719[a]	0.09	64.7	3.5	226.5	4.184	0.95
Notes/Sources	–	Invertebrate biomass	–	Hall and Moll (1975)			–
Fish (units →)	mg O_2 g^{-1} day^{-1}	g m^{-2}	mg O_2 m^{-2} day^{-1}	cal mg^{-1} O_2	cal m^{-2} day^{-1}	joules cal^{-1}	kJ m^{-2} day^{-1}
RESPIRATION	40[b]	0.29	11.6	3.5	40.6	4.184	0.17
Notes/Sources		Fish biomass	–	Hall and Moll (1975)			

[a] Example respiration of macroinvertebrate is for herbivores at Riffle 1 in size class 8.
[b] Initial respiration and biomass are for a blacknose dace (insectivore) in size class 1 at location 1.
[c] See Table 4 for areas of all sampling locations.

Where GPP_{max} is maximum gross primary productivity/photosynthesis, *Resp* is a vertical adjustment for respiration (a negative value), K_s is the solar insolation at half of GPP_{max}, and *PAR* is the sunlight adjusted for shading (*Est. PAR* from Eq. (2), see Fig. B1 and B5 in the Appendix). Note: the curve should be for values above the nighttime respiration value, not above zero (Fig. B1 and B5 in the Appendix). The Michaelis-Menten GPP_{max} parameter was fit in Excel using the "solver" function to minimize sum of square residuals. For Michaelis Menten functions ks is set to 200 ($W m^{-2}$) respiration is set to the average negative DO change at night.

STEP 4: Develop functional relations for primary production (GPP_{max}) and respiration with depth.

We did not find statistically significant correlations with depth in the benthic chambers (See Figure B4 in Appendix). Therefore, in the model, *GPP* and *Resp* were set to averages of data measured in forest and riffle sections. To extrapolate benthic community metabolism to the entire stream, values reported per m^2 were multiplied by area, 3850 m^2 in the forest and 3150 m^2 in the meadow.

2.3.6. Stocks of benthic invertebrates and fish

Stocks (biomass per square meter) of benthic invertebrates and fish were collected quantitatively as a function of depth and expressed as grams (and joules) per square meter. We subdivided mass measurements for each sample of benthic invertebrates and fish by trophic level and size class. To tabulate field data, we summed the mass of individuals within each size class and trophic level from a given sample site. We plotted abundance and subsequent biomass with depth for each size class of each trophic level; from these plots we derived linear functions with depth so that the number of individuals was modeled as a function of depth. In the model, we calculated mass of each size class within each trophic level by multiplying the number of individuals in each size class by the average mass of an individual of a size class in that trophic level (Step 1). For both field data and model results, mass was converted from grams to joules per square meter by multiplying the estimated dry mass (g) of the sub-sample by its energy density (cal g^{-1}) (Cummins and Wuycheck, 1971), an expansion factor to correct for sampling efficiency, and sample area (Step 2; Table 1). Total trophic level biomass was determined by summing all biomass estimates for each size class (Step 3). For field data, see Table 1; for model results, see Table 7. Steps 1 through 3 were done for each sample of benthic macroinvertebrates and fish.

STEP 1: Calculate the mass for each size class

$$Mass_{tl,sc} = Num_{tl,sc} * \mathrm{IndMass}_{\mathrm{tl,sc}} \quad (13)$$

Where $Mass_{tl,sc}$ is the total mass (g) of a size class (*sc*) in each trophic level (*tl*), $Num_{tl,sc}$ is the number of individuals in the size class within each trophic level in a sampled area, and $IndMass_{tl,sc}$ is the midpoint mass (g) of the size class of that trophic level.

STEP 2: Convert size class mass to energy per square meter.

$$BM/m^2{}_{\mathrm{tl,sc}} = Mass_{tl,sc} * \mathrm{EDens} * \mathrm{ExpFact}/\mathrm{Area} \quad (14)$$

Where *BM* is biomass (J m^{-2}), $Mass_{tl,sc}$ is the mass of a size class (g), *EDens* (J g^{-1}) is mean energy density of that particular trophic group, *Area* (m^2) is s area sampled, *ExpFact* (no units) is an expansion factor which is equal to the inverse of the sampling efficiency (Table 1). Energy density is calculated by converting from grams of dry weight to joules using the appropriate values (cal g^{-1}) from Cummins and Wuycheck (1971) multiplied by 4.184 (J cal^{-1}) (Tables 2, 3a, and 3b). For benthic invertebrate samples, the area of the PIB sampler was approximately 0.1 m^2 and we assumed 100 percent sampling efficiency (Pollard and Kinney 1979), therefore our expansion factor for benthic macroinvertebrates was equal to 10. The area of the fish sample sites varied (Table 4), thus we used the Seber-Le Cren method (Seber and Le Cren 1967) to derive a mean expansion factor of 3.1 (Table C in Appendix). The fish biomass of each sample was multiplied by 0.2 (wet to dry biomass conversion) to correct for wet weight before converting to joules (see Table 1).

STEP 3: Calculate total trophic level biomass, expressed in energy units.

$$BM/m^2{}_{\mathrm{tl}} = \sum BM/m^2{}_{\mathrm{tl,sc}} \quad (15)$$

Where $BM/m^2{}_{tl,sc}$ is the value for each individual size class within a trophic level derived in Eq. (14), and $BM/m^2{}_{tl,}$ is the summation of size classes within a trophic level.

2.3.7. Energy flows of benthic invertebrates and fish

For benthic invertebrates and fish, the rate of energy use by each trophic level was derived in the same fashion as biomass values, with the following exception: metabolism is very strongly related to organism size and the size of our organisms varied widely. To gain more precise estimates of respiration for a given trophic level, it was necessary to break our benthic invertebrate and fish data into size classes. Using size classes allowed us to quantify and model respiration to represent the frequency distribution of body sizes within each trophic level. Size-specific metabolism was derived for individuals of each size class and trophic level based on field-derived respiration relations with size. Eq. (16) is the respiration equation used in the model for benthic invertebrates and fish.

In addition to our own field measurements, fish respiration was calculated using the generalized Wisconsin bioenergetics model (Kitchell et al., 1977), to supplement our limited field data:

$$R = R_{max} * \mathrm{A} * \mathrm{r_R} + S * C$$

Table 4
Locations and characteristics of all sampling sites, as well as abundance and biomass for invertebrates and fish classified by trophic level.

Benthic Chambers

Sample/Transect	Location Characteristics	A – Area (m^2)	Depth (m)	V – Water Volume (m^3)	Z – Depth of Water in Chamber Z = V/A (m)	Sunlight Transmission	Estimated PAR ($kJ\,m^{-2}\,day^{-1}$)	Community Respiration ($kJ\,m^{-2}day^{-1}$)	Community GPP ($kJ\,m^{-2}day^{-1}$)	P/R Ratio	GPP_{max} ($kJ\,m^{-2}\,h^{-1}$)
C1/8	Pool (*Meadow*)	0.17	0.55	0.017	0.1	66%	3114	10	11	1.0	0.62
C2/9	Riffle (*Meadow*)	0.17	0.2	0.011	0.06	58%	2736	15	9	0.6	0.80
C3/10	Pool (*Meadow*)	0.17	0.6	0.017	0.10	64%	2976	19	21	1.1	1.70
C4/10	Riffle (*Meadow*)	0.17	0.2	0.014	0.08	63%	2942	20	22	1.1	3.04
C5/23	Pool (*Forested*)	0.17	0.5	0.027	0.16	26%	1141	23	18	0.8	1.60
C6/23	Pool (*Forested*)	0.17	0.45	0.013	0.08	52%	2302	14	14	1.0	1.44
C7/25	Riffle (*Forested*)	0.17	0.15	0.012	0.07	19%	840	11	13	1.1	1.23
C8/28	Riffle (*Forested*)	0.17	0.2	0.012	0.07	14%	643	14	11	0.8	1.02

Macroinvertebrates

Sample/Transect	Location Characteristics	Sampling Area (m^2)	Depth (m)		Herbivore	Herbivore/Detritivore	Detritivore	Insectivore	Piscivore	Mixo-troph	TOTAL
I1/1	Riffle (*Forested*)	0.1	0.19	Abundance ($no.\,m^{-2}$) →	570	190	490	180	–	–	1430
				Biomass→ ($kJ\,m^{-2}$)	13.7	23.0	9.0	22.6	–	–	68.3
I2/20	Riffle (*Meadow*)	0.1	0.18	Abundance ($no.\,m^{-2}$) →	1790	20	1200	180	–	–	3190
				Biomass→ ($kJ\,m^{-2}$)	29.5	0.2	27.0	24.7	–	–	81.4
I3/36	Pool (*Forested*)	0.1	0.49	Abundance ($no.\,m^{-2}$)→	170	10	290	0	–	–	470
				Biomass→ ($kJ\,m^{-2}$)	2.8	0.4	2.7	0	–	–	5.9
I4/8	Pool (*Meadow*)	0.1	0.33	Abundance ($no.\,m^{-2}$)→	230	0	280	70	–	–	580
				Biomass→ ($kJ\,m^{-2}$)	27.6	0	10.5	5.5	–	–	43.6

Fish

Sample/Transect	Location Characteristics	Transect Area (m^2)	Depth (m)		Herbivore	Herbivore/Detritivore	Detritivore	Insectivore	Piscivore	Mixo-troph	TOTAL
F1/33	Riffle (*Forested*)	227.1	0.1	Abundance ($no.\,m^{-2}$) →	–	–	–	0.4	0	0.0	0.4
				Biomass→ ($kJ\,m^{-2}$)	–	–	–	3.6	0	1	4.6
F2/25	Pool/Riffle (*Forested*)	133.9	0.21	Abundance ($no.\,m^{-2}$) →	–	–	–	2.2	0.2	0.5	2.9
				Biomass→ ($kJ\,m^{-2}$)	–	–	–	44.0	6.3	4.4	54.7
F3/34	Pool (*Forested*)	118.7	0.63	Abundance ($no.\,m^{-2}$)→	–	–	–	0.5	0.3	0.3	1.1
				Biomass→ ($kJ\,m^{-2}$)	–	–	–	72.2	9.8	46.8	128.7
F4/22	Pool (*Bridge*)	171.3	0.61	Abundance ($no.\,m^{-2}$)→	–	–	–	0.2	0.3	0.1	0.6
				Biomass→ ($kJ\,m^{-2}$)	–	–	–	90.1	29.3	2.6	122.1
F5/20	Riffle (*Forested*)	156.5	0.19	Abundance ($no.\,m^{-2}$) →	–	–	–	0.4	0	0	0.4
				Biomass→ ($kJ\,m^{-2}$)	–	–	–	3.6	0	0	3.6

where R is Respiration, in g O_2 g^{-1} fish day^{-1}, R_{max} is maximum respiration, A is an activity parameter "to specify respiration rates above standard" (Kitchell et al., 1977), r_R is an intermediate respiration calculation, S is the specific dynamic action coefficient, and C is consumption (see Table E in the Appendix for specifics). Stream temperature is used in calculating both R_{max} and r_R; fish size (mass) is used to calculate R_{max} and C. Thus, fish respiration will vary based on both the stream temperature and the fish size. We used the Little Sandy Creek stream temperature and the mass of our sampled fish in these calculations.

The determination of production is a very complex and time intensive process, requiring far more information than we had. Fortunately, we were able to implement Humphreys' (1979) general relation between respiration and production for both invertebrates and fish (Step 3).

STEP 1: Calculate respiration by size class and trophic level.

$$Resp_{tl,sc}(\text{gday}^{-1}) = (RespFunct_{tl,sc}) * \text{IndMass}_{\text{tl,sc}} * Num_{tl,sc} \quad (16)$$

Where $RespFunct_{tl,sc}$ is the respiration rate per gram body mass for a given size class (*sc*) and trophic level (*tl*). $IndMass_{tl,sc}$ is the midpoint mass of the size class, $Num_{tl,sc}$ is the number of individuals in the size class within each trophic level in a sampled area

For fish, a conversion factor derived from the Wisconsin bioenergetics model (described above) was used to set $RespFunct_{tl,sc}$ for each size class and trophic level. For all invertebrates, functional relations from incubated invertebrate samples were used, we tested several fits in our sensitivity analysis, ultimately we used the following in our model, $RespFunct_{tl,sc}\ (g\,m^{-2}\,g^{-1}\,day^{-1}) = 0.039 * (IndMass_{tl,sc})^{-0.0446}$. The Wisconsin model and our field calculations were generally quite close except for the largest fish. See Fig. 8 for data.

STEP 2: Convert respiration values to energy used per square meter per unit time.

$$Resp_{tl,sc}(\text{J}\,m^{-2}\,day^{-1}) = Resp_{tl,sc} * \text{OxToE} * \text{ExpFact}/\text{Area} \quad (17)$$

Where $Resp_{tl,sc}$ is the output from Eq. (16), *ExpFact* is the expansion factor as described in Step 1 of STOCKS, after Eq. (14), and *Area* is the size of the sample site in m^2. *OxToE*, is the conversion factor for mass of oxygen to energy in joules (see below or Table 3b).

STEP 3: Sum all respiration, expressed as energy, for each trophic level.

$$Resp_{tl,tot} = \sum Resp_{tl,sc} \quad (18)$$

Where $Resp_{tl,sc}$ is the respiration rate for each individual size class within a trophic level per unit area derived in step 1, and $\sum Resp_{tl,tot}$ is the summation of respiration of size classes within a trophic level.

STEP 4: Calculate production from respiration using Humphreys' equation.

$$Prod_{tl,sc} = 10^{((log(Resp/m2tl,sc) * ProdCons) - ProdCons2)} \quad (19)$$

Where $Prod_{tl,sc}$ is the production rate for each individual size class within a trophic level per unit area (J m^{-2} day^{-1}), $log(Resp_{tl,sc})$ is the log of the respiration derived in Step 2, *ProdCons* is a productivity constant from Humphreys (1979), and *ProdCons2* is the second productivity constant from Humphreys (1979). *ProdCons* is 0.978 for invertebrates and 0.834 for fish; *ProdCons2* is 0.06 for invertebrates and 0.429 for fish. For our data set, the Humphreys (1979) equation finds that production is about 75% of respiration for invertebrates and about 12% for fish.

3. Results

3.1. Overview

We display modeled stocks (e.g., biomass) and flows (e.g., energy movement through trophic levels) in Little Sandy Creek using an Odum energy circuit diagram (Odum 1983) (Fig. 3). The outputs indicate that during our study, the Little Sandy Creek ecosystem was primarily fueled by both the sun and internally-derived production, with a much smaller amount of energy coming from allochthonous material. We found that similar to terrestrial systems, stocks and flows of energy declined with each ascending trophic level. Note that all data are presented in their original form (usually grams per square meter) and then extrapolated to the entire one kilometer stream reach using functional relations with depth and units of joules. This is important because there are many more shallow areas than deep locations in the study reach.

The result of model extrapolation, and range of model uncertainty, does not support the operation of Allen's paradox in Little Sandy Creek. The data we collected on September 8, 2012 imply that the benthic macroinvertebrate production appears to be sufficient to support the fish energy requirements (Fig. 9 and Table 7). Details follow.

3.2. Sunlight

The sunlight fluctuated throughout the 24-h period, and the intensity was generally very low compared to a typical day in early September (Fig. 4). We recorded that the hill site (100% transmission of available PAR) received a total of 4640 kJ m^{-2} day^{-1}. The meadow section, which had an area of 3150 m^2, received about 63% of available PAR at the stream surface; the forest section had an area of 3850 m^2 and received about 28% of available PAR at the stream surface. Over the course of the day, meadow transects received about 2900 kJ m^{-2} day^{-1} (or 9200 MJ in total for the km reach), while forested stream transects received about 1300 kJ m^{-2} day^{-1} (or 5000 MJ in total) (Fig. 3). Sunlight inputs did not vary significantly between riffles and pools.

3.3. Whole stream metabolism

The two-station (or free water (FW)) analysis indicates that gross photosynthesis (GPP) was higher in the meadow than in the forest. In the meadow, NEP followed a bell shaped pattern; gross photosynthesis peaked in the early afternoon (Fig. 5d). In the meadow the integrated respiration over 24 h was 46 kJ m^{-2} day^{-1} and the integrated gross photosynthesis was 93 kJ m^{-2} day^{-1}. In the forest, GPP of the stream was variable during daytime; we observed a peak in the late morning (Fig. 5h); GPP fell to zero in the cloudy early afternoon, then rose above zero briefly in the late afternoon. In the forest the integrated respiration was 80 kJ m^{-2} day^{-1} and the integrated gross photosynthesis was 31 kJ m^{-2} day^{-1}. The NEP (GPP minus respiration) over 24 h was 47 kJ m^{-2} day^{-1} (3.2 g O_2 $m^{-2}day^{-1}$) in the meadow and −49 kJ m^{-2} day^{-1} (−3.3 g O_2 $m^{-2}day^{-1}$) in the forest (Table 5).

From the results of the two station analysis, we estimated the respiration, GPP, and NEP in for the wetted area meadow and forest sections of Little Sandy Creek (Table 5). Community respiration was 354 MJ day^{-1} in the forest and 169 MJ day^{-1} in the meadow (523 MJ day^{-1} for all of Little Sandy Creek). GPP in the forest was 138 MJ day^{-1} and at 339 MJ day^{-1} in the meadow (477 MJ day^{-1} for all of Little Sandy Creek). Thus, based on the two station analysis we estimate that the total NEP in Little Sandy Creek on the day of our study was −46.0 MJ day^{-1} (which is very close to zero).

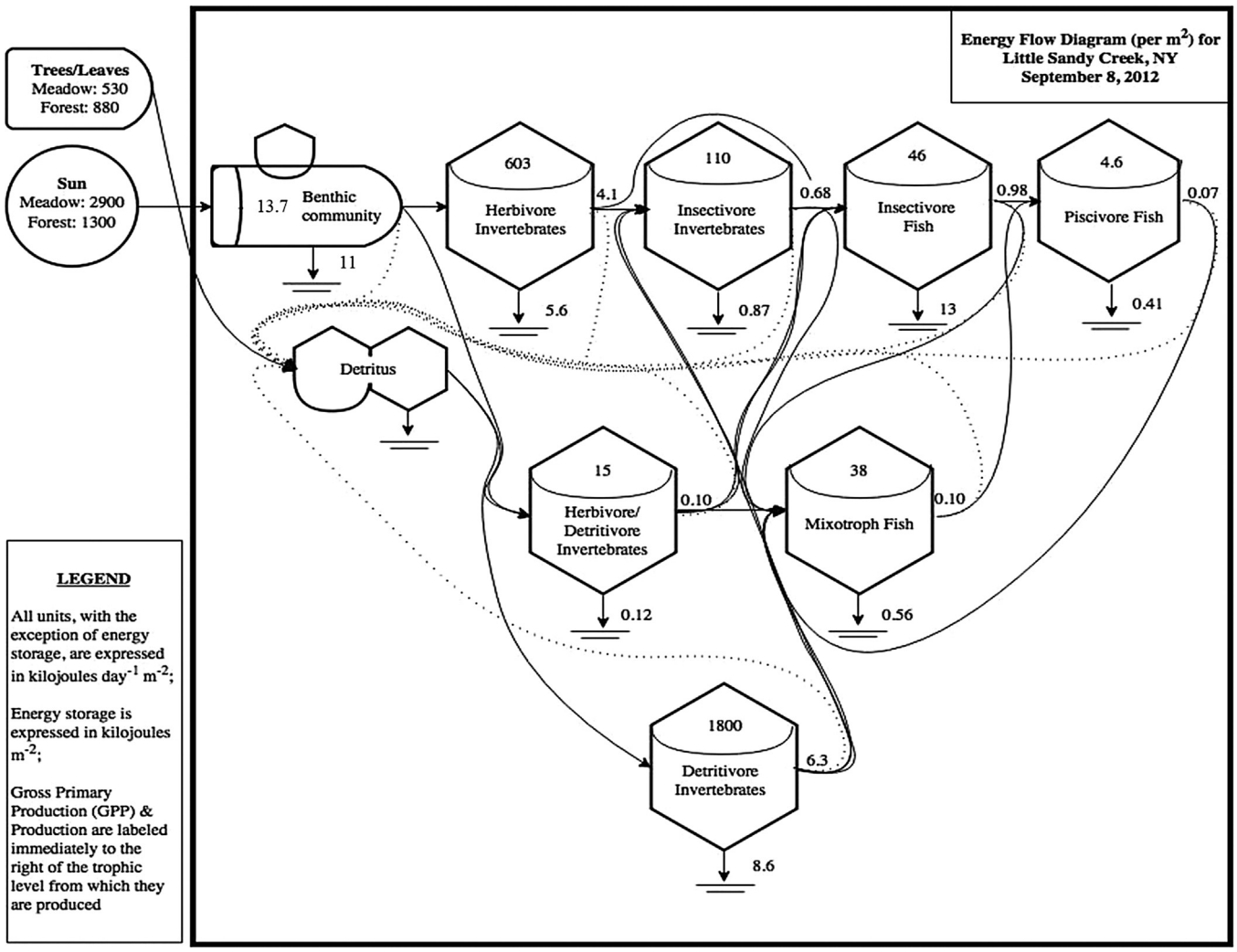

Fig. 3. Model estimates of mean energy flow in the study reach of Little Sandy Creek on September 8, 2012, using symbols from H.T. Odum. Bullet-shaped modules represent autotrophs, and hexagons represent heterotrophs. Dashed lines indicate indirect energy flow to detritivorous invertebrates. Numbers in the hexagons are biomass values and numbers on downward pointing arrows are respiration values. Gross primary production (GPP) and production values are on the horizontal lines/arrows to the right of the trophic level from which they are produced. Benthic community (BC) respiration and production are from the Little Sandy Creek 24 h chamber respiration values in Table 5, converted to kJ m^{-2} day^{-1}. To calculate the energy of the study reach, benthic community, invertebrate, and fish values were multiplied by 7000 m^2; detrital and sunlight values were multiplied by 3850 m^2 (forest) or 3150 m^2 (meadow).

Table 5
Two independent estimates of primary production and respiration from FW (two station free water) analysis and benthic chamber (BC) field data. In the MJ day^{-1} column, values in g O_2 m^{-2} day^{-1} were converted to MJ then multiplied by the area of interest: area of the meadow was 3150 m^2, the forest was 3850 m^2, for a total of 7000 m^2 in the study reach. BC values are expressed as averages of chambers 1–4 for the meadow, and chambers 5–8 for the forest. Twenty four hour NEP is reported for FW and NBP is reported for BC. Total values in g O_2 m^{-2} day^{-1} are weighted averages based on the area of the meadow and forest.

Area of Interest	24 h resp				Daytime GPP				24 h NEP/NBP			
	g O2 m^{-2} day^{-1}		MJ day^{-1}		g O2 m^{-2} day^{-1}		MJ day^{-1}		g O2 m^{-2} day^{-1}		MJ day^{-1}	
	FW	BC	FW	BC	FW	BC	FW	BC	FW	BC	FW	BC
Meadow	3.2	1.12	169	60	6.4	1.07	339	57	3.2	−0.05	170	−2.8
Forest	5.4	1.08	354	70	2.1	0.96	138	62	−3.3	−0.12	−216	−7.7
Total	4.4	1.09	523	130	4.0	1.01	477	119	−0.4	−0.09	−46	−10.6

3.4. Benthic community metabolism

Estimated daily metabolism for the benthic chambers are given in Table 4. Benthic metabolism was highly variable (Fig. B1 and B2 in Appendix) – standard deviation was calculated to be about ±40% of our mean estimates for GPP and about ±50% for our estimates of respiration. Production showed little relation to sunlight intensity above minimum levels across all chambers, even on a cloudy day when our data were primarily collected (Figs. B1, B2 and B5). The NBP and respiration inside of the benthic chambers had no significant correlation with depth after adjusting for outliers. Table 5 compares per square meter and stream section estimates of primary production between free water and benthic chamber analyses. Average GPP from the benthic chamber analysis was slightly higher (though not significantly) in the meadow than in the forest (Table 5). We plotted GPP_{max} and respiration for each chamber versus depth of chambers (Step 4) and sunlight transmission (see values in Table 4), but there was no significant linear rela-

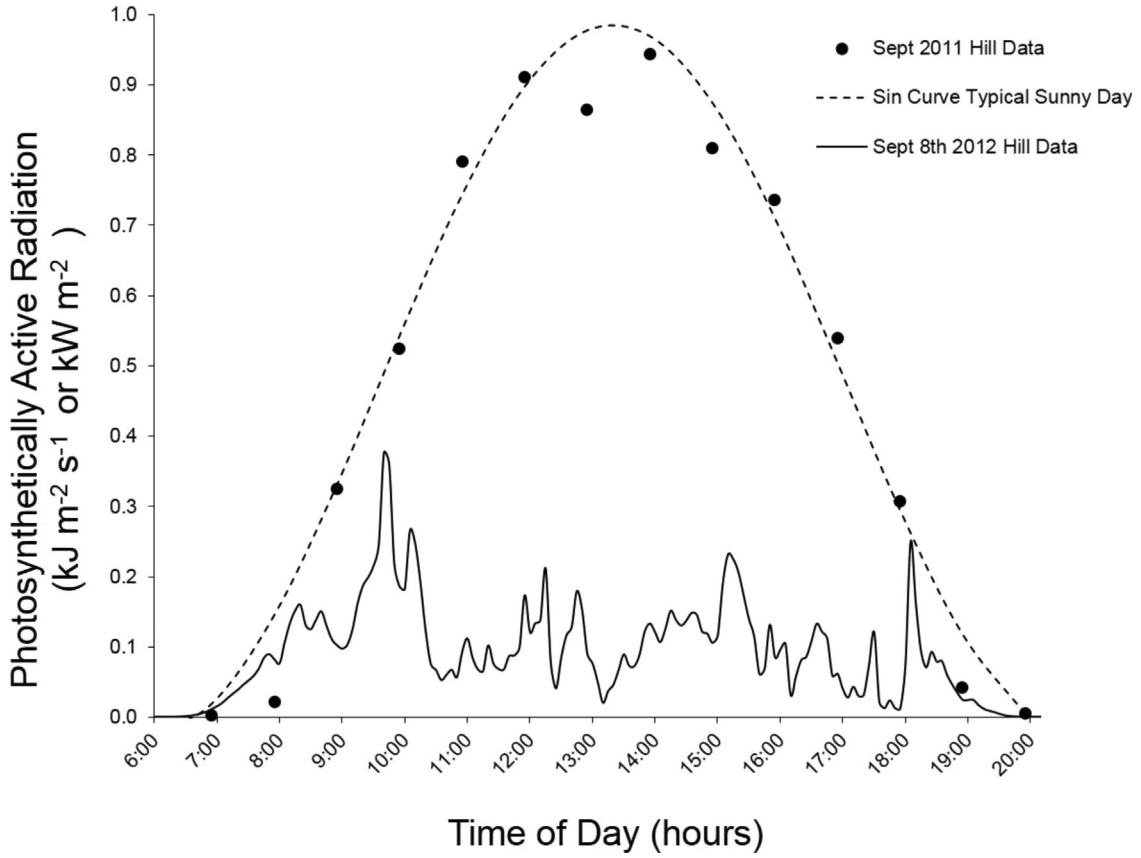

Fig. 4. Light intensity data (solid line) collected at on open field site adjacent to Little Sandy Creek on September 8, 2012 (a cloudy day) versus expected photosynthetically active radiation (PAR) on a typical sunny day in early September at 43.5°N (dotted line). PAR values from 2011 (circles) align with expected light intensities, indicating the PAR values measured in 2012 were lower than normal.

tion between GPP and depth or sunlight. Therefore, the analysis of functional relations with depth and sunlight have been excluded from our results. To the model benthic community on the day of September 8th, 2012, we used averages from the meadow and forest chambers (Table 5), and extrapolated them to the entire stream, yielding GPP of 119 MJ day^{-1} and respiration of 130 MJ day^{-1}.

3.5. Benthic invertebrate and fish stocks

Biomass (and abundance) of macroinvertebrates differed between riffles and pools, and was largely dependent on stream depth. In general, greater biomass and abundance for a given trophic level were found in riffles compared to pools (Table 4, Fig. 6). The number and biomass of invertebrates per square meter was much greater in shallower environments, while the pattern of fish abundance with depth was variable (Table 4). However, the larger fish, and hence the largest total biomass, were found exclusively in pools while smaller fish were found in all areas, but were more abundant in shallower sample sites. The taxa of biota sampled in Little Sandy Creek and their trophic level designations are listed in Table B in the Appendix. Size class designations for invertebrates and fish are shown in Table F in the Appendix.

Fish biomass in each location was largely dependent on the depth of the sample site (Fig. 7). Fish number was greatest in the pool/riffle location (transect 25). However, fish in this location (transect 25) were significantly smaller than fish sampled in pool locations (transects 22 and 34). The total mass of fish in transect 25 was smaller than the total masses of transects 22 and 34. Insectivores sampled in the pool/riffle had the greatest abundance (288 fish). Piscivores were absent in riffle locations (transects 33 and 20). Mixotrophs were also absent from transect 20 and had the lowest overall biomass. See Table 4 for additional results.

3.6. Other stocks

While our study did not address the issue of upstream inputs of detritus directly, it does appear there is roughly twice as much respiration as photosynthesis. This means that about half the energy that is running through the stream came from sources other than photosynthesis, similar to what Hall (1972) found for New Hope Creek. Specifically, we measured averages of 30 (open canopy) to 50 (closed canopy) g m^{-2} day^{-1} (530–880 kJ m^{-2} day^{-1}) of allochthonous material input (Fig. 3), which is comparatively higher that other lotic systems although similar to one autumn value (see Table G in Appendix). We did not measure other inputs (e.g., terrestrial invertebrates) or the meiofauna found within the interbed of the stream.

3.7. Benthic invertebrate and fish energy flows

For each trophic level, invertebrate respiration and production were greater in riffles compared to pools (Table 6). Insectivores demonstrated the greatest overall respiration (48.6 kilojoule m^{-2} day^{-1}) in riffles as well as the greatest variation in respiration and production between riffles and pools (average respiration was 1.16 kilojoule m^{-2} day^{-1} in pool habitats).

The per unit mass respiration of fish measured decreased with mass. The range was 0.05 g g^{-1} day^{-1} for a 3.3 g fish to 0.001 g g^{-1} day^{-1} for a 108.5 g fish. On a log–log scale, the respiration slope of the trendline of all the fish when calculated using the Wisconsin bioenergetics model equations was slightly higher than

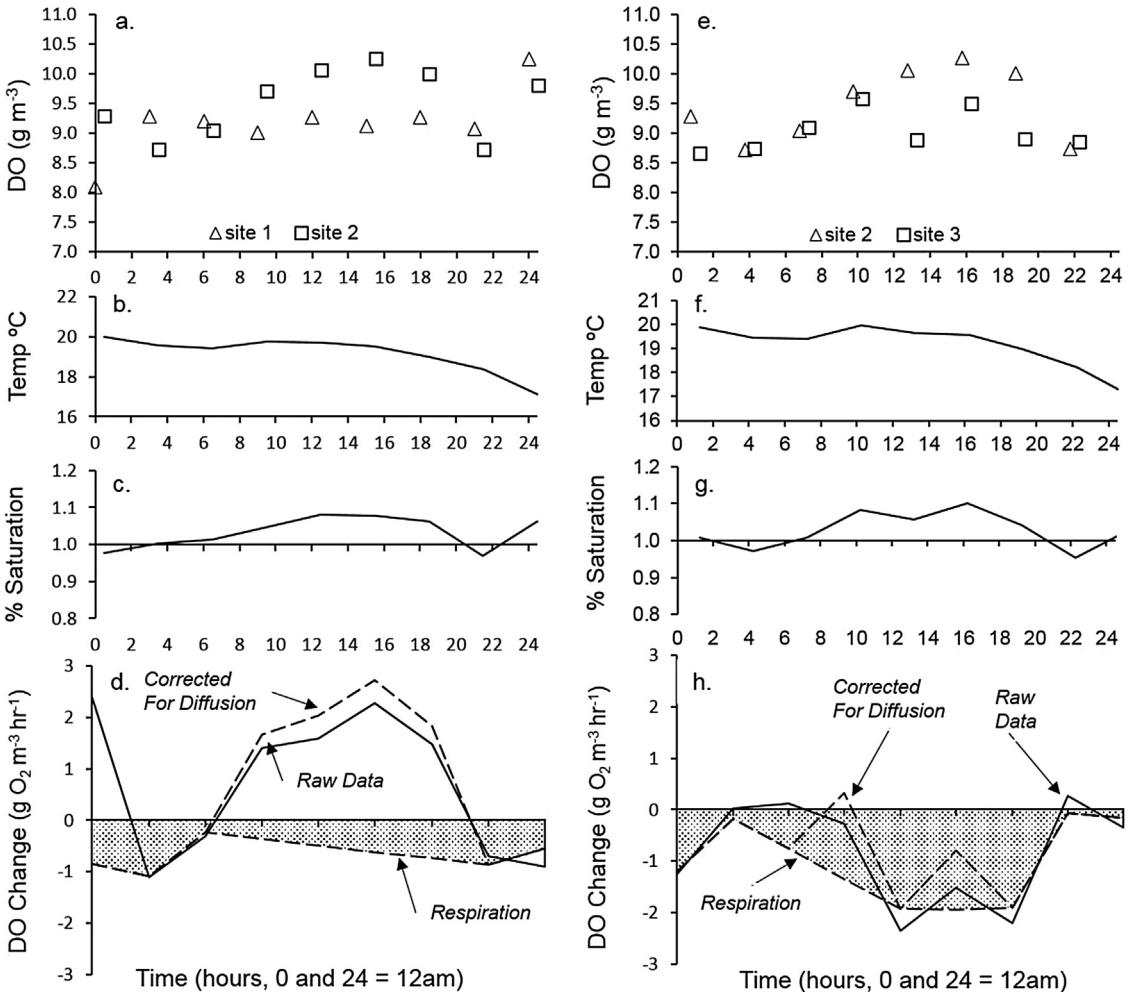

Fig. 5. Derivation of whole stream respiration and gross photosynthesis (adjusted for diffusion) in the Meadow (left, a-d) and forest (right, e-h) calculated using the two station approach. The average percent oxygen saturation calculated from temperature and dissolved oxygen (panel a and e), the raw DO change data (solid line) (panels d and h), are depicted. Data adjusted for diffusion are shown as dashed lines, and interpreted respiration is depicted in the shaded area of panels d and h.

Table 6
Macroinvertebrate and fish respiration and production results from measured field sites (note values are per square meter). Fish respiration is derived from literature equations backed up with our limited field measurements (Fig. 8). Production is derived from respiration values using relations from Humphreys (1979).

Sample	Depth (m)		Herbivore	Herbivore/Detritivore	Detritivore	Insectivore	Piscivore	Mixotroph
Macroinvertebrates								
I1	0.19	Respiration (kJ m^{-2} day^{-1})	24.3	52.5	27	48.6	–	–
		Net Production (kJ m^{-2} day^{-1})	18.1	36.3	19	0.8	–	–
I2	0.18	Respiration (kJ m^{-2} day^{-1})	161	0.2	108	6.3	–	–
		Net Production (kJ m^{-2} day^{-1})	106	0.1	73	4.6	–	–
I3	0.49	Respiration (kJ m^{-2} day^{-1})	2.67	0.2	6	0	–	–
		Net Production (kJ m^{-2} day^{-1})	2.01	0.1	4.4	0	–	–
I4	0.33	Respiration (kJ m^{-2} day^{-1})	16.5	0	17	2.2	–	–
		Production (kJ m^{-2} day^{-1})	11.8	0	12.6	1.5	–	–
Fish								
F1	0.1	Respiration (kJ m^{-2} day^{-1})	–	–	–	0.7	0	0.0
		Net Production (kJ m^{-2} day^{-1})	–	–	–	0.1	0	0.0
F2	0.21	Respiration (kJ m^{-2} day^{-1})	–	–	–	3.4	0.9	0.8
		Net Production (kJ m^{-2} day^{-1})	–	–	–	0.4	0.1	0.1
F3	0.63	Respiration (kJ m^{-2} day^{-1})	–	–	–	1.3	1.6	1.3
		Net Production (kJ m^{-2} day^{-1})	–	–	–	0.2	0.2	0.2
F4	0.61	Respiration (kJ m^{-2} day^{-1})	–	–	–	1.3	2.3	0.1
		Net Production (kJ m^{-2} day^{-1})	–	–	–	0.2	0.3	0.0
F5	0.19	Respiration (kJ m^{-2} day^{-1})	–	–	–	0.8	0	0
		Net Production (kJ m^{-2} day^{-1})	–	–	–	0.1	0	0

the trend found for our field measurements (Fig. 8). Mixotrophs had the lowest overall respiration rates (averaging 449 J m^{-2} day^{-1}, with a minimum of 6.5 J m^{-2} day^{-1}). Insectivores had the highest overall respiration and the greatest range of respiration rates. Interestingly, the two riffle transects (33 and 25) had the highest insectivore respiration (696 J m^{-2} day^{-1} and 3394 J m^{-2} day^{-1},

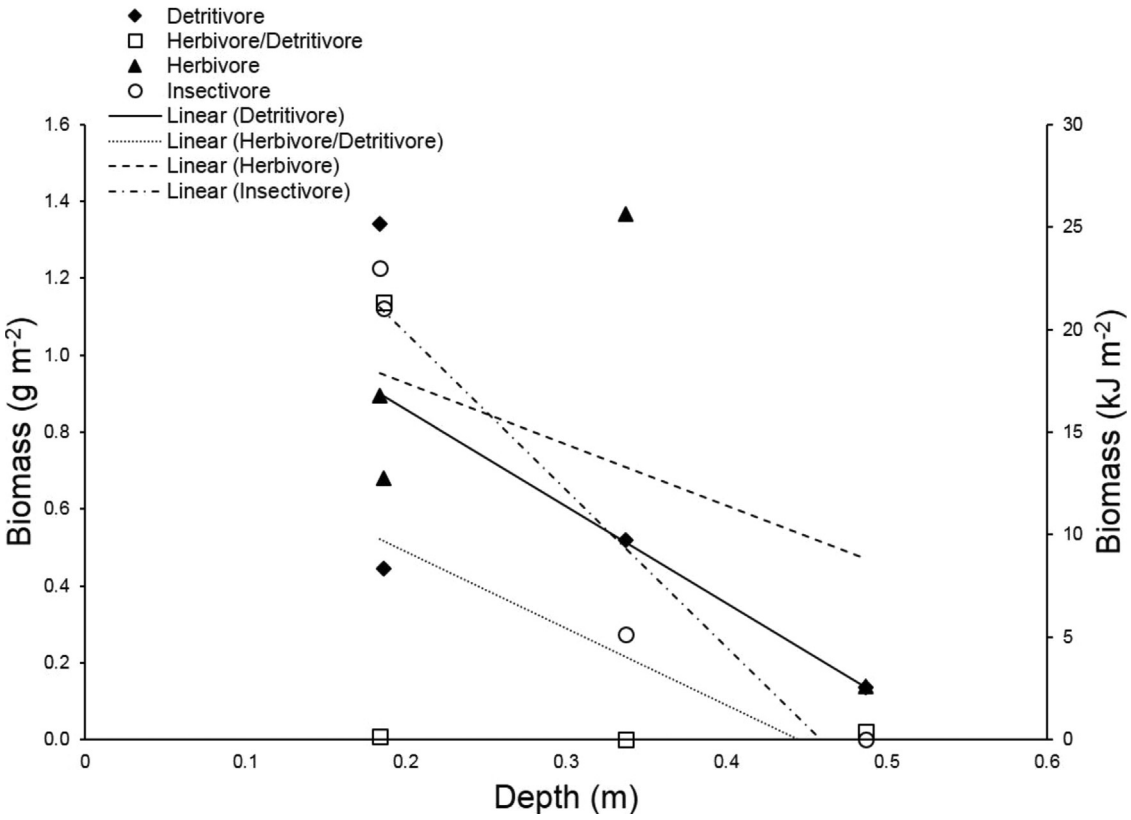

Fig. 6. Benthic invertebrate biomass (g m^{-2} and kJ m^{-2}) by trophic level as a function of depth. Detritivores = −2.52(depth) + 1.36, R^2 = 0.502; Herbivores = −1.59(depth) + 1.25, R^2 = 0.374; Herbivores/Detritivores = −1.99(depth) + 0.89, R^2 = 0.260; Insectivores = −4.08(depth) + 1.87, R^2 = 0.934.

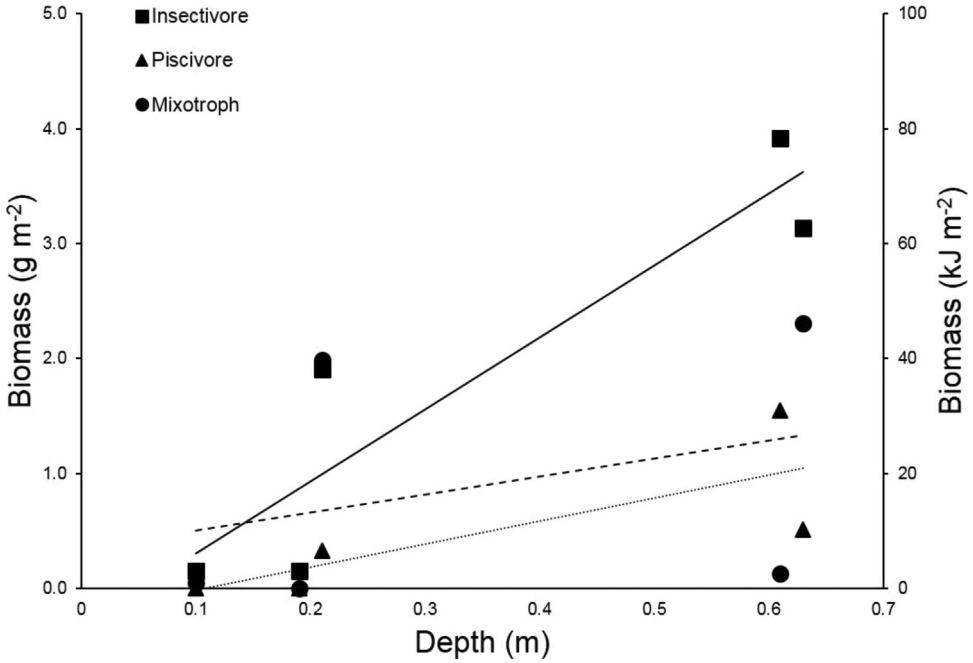

Fig. 7. Fish biomass (g m^{-2} and kJ m^{-2}, dry weight) by trophic level as a function of depth. Insectivores (solid line) = 6.25(depth) − 0.32, R^2 = 0.848; Piscivores (grey dashed line) = 2.0(depth) − 0.214, R^2 = 0.619; Mixotrophs (black dashed line) = 1.56(depth) + 0.35, R^2 = 0.117.

respectively). In contrast, piscivorous fish had higher respiration rates in deeper waters than in the riffle. As production is calculated using respiration, similar trends were found. See Table 6 for additional results.

3.8. Synthesis and extrapolation to entire reach

Depths within our study reach of Little Sandy Creek were skewed towards shallower depths, i.e. riffles were much more abundant in the stream than pools. Since we defined abundance

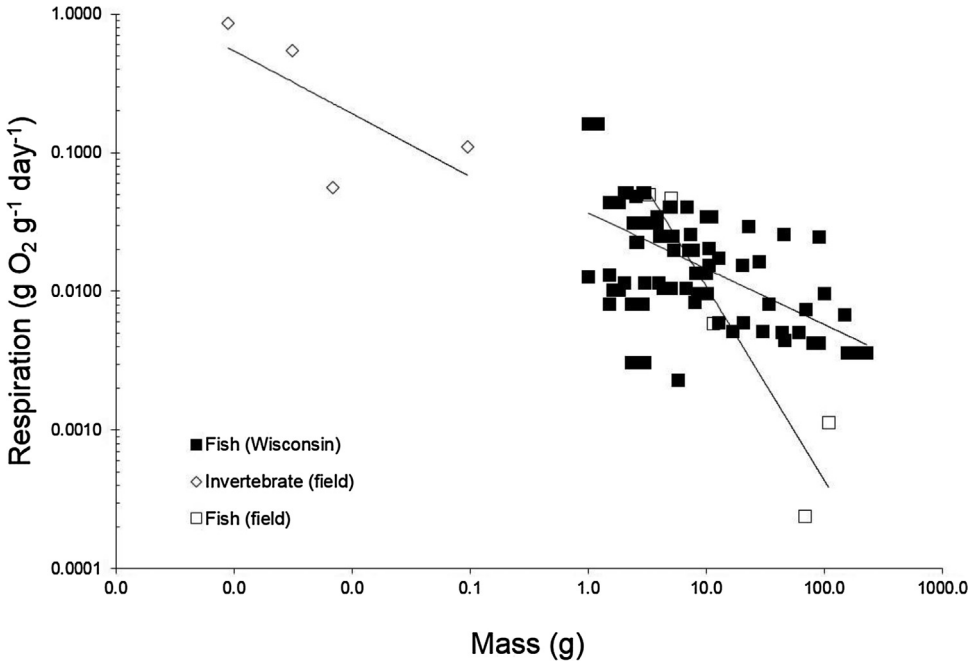

Fig. 8. Respiration rates ($g\,g^{-1}$ day^{-1}) as a function of mass (g) for invertebrates and fish. Invertebrate respiration was measured in the field (Winkler method); fish respiration was estimated in the field, and also calculated using the Wisconsin bioenergetics model (see Table E in Appendix for equations). $Respiration_{invertebrates} = 0.024(mass)^{-0.455}$, $R^2 = 0.482$; $Respiration_{fish}$ (field) $= 0.27(mass)^{-1.398}$, $R^2 = 0.869$; $Respiration_{fish}$ (Wisconsin model) = 0.039(mass)-0.355, $R^2 = 0.256$.

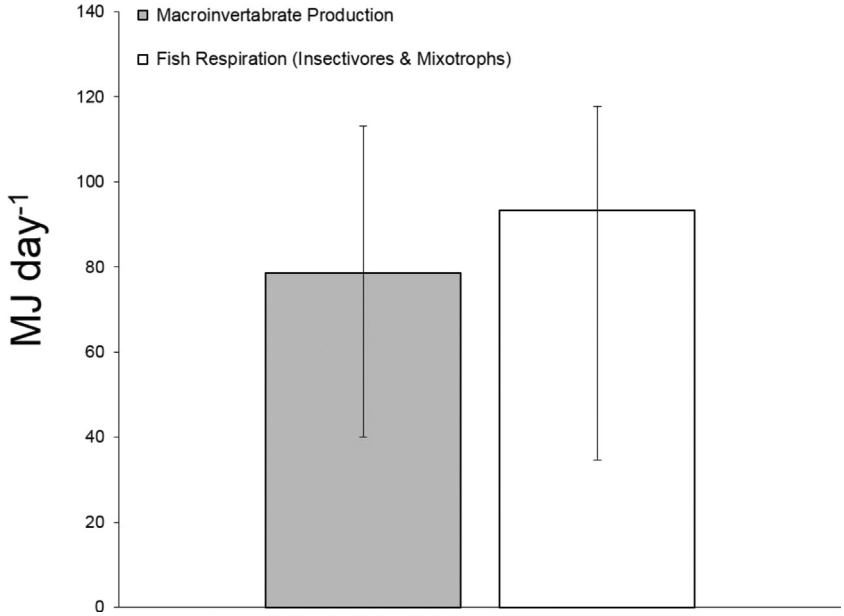

Fig. 9. Allen's paradox model outputs for total invertebrate production (grey bar) and fish respiration (white bar) in study reach of Little Sandy Creek. Estimates of error were calculated using the average positive and negative deviation of field data from the values produced by functional relations with depth.

of organisms in trophic levels and size classes by depth, our integration over the full one km area and the simulations resulted in greater biomass of trophic levels that were found more frequently in riffles, and lower biomass of trophic levels that were generally found in pools. This is one reason that our invertebrate production values are large relative to fish consumption for the entire stream section. The respective biomass, respiration, and production of the trophic levels of the entire length of Little Sandy Creek are detailed in Table 7. Stocks of benthic invertebrates (e.g., biomass) were much larger than stocks of fish. Production generally decreased with ascending trophic level (Table 7). The total respiration of invertebrates and fish in Little Sandy Creek was estimated to be about 205 MJ day^{-1}.

3.9. Allen's paradox

The calculations and the model results do not support the existence of Allen's paradox in Little Sandy Creek. As noted above, we found that shallow depths comprised the vast majority of the study reach, with relatively few deep pools (Fig. 2). When the relations between fish and invertebrate abundance with depth were extrapolated across the entire reach, we found that modeled benthic invertebrate production was about the same as modeled insec-

tivorous fish respiration (Table 7 and Fig. 9). Overall, in-stream invertebrate production of 79 MJ day^{-1} (−38, or +34 MJ) appears to be sufficient to support fish respiration needs of 93 MJ day^{-1} (−60 or +25 MJ) within the uncertainty of the data and analysis. Given an 80% assimilation efficiency for fish, the macroinvertebrate production is enough to supply 68% of the insectivorous fish needs. However, during model sensitivity tests, we found that changing the type of function (e.g. power versus log linear) for invertebrate respiration versus individual mass (Fig. 8) resulted in estimates of invertebrate production that were up to three times higher or three times lower than our final best estimate. These uncertainties highlight the difficulty of quantifying Allen's paradox.

4. Discussion

This entire exercise (and corresponding class exercises), was meant to serve as an introduction to systems ecology and more generally quantitative environmental science. As such, we, the students, were really surprised at its effectiveness in preparing us for later quantitative life. The preparation of a real manuscript was especially effective in teaching us how to do real quantitative science. We cannot emphasize enough the difference between reading about models and generating one from one's own data. This plus the uncertainty in our estimation of invertebrate and fish metabolism used to test Allan's paradox highlight the importance of having the modelers gain an intimate understanding of how data is collected and the types of error associated with the methods used. For this reason we believe that it is crucial that modelers participate directly in the planning and collection of data from field studies. In addition we believe that the basic methods given here serve as a template for more comprehensive and rigorous studies of stream ecosystem energy flow should that be of research interest.

Energy is the common denominator for all metabolic and ecological processes (Hall, 1972). With standard conversions from published literature, we converted our biomass, respiration, and production values to energy units, which allowed us to compare between trophic levels and to test Allen's paradox. We built unit conversion tables (Tables 4) so that others can easily convert to energy units with standard stream ecology data. These estimates may not be precise, but we believe that the order of magnitude of differences among trophic level values makes our analysis robust enough for the conclusions we draw.

It was unrealistic to undertake enough sampling in a few days to utilize robust statistics with our data. Hence, rather than report elaborate statistical analyses, we examined the data we obtained in 2012 with data from other years, and from Mead (2007). The results indicate that the data for 2012 were generally within the range of values collected by other Systems Ecology classes (Figs. 12 and 13 and Table 8) and Mead (2007) (Fig. 10). These values were not sufficiently different to negate our conclusions using sensitivity analysis. Specific comparisons are given by taxon below. Further, the methodologies used in this study are relatively simple, and more robust methodologies exist to quantify stream ecosystem metabolism (see Huryn et al., 2014, for example).

4.1. Sunlight

We measured PAR at each benthic chamber periodically to obtain functional responses with photosynthesis. Because PAR was not measured at regular frequent intervals at the chambers, we did not have a sunlight measurement for each benthic chamber reading. Instead, we assumed sunlight in the stream was proportional to sunlight measured at the hill, and a shading factor (Eq. (1)) was used to estimate sunlight. The use of a single shading factor eliminated the possibility of characterizing shading at different times of the day. To eliminate this source of uncertainty in future studies, sunlight estimates at each chamber could be improved by setting up solar flux meters to take regular readings in the areas of the stream near the benthic chambers. If monitoring equipment is limited then the benthic chamber team should be given a solarimeter and the solar flux measurements should be taken hourly at each chamber at the time DO readings are being recorded.

Table 7
Modeled stocks and flows of trophic levels for the wetted area (7000 m^2) of Little Sandy Creek. See Fig. 3 for an energy flow diagram with values per m^2.

Trophic Level	Biomass (MJ)	Respiration (MJ day^{-1})	Production (MJ day^{-1})
Stream Community Metabolism			
Free Water	–	523	477
Benthic Chamber	–	130	119
Primary Consumers (Herbivores and Detritivores)			
Herbivore Invert.	4272	39	29
Detritivore Invert.	12352	61	45
Herb./Det. Fish	88	1.3	0.2
Total	16712	101.3	74.2
Secondary Consumers (Insectivores)			
Invertebrates	769	6.1	4.7
Fish	412	93	7
Total	1181	99.1	11.7
Tertiary Consumers (Piscivores)			
Fish	120	4.2	0.7

Table 8
Biomass (g m^{-2}, ash-free dry weight) of benthic invertebrates collected in Little Sandy Creek by habitat type. 2013 values are only those that were measured; other benthic invertebrates were collected but their masses were not recorded.

	Riffle/Closed	Riffle/Open	Pool/Closed	Pool/Open
2011	6.9	9.2	0.9	0.3
2012	3.0	4.0	0.3	2.2
2013	0.4	0.8	0.2	0.1

4.2. Whole stream metabolism

For the entire stream, the integrated 24 h net benthic production (NBP) estimate, from the Benthic Chamber analysis of −11 MJ day^{-1} was lower than the net ecosystem production (NEP) estimate from the free water analysis of −46 MJ day^{-1} (Table 5). Both net production estimates were close to zero, which indicates that the stream used about the same amount of energy on the day of our study as it produced. Free water estimates for GPP and respiration were about 2–6 times greater than benthic chamber estimates (Fig. 10). Similarities in trends between the metabolism estimates from the meadow and the forest, in conjunction with observed weather patterns, indicate a general agreement between the free water and benthic chamber analyses despite this difference. NEP and NBP were generally above zero during the day in the morning and late afternoon, where there was higher sunlight transmission. The negative daytime NEP and NBP values are indicative of the compounding effects of low light transmission due to tree cover and heavy clouds which limited photosynthetic activity on the day of our study.

Low or negative NEP is typical of partially shaded temperate stream ecosystems, such patterns have been observed by Hall (1972), Bott et al. (1997), Mulholland et al. (2001) and others. According to Hall (1972) and Bunn and Davies (2000), the primary control on GPP in many streams tends to be riparian-zone vegetation, where a closed tree canopy during the warm season tends to reduce GPP (Young and Huryn, 1999). This was consistent with our study, as the GPP estimated in the meadow from the two station analysis (6.5 g O_2 m^{-2} day^{-1}) was greater than in the forest (2.25 g O_2 m^{-2} day^{-1}). The GPP estimates from the free water analysis for

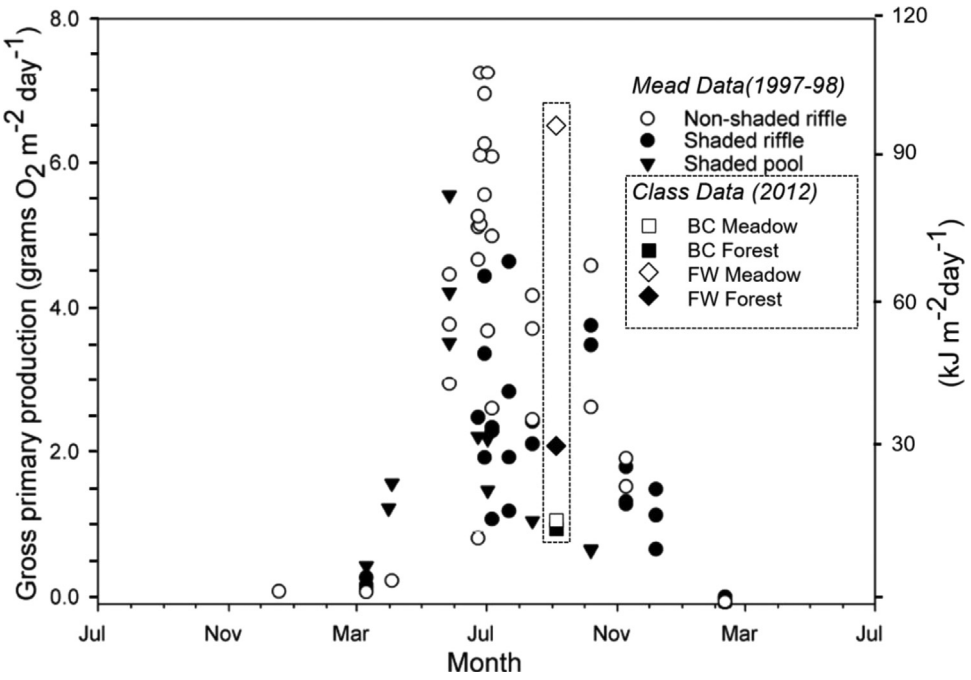

Fig. 10. Estimates of daily gross primary production (GPP) from benthic chambers on sunny and cloudy days from Mead (samples in 1997-98, circles and triangles) with September 2012 data (inside dotted line, squares and diamonds). The 2012 data points represent average benthic chamber values (from forested and meadow sites) and data from free water samples.

the meadow and the forest had a similar range to Mead's (2007) findings for open canopy and closed canopy samples sites (Fig. 10), however the meadow GPP was particularly high.

We observed some very high oxygen concentrations during the day: DO values were above 10.0 g O_2 m^{-3} at site 2 between 12:30 and 18:30, which was more than 10% above oxygen saturation. We are not sure why the DO concentration was so high in the water column in the afternoon. The heavy rains and wind and our use of a diffusion constant of 1.0 g m^{-2} h^{-1} at 100% saturation, which has been found as an approximate value in other streams (Churchill et al., 1962; Hall, 1972), have all contributed to the uncertainty of the free water analysis. Wind and heavy rain can create surface turbulence which reduces the laminar layer of the stream air interface leading to increases the rate of diffusion, however, for obvious practical reasons we were unable to quantify the influence of any of these physical forces on DO concentrations in Little Sandy Creek. Nonetheless, the data from the free water analysis gives a rough representation of what occurred September 8, 2012.

4.3. Benthic community metabolism

The estimated NBP over the entire 24-h study period was negative. The sunlight was (barely) sufficient to generate positive oxygen changes in both the free water and benthic chambers. However, it appears that at about 100–200 J m^{-2} s^{-1} (~210–420 μmol m^{-2} s^{-1}), oxygen production did not increase with increasing sunlight (Fig. B1 in Appendix). While there is a lot of scatter in the sunlight data collected by students, the basic results are similar to those of more professional analyses of Little Sandy Creek (see Mead 2007). The low amounts of sunlight and heavy rain received during our study helps to explain the very low levels of GPP. Benthic Chambers are also known to reduce productivity due to insufficient water turbulence (Hall et al., 1979). The effect of highly variable conditions (with variable sun flecks), especially in the shaded woods, and probably somewhat inexperienced investigators are apparent in the widely scattered data (Figs. B1, B2 and B5 in Appendix).

We compared adjusted GPP data for the meadow and the forest from 2012, with Mead's (2007) more abundant and presumably more sophisticatedly derived data (Fig. 10). Our mean adjusted GPP ranged from 0.96 g m^{-2} day^{-1} (in forest chambers) to 1.07 g m^{-2} day^{-1} (the meadow chambers). Our estimates from the benthic chamber analysis were on the low end of values reported by Mead (2007), who estimated GPP of about 1 g m^{-2} day^{-1} (in shaded pools) and 4.5 g m^{-2} day^{-1} (in non-shaded riffles) in August and October. The agreement between Mead's (2007) benthic chamber data and our 2012 data is satisfying given the low level of sunlight that reached the stream on Sept 9, 2012 (shown on Fig. 4). The GPP estimates from 2012 are close to what is typically observed in closed to semi-closed canopy stream ecosystems at similar latitudes. In an inter-biome comparison of streams across the United States, Mulholland et al. (2001), found GPP rates between 0.1 and 2.0 g m^{-2} day^{-1} in six closed and semi-closed canopy streams. Roberts et al. (2007) found GPP rates of about 1 g $m^{-2}day^{-1}$ in a forested reach of the Walker Branch in Tennessee.

We suspect that there may have been faulty seals on certain chambers, which would have reduced both positive (NBP) and negative (respiration) measurements of O_2 change. The benthic chambers were made of a pink or blue opaque plastic and the walls of the chambers were generally raised between 10 and 30 cm above the stream surface. Photosynthesis in the benthic chambers could have been reduced due to shading and ambient light reduction caused by the container walls. Hence, it is likely that both respiration and production were underestimated by the benthic chamber analysis. Using clear chambers and better materials to seal the chamber lids and a more comprehensive sampling procedure could improve the accuracy of benthic chamber measurements. Nevertheless, the general similarities between trends in the benthic chamber data, free water data, and values from the literature indicate that our findings were roughly representative of the activity of the benthic primary producers in Little Sandy Creek. The true primary productivity rates likely fall between the benthic metabolism and two station analysis estimates.

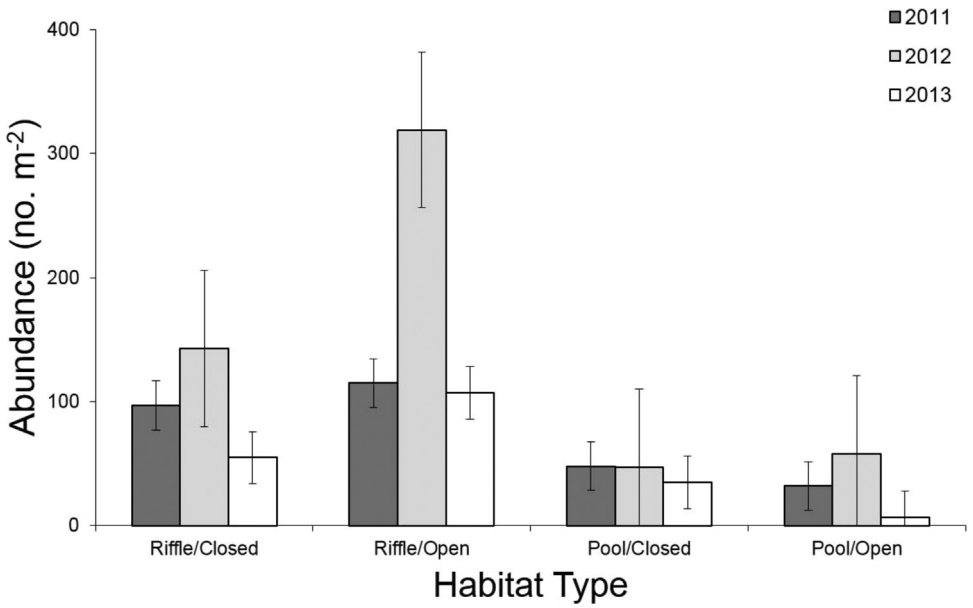

Fig. 11. Comparison of benthic invertebrate abundance values in relation to habitat type in Little Sandy Creek from 2011 to 2013. Bars represent standard error.

4.4. Benthic invertebrate and fish stocks

Benthic invertebrate biomass in lotic ecosystems can be highly variable both spatially and temporally (Merritt et al., 2008; Mead 2007), although Cummins (1973) mentions that in temperate freshwater ecosystems, biomass of aquatic macrobenthic animals is generally consistent. We found for both our own samples and those summarized by Mead (2007) that there was a general pattern of greater benthic invertebrate biomass in shallower, faster water and less biomass at deeper locations. We found the biomass of benthic macroinvertebrates in Little Sandy Creek to be roughly comparable with similar stream ecosystems. For example, Griffith et al. (1994) found shredder (detritivore) biomass ranged from 1.19 g m^{-2} to 3.77 g m^{-2} in West Virginia streams. In comparison, detritivore biomass in Little Sandy Creek ranged from 0.1 g m^{-2} to 1.3 g m^{-2}. The lower values found in Little Sandy Creek might be explained by the limited temporal resolution (e.g., approximately 24-h) in which our data were collected, thus not capturing seasonal biomass variation in Little Sandy Creek. Further, Cummins et al. (1966) quantified the biomass of macroinvertebrates in Linesville Creek, a small woodland stream in Pennsylvania, and found predators to have the highest proportional biomass (40.9%) while herbivores composed a smaller percentage (31.8%). One might predict that Little Sandy Creek trophic levels would be organized in a relatively similar manner (e.g., proportional biomasses for specific trophic levels between systems), given that both are found in similar geographic settings with forested riparian habitat. However, our results indicate that herbivores and detritivores dominate the benthic invertebrate biomass in Little Sandy Creek, comprising greater than 90% of the total community, whereas predator (insectivore) biomass was less than 1%. Differences in trophic level biomass between Little Sandy Creek and the community described by Cummins et al. (1966) suggest that different forcing functions and mechanisms across systems may be affecting how trophic levels are organized.

With the PIB sampler, we could not sample anything deeper than the top of the net frame (approximately 0.5 m). A quantitative sample of benthic invertebrates in the area of the frame must operate close to 100 percent sampling efficiency. This means we did not account for benthic invertebrates inhabiting the deepest portions of the stream. When we extrapolated these data into the depths included in our model, we assumed that the trend of benthic invertebrate biomass would continue at deeper depths.

We found herbivores were the most abundant trophic level amongst benthic macroinvertebrates, while herbivore-detritivores (e.g., filterers) were the least abundant. Note that in previous years, filtering benthic macroinvertebrates (e.g., Hydropsychidae) dominated the invertebrate community, contrary to the data collected in 2012. This may be related to the temporal variation in available suspended food particles present in Little Sandy Creek, where reduced litter fall limits filterer populations and/or higher abundance of benthic algae support a greater number of herbivores (e.g., scrapers).

We compared our results to those from the 2011 and 2013 Systems Ecology class, and found that in 2012 a much greater number of benthic invertebrates were collected (Fig. 11; see Table $H_{1\text{-}3}$ in the Appendix for raw data). Generally, benthic invertebrate biomass and abundance varied by depth across the three years analyzed; our results indicated that open (meadow) riffles had the greatest total abundance (Fig. 11 and Table 8). However, there was not an overall significant difference between habitat types (Fig. 11 and Table 8). Invertebrates collected by students in 2011–2013 ranged from 0.1 g m^{-2} in open pools to 9 g m^{-2} in open riffles (Table 8). In September 2003, simulated benthic invertebrate biomass average 1.8 g m^{-2} (see Fig. 13 on page 108 in Mead (2007)). This was smaller than the average of the 2011–2013 biomass (2.3 g m^{-2}), but well within the range of our data. Note that the actual total invertebrate mass from 2013 is higher than reported here, as mass was recorded for only select trophic levels. It is possible that the 2012 benthic invertebrate community structure was an aberration compared to other years, indicated by higher abundance values relative to 2011 and 2013 (Fig. 11 and Table 8).

There were various factors that could have reduced the effectiveness of our fish measurements. Fish were collected with the use of an electro-shocker in blocked off cross-sections of the stream. The Seber-Le Cren method used for analysis gives an expansion factor that corrects for these potential errors. We have attempted to quantify how the inclusion of second pass data would have affected our results. Since we used a combination of two factors (mass and abundance) to determine whether our sample size had decreased from the first pass to the second, we had several estimates of sam-

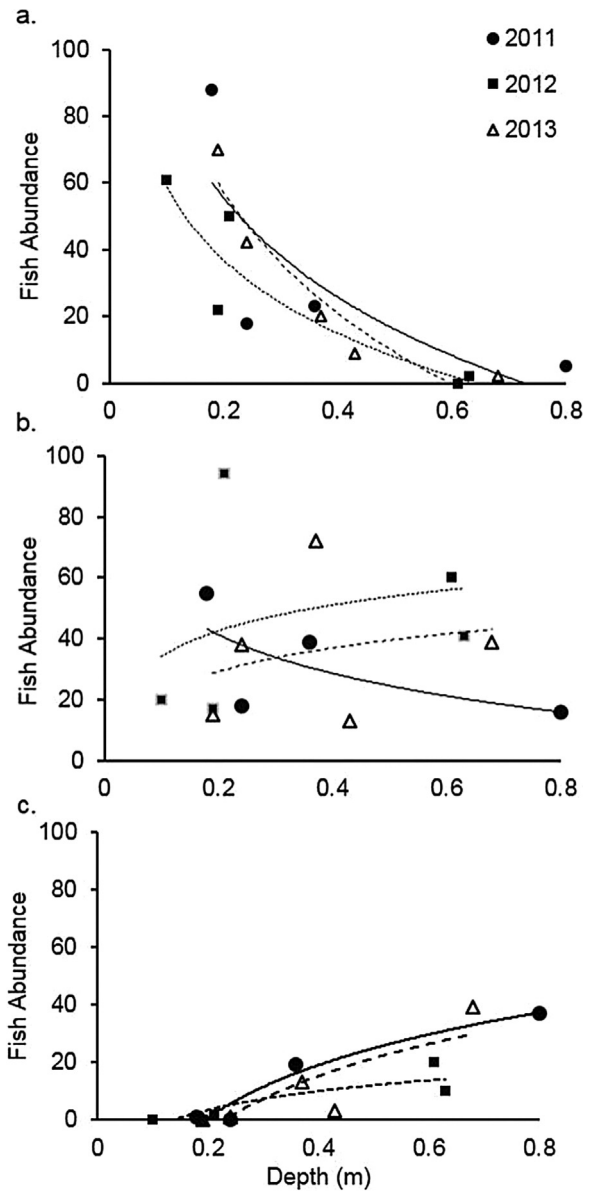

Fig. 12. Fish abundance as a function of depth for all fish sampled in 2011–2013. (a) Abundance of the smallest size class (0–2 g). (b) Abundance of the 2.1–30 g size class. (c) Abundance of fish over 30.1 g. Circles and solid black lines represent 2011 data, squares and grey lines depicted data collected in 2012, and triangles and dotted black lines are for data collected in 2013. Fish abundance estimates were similar, mostly within a factor of two, for the three years of data.

pling efficiency (see Table C) which we combined for expanding abundance and biomass from each location.

We found our fish density data (2.02 fish m^{-2}) to be comparable with similar stream ecosystems. For example, Angermeier and Smogor (1995) found density was approximately 1.95 fish m^{-2} in Jordan Creek in Virginia, and density ranged from 0.1 to 3.2 fish m^{-2} in the Sedgeunkedunk Stream in Maine (Gardner et al., 2013). Gardner et al. (2013) additionally found average fish biomass ranged from approximately 1.0 g m^{-2} to 18.0 g m^{-2} in two streams in Maine. Compared to Gardner et al. (2013), fish biomass in Little Sandy Creek had a much larger range, from 0.7 g m^{-2} to 29.8 g m^{-2}, though the area-weighted average (17 g m^{-2}) was similar.

Furthermore, we compared our results to those from the Systems Ecology classes in 2011 and 2013 (see Table $I_{1\text{-}5}$ for raw data). Fish abundance was similar for all size classes in all three years (2011–2013), with the exception of the small (2.1–30 g) size class (Fig. 12a–c). The abundance of fish of any given size in a location is strongly related to stream depth; small fish are more abundant in shallower areas while the largest fish are found almost exclusively in deeper areas. Overall, the largest number of fish caught in Little Sandy Creek was in the 2.1–30 g range. Fish in this size class were found primarily in the middle depths, between 0.35–0.65 m (Fig. 12b). Relatively few fish were caught in any given year in the largest size class (>100.1 g) (Fig. 12c). Given the relation between fish size and the depth of capture, the total mass of fish caught in 2012 and 2013 increased with an increase in stream depth (Fig. 13).

4.5. Benthic invertebrate and fish energy flows

Benthic invertebrate respiration estimates were conducted using several invertebrate taxa of different sizes to generate functional relations. These simple measurements demonstrated what is well known in physiology: that smaller individuals consumed more oxygen per gram of weight than larger individuals. For example, a 1.0 mg macroinvertebrate consumed approximately 35 μg O_2 hr^{-1}, which is in agreement with literature estimates summarized in Mead's (2007) Little Sandy Creek study, while a 4 mg macroinvertebrate consumed oxygen at a slower rate (approximately 4.5 μg O_2 hr^{-1}). We compared our *in situ* benthic invertebrate respiration values to those measured by Rostgaard and Jacobsen (2005), and found comparable respiration rates. For example, the respiration of stoneflies in Little Sandy Creek at 20 °C was measured at 4.57 mg O_2 g^{-1} h^{-1}, while Rostgaard and Jacobsen (2005) found a respiration rate across all taxa sampled (87 individuals) at 20 °C to be 4.89 mg O_2 g^{-1} h^{-1}.

The general functional relations from our *in situ* measurements were subsequently used to estimate respiration of size classes of each trophic level for the benthic invertebrate community sampled in the stream, and respiration rates were converted to generate production estimates. As energy is consumed, a proportion will be used to maintain metabolic functioning of the individual, with the remaining energy (generally) utilized for growth and reproduction (i.e. production). Humphreys (1979) demonstrated that a greater proportional production is observed as respiration increases, up to an organism's temperature optimum. In other words, as the respiration of an individual increases, the difference between respiration and production also increases due to a greater amount of total energy available for growth (assuming food is unlimited).

We estimated fish respiration in the field using fish of varying sizes from different taxa; these data were then used to generate functional relations. However, due to inappropriate container size along with questionable seals, the respiration data were not successful for all of the species sampled. Thus, we used the Wisconsin bioenergetics model (refer to equations in Table E of the Appendix) as our primary method of calculating fish respiration rates per gram of fish and to generate functional relations to use in the Little Sandy Creek system model. We subsequently compared our field results to those from the Wisconsin bioenergetics model output. Variability in fish respiration (from 2 to 3400 J $m^{-2}day^{-1}$, see Fig. 8 and Table 6) in Little Sandy Creek was primarily a function of fish mass. Nonetheless, it seems likely that fish species and the depth of measurement also caused small amounts of variability in fish respiration. The constants in the Wisconsin bioenergetics model equations vary by fish species, thus contributing to some of the variability in respiration. In addition, respiration and production of aquatic animal populations can vary depending on activity, environmental stress, such as oxygen levels, food availability, and stream temperature (Warren and Doudoroff, 1971).

The fish respiration rates we measured in the field were similar to the results produced by the Wisconsin bioenergetics model for similar sized fish (Fig. 8). Our field results were also comparable to those in the literature. For example, Beauchamp et al.

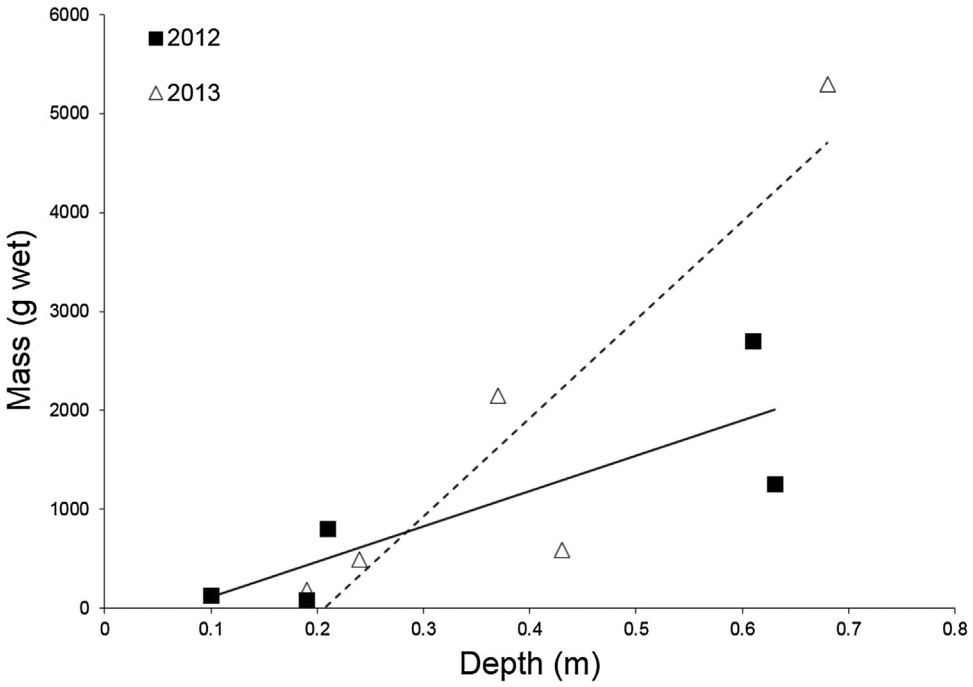

Fig. 13. Fish mass (g, wet weight) as a function of depth in Little Sandy Creek for fish sampled in 2012 and 2013. Note that insufficient fish community data was available for 2011, and thus not included in the comparison among years. $Mass_{2012}$ (solid line) = 3576(depth) − 247, R^2 = 0.704; $Mass_{2013}$ (dashed line) = 9948(depth) − 2058, R^2 = 0.811.

(1989) found that the respiration of juvenile sockeye salmon in Babine Lake, Canada was approximately 0.04 g g^{-1} day^{-1} (see Fig. 4 in Beauchamp et al., 1989) in September, slightly less than the maximum fish respiration we measured in the field (0.05 g g^{-1} day^{-1}). Further, Kitchell et al. (1977) reported simulated yellow perch respiration rates ranging from approximately 1 mg O_2 g^{-1} day^{-1} in early September to 7.5 mg O_2 g^{-1} day^{-1} in late September. By comparison, our field measurements of fish respiration ranged from 0.24 mg O_2 g^{-1} day^{-1} to 50 mg O_2 g^{-1} day^{-1} (Fig. 8). While there was a large range of respiration values in the modeled Little Sandy Creek results, due to fish of many sizes and types (2.3.–163 mg O_2 g^{-1}fish day^{-1}), respiration values found in the literature for similar ecosystems generally fall within this range. For example, the average respiration value for New Hope Creek was 0.0034 g O_2 g^{-1}fish day^{-1} (Hall, 1972). The rate of oxygen use by the fish community of Little Sandy Creek at location 2 (transect 25), which had an average depth of 0.21m, was 4.73 Cal m^{-2} day^{-1} compared to 0.79 Cal $m^{-2}day^{-1}$ in the upstream fish community of New Hope Creek, which had an average depth of 0.28 m (Hall, 1972). However, Hall (1972) did not report fish respiration as a function of mass, so it is difficult to make a direct comparison.

4.6. Allen's paradox

Allen's paradox was famously shown to be operating in Horokiwi Stream, New Zealand (Allen, 1951; Harvey and Marti, 1993; Huryn, 1996). Allen estimated that fish predation utilized 40–150 times the aquatic macroinvertebrate production (Allen, 1951; Williams et al., 2003), a much clearer case for Allen's Paradox than we found. Benthic invertebrate production must be greater than or equal to fish respiration in order to support the presence of a fish community through time. Benke (1976) has attributed Allen's paradox to inadequate sampling methods for the macroinvertebrate community, especially macroinvertebrate secondary production. This might also apply in Little Sandy Creek, especially due to our exclusion of the hyporheic community, which Stanford and Ward (1993) suggest may be more important in some systems than conventionally sampled benthic invertebrate communities.

We hypothesized that Allen's paradox would be extant in Little Sandy Creek on September 8th, 2012. The hypothesis was tested by modeling benthic invertebrate production and fish respiration. Considering the limitations of our analysis, we conclude that Allen's paradox was not observed in our study reach. Although the benthic invertebrate production and fish respiration are similar, total benthic invertebrate production (78 MJ day^{-1}, uncertainty range: 40–113 MJ day^{1}) is sufficient to support insectivorous fish respiration (93 MJ day^{-1}, uncertainty range: 35–117 MJ day^{1}). The two outputs generated by the Little Sandy Creek model are not significantly different after considering sensitivity tests and the error estimates of functions used in the extrapolation to the entire stream. We can highlight several other important factors that contribute to uncertainty surrounding modeled Allen's paradox outputs. These factors include additional food sources for fish; seasonal and inter-annual variability in species abundance and size, spatial heterogeneity in the stream, such as depth, substrate and physical forces (Benke et al., 1988). Although there is a large amount of uncertainty surrounding our results, when we account for energy transfer between trophic levels, there does appear to be enough invertebrate production to support the insectivorous fish respiration needs.

We did not measure additional potential food sources for fish such as terrestrial insects falling into the stream, hyporheic macroinvertebrates, or meiofauna. Huryn (1996) incorporated macroinvertebrate samples from the terrestrial and hyporheic zones into an analysis of Allen's paradox in Sutton Stream in New Zealand, and found that primary consumer production was greater than that of secondary consumers (e.g., fish). Thus, a surplus of prey production was available to the fish community in Sutton Stream. The link between hyporheic invertebrates to fish production is often overlooked, likely due to hyporheic invertebrates being under represented in standard stream benthic sampling (Waters, 1993; Huryn, 1996).

Waters (1993) conducted a literature review of Allen's paradox and found that in certain streams during certain times of the year, ample invertebrate production is present to support to fish energy demand. Mead's (2007) study in Little Sandy Creek reported that

invertebrate biomass and production were highest in September. Variables such as temperature, stream community biomass, and composition vary significantly throughout the year. Respiration rates of all organisms are tightly related to temperature, which varies from 0 °C to about 25 °C in Little Sandy Creek. Without further modeling and analysis it is difficult to assess how seasonal changes alters the balance of in-stream fish respiration and invertebrate production. Collecting data on a quarterly or even biannual basis would allow students to more adequately address questions that vary on a temporal scale.

Inter-annual variability in trophic level abundance and biomass is likely to have affected the magnitude of Allen's paradox between 2011 and 2013. Fish abundance was not significantly different from 2011 to 2013 (Fig. 12). In 2013 fish mass was higher than in 2012 (Fig. 13), however invertebrate biomass and abundance was much lower (Table 8, Fig. 11), which suggests that Allen's paradox was in operation in 2013. The 2011data are more ambiguous. Invertebrate samples from 2012 had high abundances relative to 2011 while total biomass was much lower (Fig. 11 and Table 8). This indicates that the 2012 community was comprised of smaller individuals, which led to higher estimates of respiration and production. Given the similar abundance and mass of fish in 2011 and 2012, compared to the relatively low abundance and high biomass of benthic invertebrates in 2011, it is possible that Allen's paradox was operating in September of 2011.

From annual sampling of the stream by the SUNY-ESF Systems Ecology course, plus additional studies from Mead (2007), we know that fish and benthic invertebrates have inhabited Little Sandy Creek at roughly similar levels over a long-term period. However, it seems as though interannual invertebrate population changes may be large enough shift the balance of estimate invertebrate production and fish respiration. We measured benthic invertebrate biomass and respiration over a very short period of time (approximately 24-h) and we used a somewhat crude and generalized approach to estimate production (an equation from Humphreys (1979)). With a more robust dataset, stronger statistical relations could be developed and the range of model uncertainty be reduced.

4.7. A student's perspective: what did the field trip and modeling the results teach us?

The Systems Ecology course began with an invitation to the students to hypothesize about the various explanations of ecosystem processes. We learned that systems ecology was defined by Odum (1964) as the "structure and function of levels of organization beyond that of the individual and species." Specifically, it is the idea that there is "a *set of elements* connected and related in order to form a whole, whose properties are not (just) those of the component elements but are properties of the whole itself" (Peet, 1992). As developing systems thinkers, we learned to look for the connections between elements and think about how they impact ecosystem structure.

We were immersed in process of in-class literature discussions, hypothesis formation, field sampling, data analysis, deep thinking when our hypotheses were not supported, and modeling. Quantifying stocks and flows in Little Sandy Creek and conceptualizing them in a flow diagram allowed us to learn how the stream operates over much of its length, though we examined only individual components in discreet locations within the stream. This allowed us to engage in systems thinking and enhance our understanding of Little Sandy Creek, specifically how each individual component of the stream contributes to the overall function of the ecosystem – such as organic debris imported by rain storms as an energy input to detritivores and ultimately fish.

Ultimately this iterative learning experience left us with humility for the aspects of the ecosystem we didn't immediately understand and/or could not capture with our sampling techniques (e.g. nutrient dynamics) and a deeper knowledge of stream ecosystems and their complexity. This class enlightened us to the utility of formally identifying system components and interactions with observation and modeling and imbued us with a fundamentally different view of the world by learning to look for connections between system components everywhere we go.

4.8. Teaching systems ecology

We have found that students learn about systems thinking and modeling much more concretely when they observe, measure, and derive relations from a real, specific ecosystem rather than abstractions from books or equations. From our perspective, models are simplifications of complex systems that ideally capture the most important behavior of interest.

More than twenty years of data have been recorded at Little Sandy Creek, which we have come to know as a thriving ecosystem driven by allochthonous energy inputs. This has been a result of hard work, borrowed equipment, good land-owner relations, and overall extremely low cost of implementation. With such copious data archived, this Systems Ecology class can be seen as a mini Long Term Ecological Research project. It allowed for an enormous amount of student involvement as well as support by many other volunteers. The legacy of research on this stream facilitated the development of a state-of-the-art benthic invertebrate model (Mead, 2007). One future possibility is making the entire data set digitally available so that more studies can be performed on this creek.

In addition, many students have indicated that experiencing, or watching, the use of quantitative methods, including Winklers, stream morphology measurements with meter sticks and meter tapes, solarimeters, PIB invertebrate samples, electric fish sampling equipment and so on has equipped them well for later careers in ecology and environmental science. Then, of course, taking their field measurements and figuring out how to handle them in spreadsheets and computer modeling gave many a leg up for everything from field positions to environmental NGOs to faculty positions.

Our hope is that this paper will be useful as a resource for young scientists in training, and teaching tool for early career professors. One of the key components of the systems ecology course was in class discussion of papers in ecology. The seminar style exercise forced students to be critical of what they read and to think in real time. Rather than training technicians, the goal is to train thinkers. This paper reflects the thought pathways Dr. Hall encouraged students to use when thinking about ecosystems. We encourage readers of this paper to think not just about how we applied technical approaches in field methods and data analysis, but how we have defined the ecosystem in terms of functional components, and how this exercise might apply to the ecosystems that each reader studies. For those readers who are interested further conceptual development and teaching ecology using a systems approach, Jørgensen (2012) is a good source to start. For the Systems Ecology class at SUNY-ESF, Dr. Hall used a compilation of literature, including many of the works cited in this paper (e.g., Odum, 1957; Warren and Doudoroff, 1971; Hall, 1972; Hall and Day, 1977; Odum, 1983) as well as Lindeman (1942).

5. Conclusions

Our original intent for this paper was to describe a very successful (but difficult) teaching tool for systems thinking and, eventually, modeling. At the suggestion of the editor of this journal, we have written it up as a research report, and recognize that the modeling

approach used here (simple functional relations with stream depth) are simplified in order to be applied in a semester-long course. Given the lack of sampling experience of most students, we are pleased that the results are as good as they are. We are also pleased to report that whole ecosystem studies, new and exciting when the first author was a graduate student, still have a lot to offer in terms of understanding ecology. Over the last several decades there has been an apparent decline in quantitative ecosystem ecology and an emergence of more defensible sub-disciplines within ecology and academics in general. As researchers become more specialized gaps in whole system understanding will emerge, especially without encouragement of truly interdisciplinary research in academia and funding agencies. With ever increasing human impacts, and ability to monitor ecosystems, it is difficult to conduct actionable science by only looking at a few independent and response variables. Identifying problems, system boundaries, developing management strategies, and adapting them in a timely fashion, can be done only if a comprehensive systems approach is utilized. For example, warming air temperatures will potentially lead to insufficient energy for fish reproduction, which could ultimately affect the fishing industry. However, the initial impacts of warming air temperature cannot be fully understood without using a systems approach to study the problem. Our exercise taught students the process of modeling and studying a whole system. The one weekend process of collecting data in a small stream allowed students to gain a whole ecosystem perspective, and even to test hypotheses by integrating data from different components of the system. Using a systems approach can lead to many useful and unexpected research outcomes. For example, by sampling the entire ecosystem, we had sufficient data to test Allen's paradox, even though that was not the initial goal of the systems ecology field trip. Another useful outcome is that we were able to examine the influence of various forcing functions on our measured ecosystem components. We hope that this exercise will encourage other professors or high school teachers to undertake such studies with their own students, whether or not the results are eventually modeled as we have done.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2017.12.014.

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