THE EFFECTS OF SPACE AND ENERGY ON PARASITE COMMUNITIES

By

RITA L. GRUNBERG

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Peter J. Morin
And approved by

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ABSTRACT OF THE DISSERTATION

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by RITA LYNN GRUNBERG

Dissertation Director:

Dr. Peter Morin

Parasites are ubiquitous in nature, and yet their contribution to biodiversity and ecosystem processes is poorly understood. This knowledge gap has provoked a plea to include parasites into ecosystem ecology. Still, incorporating parasites into our purview of ecology is a nuanced task because it requires the careful consideration of the spatial scale of host-parasite interactions and the use of common ecological currencies. In this dissertation, I explore the effects of host community structure, spatial scales and energetics on patterns in parasite assemblages.

First, I test for concordance between the patterns of similarity of parasite assemblages, host communities and environmental factors. I used multivariate tests to assess if parasite assemblages mirror changes that occur along a stream width gradient in two riverine ecosystems. Overall, I observed no concordance between patterns in parasites and hosts assemblages suggesting that parasites and their hosts are not responding similarly to changes in environmental factors that occur along rivers.

Next, I contrast patterns in parasite body size-density relationships at different spatial scales to highlight scale sensitivity in macroecological patterns. Here, I varied the
focus of the analysis (e.g. local and global) and spatial grain of the data (e.g. parasite populations nested within their host or within an ecosystem). At local scales, I found wide variation in the relationship between parasite density and body size, while the global analysis generally fit the pattern posited by theory. However, this result was also contingent on how parasite populations were delineated. Given these results, I advocate for a more consistent use of spatial scales that reflect the processes generating the pattern being tested.

Last, I extend ideas from the metabolic theory of ecology to develop scaling relationships that explain the energetics of parasite communities nested within their hosts and ecosystems. Across host species, I found parasite community-level energetics scales allometrically with host energetics. At the ecosystem-level, wide variation in parasite productivity is better explained by host productivity rather than host biomass measures, suggesting that accounting for variation in how hosts and parasite use energy need to be considered in the future.

My research approach broadly demonstrates ways to link parasite diversity and energetics to their hosts across biological scales and provides new avenues of research to incorporate parasites into metabolic theory.
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INTRODUCTION

Parasite infections are ubiquitous in nature, making them another core component of ecosystems. Yet, the discourse in the field of parasite ecology has been limited to their detrimental effects on host individuals. As a result, the current paradigms in parasite ecology are often host centric, rarely quantifying the potential broad scale impacts of parasitism on ecosystems. While parasites are defined as having a negative impact on host individuals (Booth et al. 1993, Jensen et al. 1998, Hechinger 2010, Orlofske et al. 2013), it is clear parasitism does not occur in a bubble. Parasites are embedded in ecological food webs (Marcogliese 2002, Hernandez and Sukhdeo 2008, Lafferty et al. 2008, Anderson and Sukhdeo 2011), and consequently there are a myriad of indirect effects of parasitic infections on host communities (Wood et al. 2007, Bernot and Lamberti 2007, Mouritsen and Poulin 2009) and ecosystem processes (Sato et al. 2012, Bernot 2013, Mischler et al. 2016, Brunner et al. 2017). Therefore, understanding their diversity and their energetic relationships with their hosts at multiple biological scales is necessary to incorporate parasites into our general view of ecosystem ecology.

I. PARASITE DIVERSITY IN ECOSYSTEMS

Parasites are one of the most diverse consumer groups on the planet (Poulin and Morand 2000, Dobson et al. 2008), but their contribution to biodiversity in freshwater ecosystems is still poorly characterized. This is problematic since their diversity may in part impact the outcome of species interactions amongst hosts and other parasites (Friesen et al. 2017, Halliday et al. 2017b) and this may in turn alter ecosystem processes (Anaya-Rojas et al. 2019, Paseka and Grunberg 2019). For example, at the host
individual-level parasite co-infections can result in facilitation or reduction of other parasite species, and ultimately the outcome of these interactions is contingent on the parasite community and order of infection (Halliday et al. 2017b). Furthermore, the consequences of parasite diversity within host individuals scale up to alter populations-level transmission dynamics (Halliday et al. 2017b). Thus, understanding the factors that structure parasite communities at multiple scales will help link parasites to community and ecosystem processes.

Parasite diversity, like other forms of biological diversity, is generally influenced by heterogeneity and availability of their resources. It follows the resource for a parasite is their host, and thus, host availability (e.g. density) and host heterogeneity (e.g. richness) are likely major drivers of parasite diversity. Strong relationships between host and parasite richness are reported throughout the literature, suggesting host diversity is a major contributor to the diversity of parasites (Hechinger and Lafferty 2005, Thieltges et al. 2011, Kamiya et al. 2014, Johnson et al. 2016). This can be attributed to the postulated high level of host specificity, so the addition of more host species means more parasite species. Comparative studies also show a positive relationship between host abundance and parasite richness across hosts (Morand and Poulin 1998, Arneberg 2002, Nunn et al. 2003). Correlations between parasite diversity and host density may occur (Bell and Burt 1991) because certain parasites require a specific host density threshold to persist within host populations (Anderson and May 1978, Holt et al. 2003). Thus, higher host abundances may increase the likelihood of persistence for a wider diversity of parasites.

While quantifying coarse univariate relationships of parasite richness is informative, it is also essential to assess the multivariate relationship between host and
parasite communities. Experimental studies on plant communities show host composition is a better indicator of disease severity (analogous to parasite intensity) rather than host richness, and this is proposed to be due to variation in disease proneness among members in a community (Mitchell et al. 2002). Nonetheless, the joint effects of both host composition and their relative abundances can produce variable outcomes for parasite assemblages. Generally, variation in host community structure can result in parasite amplification or dilution within ecosystems (LoGiudice et al. 2003, Strauss et al. 2015, Halliday et al. 2017a). The factors that lead to these contrasting results are not well understood. One potential mechanism is variable levels of host specificity. A study on highly host specific parasites, showed host richness generally decreased disease severity likely due to lower abundance of other competent hosts (Mitchell et al. 2002). While another study in a similar system found evidence for disease amplification and dilution postulated to occur because of varying levels of host specificity (Halliday et al. 2017a). Clearly, the relationship between biodiversity and parasite infections is more nuanced than a correlation between host and parasite diversity.

II. METABOLIC THEORY OF ECOLOGY

The metabolic theory of ecology is a conceptual framework that aims to synthesize patterns in ecology across biological scales. It is proposed the drivers of broad scale patterns in ecology stem from fundamental physiological processes, because all organisms are ultimately constrained by the same basic chemical and physical reactions (Brown et al. 2004). As a result, metabolic theory converts ecological interactions into common currencies of mass and energy, as it focuses on the exchange of matter and
energy in biological systems (Brown et al. 2004, Sibley et al. 2012). It follows, metabolism largely determines the rate at which individuals acquire, process and cycle materials in ecosystems, and as a result is proposed to be a unifying constraint across species. Furthermore, it is rationalized that the metabolic constraints associated with being a living thing are readily applicable at the lowest level of the cell and scale up to an individual organism. It is argued these basic physiological constraints will ultimately impact ecological interactions at all scales: individual, population, community and ecosystem level, thereby unifying ecology across biological scales (Brown et al. 2004, Savage et al. 2004, Otto et al. 2007, Ings et al. 2009).

Variation in metabolic rate across species is linked to body size and temperature, making these variables powerful predictors in large-scale comparative studies. I will briefly explain the effects of body size and temperature on metabolic rate.

(1) Body size: Most relationships described in metabolic theory are described by a power function and take the form of an allometric relationship, often pertaining to the scaling of a given variable (e.g., metabolic rate, population density) with body size. In the field of biology, there are an abundance of allometric relationships that exist describing scaling relationships for numerous traits across a wide diversity of taxa. A fundamental allometric relationship in metabolic ecology is the scaling of metabolic rate with body size, and the equation is described below.

\[ R = a \times M^b \]

Where R is metabolic rate, M is body size of a species, a is a taxon specific normalization constant, and b is the scaling exponent.
It was originally proposed that the value of ‘b’ is consistent across all taxa, with normalization constants (i.e. intercepts) that vary depending on the taxonomic group being examined (Gillooly et al. 2001). Nonetheless, the specific value of the slope (b) for the scaling of whole organismal metabolic rate and body mass have been of great interest and controversy for decades (Rubner 1883, Kleiber 1932, Donhoffer 1986, Agutter and Wheatley 2004, Glazier 2005, Marquet 2005, White 2005, White and Kearney 2014). The current opinion is that metabolic rate and body size scale with an exponent of 3/4 across taxa, and this is referenced as Kleiber’s Law (Kleiber 1932, Gillooly et al. 2001, Savage et al. 2004). However, there are also those that promote a 2/3 metabolic scaling and this is hypothesized to be a product of surface area and heat loss in individuals (Rubner 1883, White and Seymour 2003, White 2005). Most models in metabolic theory rely on an assumption of 3/4 scaling for metabolic rate, due to the pervasive nature of this relationship. It is important to note there are still cases in which the 2/3 and 3/4 metabolic scaling is not supported from data, and a common metabolic scaling exponent is still frequently questioned (Glazier 2005, 2008, 2010, Reich et al. 2006, Duncan et al. 2007, Capellini et al. 2010, Kolokotrones et al. 2010).

A convincing mechanistic explanation for the 3/4 metabolic scaling lies in the structure of transport systems within an organism. It is argued that several allometric relationships in metabolic theory follow a quarter power rule, and it is posited that this is due to the presence of fractal networks that emerge across both animal (West et al. 1997) and plants (West et al. 1999). Fractal networks consist of reoccurring geometric patterns. The fractal theory of geometry proposes that since biological interactions are influenced by the rate at which resources are delivered in a system, the structure of transport vessels,
for example capillaries, should evolve to minimize the amount of energy lost within the transport system and consist of repeating fractal like patterns (West et al. 1997, 1999). Nonetheless, no single hypothesis has completely explained the mechanism behind the proposed universal scaling of metabolic rate with body size (Kooijman 1986, West et al. 1997, Kolokotrones et al. 2010).

(2) **Temperature:** Temperature affects all life and is a critical determinant of species abundance and distribution (Root 1988). Relationships in metabolic theory are better explained with the addition of a temperature term. This is because temperature directly influences enzymatic reactions and in turn biological rates, and temperature varies across broad ecological groups (e.g. ectotherm and endotherm) and geographic regions. Temperature effects can be described by the Arrhenius equation:

\[ K = A e^{-E/kT} \]

Where \( K \) is reaction constant, \( A \) is the rate constant, \( E \) is the activation energy, \( k \) is the Boltzmann’s constant, and \( T \) is the absolute temperature in Kelvin. Arrhenius plots are used to empirically derive \( E \), activation energy, for chemical reactions, in which \( A \), the rate constant, is plotted again the inverse temperature \( (1/T) \) (Figure 1A-B). Values of \( E \) tend to range from 0.6 to 0.7, with the average estimated to be 0.65 eV. This range of values for \( E \) are also affirmed within metabolic scaling studies (Gillooly et al. 2001).

The relationship between temperature and metabolic rate is robust across taxa (von Brand 1942, Gillooly et al. 2001, Clarke 2006). Therefore, the addition of a temperature term in metabolic models is essential, since temperature influences chemical reactions and whole organismal metabolic rate is the result of several biochemical
reactions occurring within an individual. The influence of temperature on metabolic rate is described by a general equation below (Gillooly et al. 2001).

\[ R = a \cdot m^b \cdot e^{-E/kT} \]

An Arrhenius plot for metabolism, which includes plotting mass corrected metabolic rate and inverse temperature (1/kT), shows a strong negative relationship, meaning as temperature increases metabolic rate concurrently increases (Figure 1A-B). The activation energy, E, which is the slope of this relationship, is reported to be 0.65 across taxa and the intercept for this relationship differs based on taxonomic group (e.g. plant, reptile, fish, amphibians) (Gillooly et al. 2001).

(3) **Size-density relationships and energetic equivalence:** Body size is a key variable in ecology and sets the pace for various life history tradeoffs: lifespan, home range, growth rate and population abundance (Jetz et al. 2004, Savage et al. 2004).

Specifically, the relationship between abundance and body size provides a critical link between individual and population level traits. It can help explain how energy flows in ecosystems (Damuth 1981, 1987), the division of resources in a communities (Taper and Marquet 1996, Ernest 2005), and biodiversity on Earth (Brown and Maurer 1986).

Damuth (1981) described the relationship between density and body size across a wide diversity of terrestrial herbivorous mammals, and reported the slope of this relationship to be -0.75, which has gained wide support and is commonly cited as Damuth’s Rule (Damuth 1987, Marquet et al. 1990, Nee et al. 1991, Cermeño et al. 2006, Hechinger et al. 2011). It is proposed that this strong negative relationship is driven by energetics, and Damuth noted this size-abundance scaling, was the inverse of Kleiber’s Law, which describes the scaling of body size and metabolic rate (Kleiber 1932, Peters 1983). It
follows when patterns describing metabolic and density scaling relationships hold true and are the inverse of one another, it gives rise to the Energetic Equivalence Rule. This rule stipulates the amount of energy a local population uses is invariant with respect to body size (Damuth 1981, 1987) (Figure 2), and this can be interpreted as there being a fixed proportion of energy a population can use.

The concept of Energetic Equivalence is quite controversial, because there are several cases in which certain taxonomic groups do not align with Damuth’s Rule and consequently the Energetic Equivalence Rule (Ward et al. 1998, Arneberg and Andersen 2003, Isaac et al. 2011, Ehnes et al. 2014). For example, Amazonian bird communities exhibit a shallow, but still negative slope, for the scaling of density and body size, and when the data is parsed out into functional guilds there is a substantial amount of variation in slopes, with some guilds showing positive size-density scaling and others showing no relationship (Russo et al. 2003). The positive within guild scaling was suspected to be a result of competitive dominance by larger species, which in turn would lower the population density of smaller species that share a common resource (Brown and Maurer 1986, Nee et al. 1991). The inconsistency of the Energetic Equivalence Rule warrants further investigation that encompasses even more species and explores alternative mechanisms driving this pattern, to evaluate the potential ecological or evolutionary factors associated with these discrepancies.

(4) Parasites and metabolic theory: Parasites provide a unique system to test hypotheses from the metabolic theory of ecology. Hosts represent tractable, well replicated ecosystems (Goater et al. 1987) because parasitic assemblages form spatially explicit populations and communities within their host (Bush et al. 1997). Therefore, at
the individual host-level it is possible to quantify the energetic inputs and outputs when treating the host as an ecosystem. This allows the approximation of the resource supply rate for parasites, something that is hard to quantify in natural systems. In addition, parasites are an extremely diverse group of consumers and present a novel system to test metabolic theory.

In the previous studies that incorporated parasites into metabolic theory, the primary focus has been to describe interspecific differences in parasite biomass or abundance at both the population (Arneberg et al. 1998, Hechinger et al. 2011) and community levels (George-Nascimento et al. 2004, Poulin and George-Nascimento 2007) to reveal energetic or spatial constraints. The assumptions and theory described in such analyses have changed as the field progressed. Initially emphasis was placed on host induced energetic constraints (George-Nascimento et al. 2004, Poulin and George-Nascimento 2007, Muñoz et al. 2015) and now it is generally accepted that parasite and host constraints need to be considered simultaneously (Hechinger 2013). Hechinger (2013) synthesized a metabolic framework to study parasite populations and communities within hosts using currencies of abundance, biomass and energy. However, this proposed framework has not been widely utilized. An issue here is potentially a lack of questions and hypotheses presented in this synthesis. Also, such metabolic scaling analyses have been restricted to describing parasites within their hosts and these studies have yet to capitalize on the multi-scale nature of the metabolic ecology.

A novel addition to the field of disease ecology is the development of disease models that are informed by paradigms in metabolic theory (Molnár et al. 2013a, 2013b). Specifically, these models incorporate the non-linear effects of temperature on parasite
biological rates and life history components, which has been a pervasive problem in climate-disease models due to the complex nature of parasite life cycles. Such models can then be used to predict changes in disease dynamics in the face of climate change (Molnár et al. 2013a, 2013b). Furthermore, metabolic theory provides general predictions on the value of temperature dependence terms and this has been proven to be useful in parametrizing data poor systems (Molnár et al. 2013b). Though, more data is required to affirm whether enzymatic activation energies used to model the effects of temperature on parasite infections actually mirror that of free living taxa (Molnár et al. 2017).

OVERVIEW OF DISSERTATION: The overarching aim of my dissertation is to quantify the role of space and energy in mediating patterns in parasite diversity and metabolic theory. (1) In my first dissertation chapter, I will use multivariate techniques to test for compositional concordance between parasites, their hosts and riverine environment. This chapter will give insight into whether parasites respond to a natural environmental gradient within a river and whether this is mediated through changes in host community structure. (2) Next, I will contrast patterns of local and global size-density relationships described in Damuth’s Rule. I aim to highlight the importance of choosing an appropriate spatial extent for an analysis to best reflect the nature of this question. (3) In my final chapter, I will extend ideas from metabolic theory to help answer a large standing question in parasite ecology: What is the energetic cost of parasitism and can we predict it across systems? I will develop scaling relationships for host and parasite energetics that can readily be applied within hosts and ecosystems.
REFERENCES:


**Figure 1A-B.** The effect of temperature on the metabolic rate of *Eustrongylides* infecting the fish *Fundulus heteroclitus* (redrawn from von Brand 1943). A. Original, untransformed data. B. Arrhenius plot, in which the inverse temperature in kelvin is plotted against the natural log transformed metabolic rate of *Eustrongylides*. The empirically derived value for E based on the Arrhenius plot is -0.59 (95% CI: -0.68, -0.58).
Figure 2. Theoretical basis for the energetic equivalence rule based on Kleiber’s law and Damuth’s Rule. When the slope describing metabolic-body size and population density-body size scaling relationships are the inverse of each other (proposed slopes: metabolism = 0.75; population density = -0.75), this will result in an invariance between population energy usage (metabolism x population density) and body size across taxa. This outcome suggests there is a fixed proportion of energy that a population can use independent of body size.
Figure 3. The relationship between body size of larval and adult *Taenia taeniaeformis* (redrawn from (von Brand and Alling 1962) under aerobic and anaerobic conditions. Note the higher intercepts in the anaerobic metabolism study.
CHAPTER 1

CONDITIONAL CONCORDANCE BETWEEN PARASITES, THEIR HOSTS AND RIVERINE ENVIRONMENT

ABSTRACT: Parasites are proposed to be useful indicators of free-living species and ecosystem change because of their co-dependent relationship with their hosts. Yet, it remains unknown whether univariate relationships between host and parasite diversity reflect changes in community structure at the level of species composition. To address this question, I tested for compositional concordance between patterns of similarity in parasites, their fish hosts and environmental factors at multiple samples collected in two river ecosystems. In both rivers, host and parasite communities were quantified in four seasons along three spatial sites representing a stream width gradient. I constructed ordinations of parasites, fish, physical stream characters and water quality variables to establish the patterns of samples in multivariate space. Then I used Procrustes rotational analysis to evaluate the similarity among these ordinations. Absence of concordance between host and parasite communities indicated that there was no pattern of similarity in host and parasite community structure. However, there was concordance between parasite community similarity patterns and the physical stream environment, but only in one river system. There was also concordance between fish communities and the physical environments in both river systems. My analysis of concordance in community similarity patterns suggests that parasites may be responding to changes in river ecosystems that result in differences in their community structure, but not in a way that generates concordance between parasites and their hosts.
INTRODUCTION

Assemblages of different organisms, such as parasites and hosts, may respond similarly to a suite of environmental factors resulting in compositional concordance among unrelated taxonomic groups. When there is concordance, a high degree of similarity in patterns of community structure emerges (e.g., concordance between benthic invertebrates and fish assemblages, Jackson and Harvey 1993), and this phenomenon of community concordance has been documented across a wide diversity of taxonomic groups inhabiting aquatic ecosystems (Jackson and Harvey 1993, Paszkowski and Tonn 2000, Backus-Freer and Pyron 2015). The high degree of concordance observed between species assemblages and their environment supports the use of biological indicators to represent ecosystem change. Nonetheless, the degree of concordance reported in studies can be variable across taxonomic groups, ecosystems and spatial scales (Paszkowski and Tonn 2000, Paavola et al. 2003, 2006). At broader geographic scales encompassing multiple ecosystems concordance was reported to be higher relative to analyses conducted on single ecosystems, suggesting local environmental filters are perhaps more taxon-specific and more variable than regional filters (Paavola et al. 2006). Groups like benthic invertebrates can also reveal scale dependent results. Some invertebrates are very sensitive to environmental gradients producing a direct relationship between their composition and local water chemistry conditions (Lammert and Allan 1999, Freund and Petty 2007), but these organisms also have higher temporal turnover and shorter generation times relative to other longer-lived organisms sampled in an ecosystem. Longer-lived organisms could result in asynchronous or no concordance with environmental factors due to differences in the time scales over which they respond to the
environment, or each other. Based on this information, Paszkowski and Tonn (2000) posited there is likely a gradient of concordance among groups based on life history traits. To further explore the utility of community concordance, it is important to extend these analyses across more taxonomic groups that vary in life history traits, and parasites and their hosts are particularly promising in this regard.

Although commonly overlooked in ecosystems, parasites are also promising candidates as biological indicators (MacKenzie 1999, Marcogliese 2005, Palm et al. 2011). Foremost, it is well established that parasite diversity and abundance are directly influenced by host diversity and community composition (Mitchell et al. 2002, Johnson et al. 2013b, Anderson and Sukhdeo 2013). Many parasites have complex life cycles, making them sensitive to changes in food web structure, because removal of a single host species within a parasite life cycle can compromise parasite persistence (Marcogliese 2002, 2005). Thus, changes in parasite communities may reflect changes in multiple trophic levels and provide a powerful measure of free-living communities and environmental change. For example, the richness and prevalence of larval trematodes infecting snail hosts were correlated with the richness and abundance of their final bird hosts (Hechinger and Lafferty 2005). Despite this strong association with bird species richness, comparable relationships between parasitic trematodes and fish richness were not detectable and trematode and small benthic invertebrate relationships were variable across systems (Hechinger et al. 2007). These contrasting results are likely a consequence of the small spatial extent of sampling used in these studies (Hechinger and Lafferty 2005, Hechinger et al. 2007), but they also hint at potential caveats associated with parasites as biological indicators for multiple host groups. Furthermore, metrics such as
species richness and abundance are relatively coarse univariate measures of communities. As such, revisiting these ideas with multivariate tests of community concordance between parasites and other trophic groups may further corroborate whether parasites are useful indicators of ecosystem change.

In this study, I test for concordance between parasites, their fish hosts and environmental variables to evaluate whether parasites respond to changes in ecosystems, and if they do so whether they mirror responses of their fish hosts. I sampled fish communities and their associated parasite fauna along a gradient of stream width to test for concordance along a natural environmental gradient in two riverine ecosystems. I quantified fish and parasite communities over the course of four seasons at three sites to encompass both spatial and temporal variation in community structure. I predict if both hosts and parasites are responding similarly to changes in the local environment, then I will find concordance between these two consumer groups (Figure 1-1). This should be evident when parasite display high levels of host specificity. However, parasites may be indirectly responding to environmental changes through other host taxa within their life cycle or exhibit low host specificity. Thus, there also is potential for patterns in parasite communities to be asynchronous with environmental parameters, and this could result in a lack of concordance between patterns in fish communities and their associated parasites.

River landscapes provide an ideal system to test for concordance among taxonomic groups because the patterns of the distribution of energy and individuals vary naturally within river systems. The river continuum concept is a framework describing differences in the structure and function of riverine systems along a spatial gradient.
ranging from headwaters to larger order streams (Vannote et al. 1980). Within this framework, it is proposed that composition of groups of consumers change along a river course because of differences in environmental conditions, including shifts in the primary energy input of river food webs from allochthonous, terrestrially derived organic matter, to more autochthonous forms such as algae and suspended organic material (Minshall et al. 1983) with increasing stream order. These changes in resource types imply that macroinvertebrate functional feeding groups will vary spatially (Cummins and Klug 1979, Rosi-marshall and Wallace 2002, Rosi-Marshall et al. 2016), with concurrent shifts in the community structure in higher-order consumers such as fish (Schlosser 1982, Goldstein and Meador 2005, Curtis et al. 2018). While it is established that the composition of certain consumer groups, such as macroinvertebrates and fish, vary with the stream order few studies have addressed this relationship with parasite species (Barger and Esch 2001, Barger 2006, Loot et al. 2007, Blasco-Costa et al. 2013). Because parasite diversity is strongly related to host diversity, changes in communities of free-living organisms occurring within rivers should also be reflected in parasite assemblages. The co-dependent nature of host-parasite interactions suggests that there should be an overall concordance between patterns in community structure of parasites and their hosts, and these shifts in communities are likely driven by differences in habitat variables that occur along stream width gradients following the river continuum concept.

METHODS

1. Field sites and sampling protocol
I sampled three 100-m long plots along a stream width gradient in both the Raritan (RR) and Passaic (PR) rivers in New Jersey, USA (Figure 1-2). The plots were chosen based on similarity of stream width between river systems, with plot 1 being the most upstream river site (width RR plot 1= 9.48m; PR plot 1= 7.12m), plot 2 midstream (RR plot 2 = 13.70m; PR plot 2= 13.00m), and plot 3 the most downstream (RR plot 3 = 21.32m; PR plot 3= 19.86m). Each 100-m plot was subdivided into five, 20-m long subplots and seining occurred continuously for 10 minutes in each subplot, starting in the most downstream subplot and making my way upstream to reduce disturbance in the water column. All fish captured during the collection period were euthanized, kept on ice in the field, and then frozen for later necropsy. I measured stream depth (m), width (m), pH, salinity (ppm) and temperature (°C) within each subplot using a multiparameter meter (Oakton PCSTestr 35) to characterize the local habitat at each sampling time point.

I sampled each plot four times over the course of a year to encompass temporal variation in communities. Raritan river samples were taken 10/28/2016, 2/19/2017, 5/21/2017, and 8/10/2017. Passaic river samples were taken 10/29/2016, 2/26/2017, 5/7/2017, and 8/2/2017. The New Jersey Department of Environmental Protection Division of Fish and Wildlife granted me permission to collect fish (scientific collecting permit #17-017).

I necropsied all fish hosts collected to quantify their macroparasite communities. Before each host necropsy, I measured standard length (distance from fish’s snout to end of their caudal peduncle) and wet weight. Then all host organs were removed and examined for endoparasites under a stereomicroscope. Fish muscle and connective tissue was also examined for parasites. After initial visual inspection of each organ, I then examined host tissue under a thick glass plate to compress the tissue and count encysted
parasites. All endoparasites were then counted and their associated infection sites within their host were recorded. Voucher parasite specimens were preserved, dehydrated in an alcohol series and stained with carmine for morphological identification. After parasite counts, all hosts were individually packaged into aluminum foil packets and oven-dried for <5 days and weighed on a microbalance (0.0001g). I removed all host reproductive tissue (eggs and gonads) and gut contents before dry weight measurements. Fish under 0.50 grams were not dissected in this study, but their individual dry weights and abundances were measured and included in the analysis to describe host biomass (g dry weight/m$^2$) and numerical density (n/m$^2$).

2. Analysis

All analyses were conducted in R v. 3.5.1 (R Core Team, 2018). I tested for compositional concordance between parasite, fish communities and their habitat using methods adapted from Paavola et al. (2006). This analysis includes generating separate ordinations for each taxonomic group (e.g., parasite and fish) and the associated habitat variables, and then using a Procrustes rotational analysis followed by PROTEST to determine similarity of ordinations (Figure 1-3). The analysis described above is a strict test for concordance. While there are other multivariate techniques that could address similar questions (e.g., constrained ordinations, canonical correspondence analysis), the proposed analysis using Procrustes does not rely on linear relationships between variables.
The following community analyses used numerical density values (individuals/m$^2$). I calculated the mean density of fishes and their parasites in each river based on the five replicate sub-plot samples for each plot (N=3) by season (N=4) combination, this yields 12 plot x season observations for each river. The first step for this analysis is to create ordinations of each dataset to establish patterns of similarity. For the parasite and fish community data, I used non-metric multidimensional scaling (NMDS) with Bray-Curtis distances and the function metaMDS in the ‘vegan’ package (Oksanen et al., 2013) to generate ordinations. Prior to this analysis, I standardized density values based on each species maximum density; so, all values are expressed as a proportion relative to their maximum. I did this to facilitate a more uniform weighting across species. The parasite NMDS was conducted at compound community level, which describes all parasites infecting all hosts within the sampling location. The compound community is represented as the mean numerical density of all parasite individuals recovered from a season x plot combination for each river. For the fish communities, I used NMDS on both numerical density and biomass (g dry weight/m$^2$) in each plot by season combination. I did this to assess if composition of host biomass, a surrogate for the distribution of energy, is more likely to result in concordance with parasite communities. Next, the river habitat data was partitioned into two general components: physical (stream width, depth, area sampled, water flow) and water quality (pH, conductivity, TDS, salinity, temperature). I then used a principal component analysis (PCA) on each environmental dataset to test for concordance with fish and parasite communities based on these two abiotic components.
Before I assessed the degree of concordance between groups, I determined whether parasite and fish communities differed across the three plots sampled along each river system. I used a permutational multivariate analysis of variance (PERMANOVA) with the *Adonis* function, on the Bray-Curtis distances to test for differences in communities across plots within each river (permutations = 999). I affirmed whether these relationships were based on both composition and abundance by rerunning the previously stated analysis using a presence-absence matrix (i.e., Jaccard distance) for both the parasite and fish data.

After creating the ordinations (e.g., biotic community data NMDS and abiotic stream data PCA), I used a Procrustes rotation analysis to determine the similarity of ordinations. The Procrustes analysis rotates, dilates and scales landmarks (in this case communities) from one ordination to superimpose it on another ordination. This method employees a least-squares criterion, minimizing the sum of squared residuals between the configurations of the two ordinations. It thus gives an indication of similarity between ordinations (SFig. 3. example high concordance and similarity; SFig. 4. example of low concordance). As a measure of the degree of concordance between ordinations, I used the $m^2$ statistic, which is the sum of squared differences between ordinations. A lower $m^2$ indicates a strong association between ordinations ($m^2$ ranges from zero to one). In the Procrustes analysis I used the abundance-based matrices, not presence-absence, for both the fish and parasite community data.

To evaluate the significance of the observed concordance, I used the function *PROTEST* which is an extension of Procrustes. This permutation test reorders samples within one configuration while maintaining the structure within the other configuration. It
then compares the original $m^2$ derived from the original two configurations and the newly calculated $m^2$ from the randomly generated-original configuration comparisons. Significance is based on the proportion of $m^2$ statistics that are smaller than or equal to the observed configurations. This analysis was conducted on pairwise comparisons of the fish, parasite and habitat (both physical and water quality) ordinations.

RESULTS

The fish data comprised a total of 1,141 individuals, representing 23 fish species across all samples. I quantified 38 unique parasite species: including 12 acanthocephalans, 6 cestodes, 8 nematodes and 12 trematodes. A summary of all fish and parasite species recorded in this study are provided in supplemental material (SFig 5 and 6). The number of fishes captured differed between rivers, 846 in the Raritan and in the Passaic 295. In the Raritan River I recovered 17 fish species and 35 parasites species, and the Passaic River 22 fish species and 29 parasite species.

Within the Raritan River the parasite communities differed in compositional abundance across plots (PERMANOVA: Pseudo-F = 1.58, DF = 2, p = 0.03, $R^2 = 0.28$), and this was also confirmed with the parasite presence-absence (hereafter abbreviated P/A) matrix (Pseudo-F = 3.52, DF = 2, p = 0.004, $R^2 = 0.47$). There was no significant difference between fish communities within the Raritan river plots when using both the numerical (Pseudo-F = 1.43, DF = 2, p = 0.12) and biomass (Pseudo-F = 1.45, DF = 2, p = 0.10) density-based matrices (SFig 1-1), however, there was a significant difference between Raritan fish communities when using the P/A matrix (Pseudo-F = 3.34, DF = 2,
p = 0.004, R² = 0.46). The PCA on Raritan River water quality variables yielded PC1 representing 70% and PC2 20% of the variance in the dataset. The physical components of Raritan River yielded PC1 representing 83% and PC2 13% of the variance.

In the Raritan River the parasite pattern in community similarity were not concordant with either metric used to describe fish community similarity patterns (PROTEST: fish abundance, p = 0.12; fish biomass, p = 0.19) and the local environment (physical, p = 0.34; water quality, p = 0.21) (Table 1-1, Figure 1-4). Yet, there was concordance between fish community similarity patterns and both physical (fish abundance, p = 0.03; fish biomass, p = 0.05) and water quality (fish abundance, p = 0.02; fish biomass, p = 0.01) stream parameters. Fish community biomass and abundance patterns were concordant (p = 0.001, SFig. 1-3).

The Passaic river parasite communities did not differ in compositional abundance among plots (PERMANOVA: Pseudo-F = 1.33, DF = 2, p = 0.14), but this finding was not corroborated with the presence-absence data (Pseudo-F = 1.76, DF = 2, p = 0.05, R² = 0.28). Nonetheless, the fish communities were different across plots and this was consistent when using all fish metrics: numerical (Pseudo-F = 1.84, DF = 2, p = 0.002, R² = 0.29) biomass (Pseudo-F = 1.95, DF = 2, p = 0.001, R² = 0.30) and P/A (Pseudo-F = 3.34, DF = 2, p = 0.002, R² = 0.43) (SFig 1-2). The multivariate analysis on Passaic River water quality variables yielded PC1 representing 67% and PC2 25% of the variance in the dataset. The physical Passaic River PCA yielded PC1 representing 79% and PC2 19% of the variance.

Patterns of concordance were variable among groups in the Passaic River (Table 1-1, Figure 1-4). There was no concordance between fish and parasite community
similarity patterns in the Passaic River (PROTEST: fish abundance, \( p = 0.44 \); fish biomass, \( p = 0.85 \)). However, there was concordance between parasite community patterns and the physical environment (\( p = 0.02 \)) but not stream water quality (\( p = 0.36 \)). Similarly, fish community abundance was concordant with the physical (\( p = 0.006 \)) but not water quality (\( p = 0.45 \)) of the river. Fish community biomass and abundance patterns were not concordant (\( p = 0.60 \), SFig. 1-4).

**DISCUSSION**

Parasites are known to be sensitive to changes in host diversity and community composition (Mitchell et al. 2002, Johnson et al. 2013a). Yet, it is unclear whether parasites and their hosts respond to differences in local environmental conditions similarly, resulting in similar patterns in community composition and thus concordance among groups. My analysis on fish and their parasites sampled along stream width gradients revealed no concordance between fish and parasite community similarity patterns. However, I did find concordance between parasites and physical stream characteristics, but this was only apparent in one of the two ecosystems sampled. In both rivers there was concordance between fish communities and the physical stream environment. These results suggest patterns in parasites community structure are not analogous to those observed in their host communities even though both may be responding to differences in environmental conditions (Figure 1-4). Taken together, this multivariate approach indicates that parasites and their host are responding independently to local environmental factors and highlight system specific differences in concordance among taxonomic groups.
My initial expectation was to observe a strong association between the structure of host and parasite communities due to potentially high levels of host specificity. Specifically, if parasites are highly specialized to infect a single host taxon there should be a high degree of similarity between host and parasite community structure. However, I detected no concordance between parasite and fish communities in both rivers. These results are unexpected, as parasites have been shown to respond strongly to changes in food webs and community structure (Marcogliese 2002, Lafferty 2012). These results suggest that parasites may still be responding to differences in host community structure, but not in a way that results in strong concordance between these two groups. This could be due to a myriad of factors. Foremost, host specificity amongst parasites infecting sympatric host species may be lower than expected. Low host specificity is commonly reported in nature (Bolek and Coggins 2003, Koehler and Poulin 2010, Lagrue et al. 2011, Friesen et al. 2017). Host sharing tends to occur in host species that are similar in their ecology and feed on similar prey or in habitat similar microhabitats (Brooks et al. 2006). Thus, if the fish parasites in the Raritan and Passaic rivers are largely generalists, then shifts in host community composition of ecologically similar species may have little to no effect on the emergent parasite community. In this scenario, host species composition is not driving variation in parasitism, but changes in functional diversity of hosts would be more likely to impact patterns in parasite diversity. On the other hand, systems exhibiting high host specificity found support for the importance of host composition in mediating parasite diversity and abundance (Mitchell et al. 2002). If such cases of low host specificity are prevalent across systems, this can complicate discussions of the relationship of host and parasite diversity, as functional host diversity, and not
necessarily taxonomic diversity, can be driving these relationships for generalist parasites.

Parasites are one of the most diverse consumer groups on the planet (Poulin and Morand 2000) and possess variable life history traits and transmission strategies. As posited by Paszkowski and Tonn (2000), life history can be mediating patterns in concordance between groups. The parasites sampled in this study primarily have complex life cycles and some are transmitted trophically, requiring the consumption of infective prey. Consequently, the variables measured directly here, fish and environmental factors, are not the only factors structuring parasite communities. The transmission of complex life cycle parasites is contingent on the presence of multiple host species interacting within a food web (Lagrué et al. 2011, Cirtwill et al. 2015), which makes them unique in their ability to be indicators of other host taxa (Hechinger and Lafferty 2005, Hechinger et al. 2007). However, this can also lead to contrasting patterns of concordance between host groups since trophically transmitted parasites are also reflecting differences in host diet (Stutz et al. 2014, Grunberg et al. 2019). For example, a parasite that first infects aquatic insects and then fish, may respond first to differences in insect communities and only later to their fish host. Sampling parasite communities infecting fish at a given time point may not reflect current differences in fish communities, but instead the communities of the host’s prey (e.g. aquatic insects). This could result in asynchronous temporal patterns of concordance between parasite and fish communities, if parasite community structure is indeed responding to multiple host groups. The role of parasite life history in generating patterns of concordance could be tested in the future by focusing
on direct life cycle and non-trophically transmitted parasites (e.g. ectoparasites), which I could not do here as I only sampled endoparasitic helminths.

Environmental conditions are also expected to impact parasite infections because their free-living infective stages are directly susceptible to abiotic factors such as pH and salinity in aquatic ecosystems (Pietrock and Marcogliese 2003, Anderson and Sukhdeo 2010). Interestingly, there was concordance between parasite communities and the physical environment (e.g. stream depth, width), but this was only observed in one of the river ecosystems. The similarity between physical river variables and patterns in parasite community structure agrees with the river continuum concept (RCC). The RCC hypothesizes that community structure of consumers change along a stream width gradient due to predictable shifts in flow regime, canopy cover and channel structure (Vannote et al. 1980). Yet, I still did not detect concordance between parasite communities and water quality (e.g. pH, salinity) in both rivers. Differences in water quality that occur within these ecosystems may not be large enough to result in concordance between patterns of similarity in parasite communities and the local environment. Also, I focused on characterizing a natural width stream gradient, and there are other factors such as historical pollution, urbanization of the surrounding environment, or heavy metals that are known to structure parasite communities (Blanar et al. 2011). It is important to note that relationships between parasite and water quality variables may be scale dependent. The degree of concordance has been shown to be more robust at broader geographic scales, where concordance within a local drainage system was weaker than regional patterns (Paavola et al. 2006).
The lack of concordance shown in these river systems has implications for the use of parasites as indicators of changes in host community structure and/or environmental factors. Prior work has advocated for the use of parasites as indicators of free-living diversity, host abundance and overall ecosystem health (Huspeni et al. 2005, Marcogliese 2005, Byers et al. 2011). Support for this notion is drawn by correlations between host and parasite richness (Hechinger et al. 2007, Palm et al. 2011) and by comparison of parasite community structure of a single host taxon across disturbed and undisturbed sites (Dutton and Barger 2017). Indeed, these studies show parasites are responding to changes in host richness or ecosystem properties, but whether they correspond simultaneously to changes in host and habitat structure remains unclear. Here, I detected no patterns of concordance between parasite and fish community structure, although the fish communities demonstrated concordance with the river environmental gradient. Interactions among trophic groups and the abiotic environment govern the formation of parasite communities. However, I could only quantify a subset of those interactions. As characterizing an entire ecosystem is not feasible, a more realistic goal is to identify a more consistent subset of variables (e.g., parasite, fish, macroinvertebrates communities) that inform patterns in ecosystem change. The value of parasites as biological indicators consequently remains uncertain; according to my data, the utility of this method could be system-specific, urging caution in the broad implementation of this approach as a means of assessing biodiversity and ecosystem health.
REFERENCES:


Table 1-1. Results from pairwise Procrustes analyses on ordinations of habitat (partitioned into physical and water quality variables), fish and parasite community abundance data. Values in the table are $m^2$ (sum of squares) where lower values indicate stronger associations and bolded values represent significant concordance between ordinations based on PROTEST (permutations = 999).

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<tr>
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<th>Raritan River</th>
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<th>Passaic River</th>
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<td>Water quality</td>
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<td>Biomass</td>
<td>0.665</td>
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<tr>
<td>Parasite</td>
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<td>0.782</td>
<td>0.722</td>
<td>0.760</td>
</tr>
</tbody>
</table>

### Raritan River
- Physical: 0.602
- Water quality: 0.565
- Abundance: 0.602
- Biomass: 0.665
- Parasite: 0.828

### Passaic River
- Physical: 0.508
- Water quality: 0.864
- Abundance: 0.508
- Biomass: 0.915
- Parasite: 0.607
Figure 1-1. Hypothetical compositional concordance between host (triangle) and parasite (circle) assemblages along an environmental gradient: colored shapes represent different species nested within an assemblage (different assemblages are delineated by larger greyscale shapes, representing different sites). The host assemblage shows clear separation between sites (NMDS graphic). Hypothetical patterns in parasite community similarity that may occur are as follows: (1) parasite communities are highly similar to their hosts resulting in high concordance, (2) homogenization of parasite communities resulting in no concordance with host assemblages, and (3) differences in dissimilarity patterns (black and white sites are more similar) resulting in no concordance with host assemblages.
Figure 1-2. Map of Raritan (blue) and Passaic (yellow) river collection sites in New Jersey.
Figure 1-3. Workflow for statistical analysis of concordance between biotic and abiotic variables. Note Procrustes and PROTEST are performed on pairwise comparison of ordinations.
**Figure 1-4.** Graphical summary of concordance results on pairwise Procrustes rotational analysis on habitat, fish and parasite communities. Green check marks indicate when concordance was found within a single river ecosystem and red crossed circled indicate when no concordance was detected. Results are based on PROTEST. Concordance between hosts and their environment (either chemical or physical) was reported in both rivers. However, concordance between parasite communities and the environment occurred only within the Passaic River. While there was no concordance between host and parasites in both rivers.
SFigure 1-1. Series of ordinations of habitat, fish and parasite community data from the Raritan river. The corresponding stress values for the NMDS are as follows: fish density (0.100), fish biomass (0.125) and parasite (0.162).
**Figure 1-2.** Series of ordinations of habitat, fish and parasite community data from the Passaic river. The corresponding stress values for the NMDS are as follows: fish density (0.144), fish biomass (0.126) and parasite (0.129).
SFigure 1-3. Example of high degree of concordance shown between host communities based on their biomass and their abundance within the Raritan river (PROTEST: $r^2 = 0.161, p = 0.001$). Points drawn are the coordinates of the NMDS of host communities based on abundance and blue arrows indicate how those points need to be scaled, dilated and rotated to fit the NMDS configuration of host communities based on biomass values.
SFigure 1-4. Example of low degree of concordance shown between host communities based on biomass and abundance within the Passaic river (PROTEST: $m^2 = 0.892$, $p = 0.57$). Points drawn are the coordinates of the NMDS of host communities based on abundance and blue arrows indicate how those points need to be scaled, dilated and rotated to fit the NMDS configuration of host communities based on biomass values.
**SFigure 1-5.** Presence absence matrix for fish species captured in Passaic and Raritan sites. Black indicates presence and light grey absence.


**Figure 1-6.** Presence absence matrix for parasite species recovered from fish located in Passaic and Raritan sites. Black indicates presence and light grey absence.
CHAPTER 2

ALLOMETRIC SCALING IN PARASITE POPULATIONS: LOCAL AND GLOBAL PATTERNS

ABSTRACT: Damuth’s Rule describes the negative scaling of population density with body size, and postulates that a common slope can describe this relationship across taxa. Although this ‘rule’ has gained support in many free-living taxa, results based on parasite species are variable. I contend many of these discrepancies can be attributed to differences in the spatial scale used in the analysis. Macroecological patterns such as Damuth’s Rule should be fitted with macroecological data, and when investigations occur at local scales these patterns often do not fit the general rule. Furthermore, parasite populations are delineated differently, sometimes within their host and sometimes within ecosystems, representing different spatial grains. Here, I show the effects of spatial scale (spatial grain and focus) on body size-density relationships in parasites when representing parasites within their hosts and within ecosystems and using local (e.g. single ecosystem) and global (e.g. across multiple ecosystems) data. I found that scaling exponents varied locally and that the relative importance of parasite body size varied considerably. After aggregating the data into a global dataset, I found a strong relationship with parasite body size and population density that conformed with Damuth’s Rule. However, this pattern was only apparent when delineating parasites nested within ecosystems. At the within host-level, there was no significant relationship between parasite body size and density. These analyses highlight discrepancies that may emerge when comparing analyses using local and global data and when delineating parasite populations. Thus, when trying to fit
parasites into macroecological patterns, the data used needs to reflect the spatial scale of the question and I suggest a more consistent path forward when incorporating parasites into comparative analyses.

INTRODUCTION

The relationship between abundance and body size provides a critical link between individual-level and population-level traits in ecology. Damuth’s Rule states that a slope of -0.75 describes the size-density scaling relationship across terrestrial mammals (Damuth 1981). The generality of this pattern has been extended by inclusion of a wide diversity of taxa across ecosystems (Damuth 1987, Marquet et al. 1990, Nee et al. 1991, Cermeño et al. 2006, Hechinger et al. 2011a). The pervasiveness of Damuth’s Rule led to investigation of the biological bases underpinning this ‘rule’ and the processes generating this ubiquitous pattern (Brown et al. 2004, White et al. 2007). It is generally argued that the emergence of some broad scale macroecological patterns such as Damuth’s Rule is a product of fundamental constraints operating on all organisms, such as energetic metabolism (Damuth 1981, Brown et al. 2004) and the basic structure of biological systems (West et al. 1997, 1999). The allometric scaling of metabolic rate and body size across taxa is the foundation of the metabolic theory of ecology, a framework that unifies patterns across scales from individuals to ecosystems and is founded on the basis of energetic constraints (Brown et al. 2004).

The negative relationship between the population density of a species and its body size is an enduring tenet in ecology, but support for this pattern is inconsistent in the
parasite ecology literature. The concordance of parasitic organisms with the theory described in Damuth’s Rule has been investigated across a diversity of parasite taxa (Arneberg et al. 1998, George-Nascimento et al. 2004, Poulin et al. 2008, Hechinger et al. 2011a, Muñoz et al. 2015). Nevertheless, based on these current studies there is no real consensus on how parasites fit into Damuth’s Rule, nor the ecological and evolutionary factors responsible for the apparent diversity of size-density relationships reported. Some studies are consistent with Damuth’s Rule, and in an ecosystem-wide analysis of the population densities of parasites, invertebrates, fish, and birds all species could be described by a single allometric equation relating body size to density, and the scaling exponent for this relationship was -0.75 after correcting for temperature and trophic level (Hechinger et al. 2011a). Studies that focused only on parasite communities within their host also fit into this theory, supporting a potential energetic equivalence for parasitic species at the community scale (George-Nascimento et al. 2004). However, there are also several cases in which parasites deviate significantly from predictions based on Damuth’s Rule (Arneberg et al. 1998, Lagrue et al. 2015, Muñoz et al. 2015). While the general negative relationship often holds true, the scaling exponents can differ significantly depending on study system. For example, Arneberg et al. (1998) report a negative relationship between parasite intensity (surrogate for population density) and parasite body size across taxa, but the scaling exponent was strikingly shallower than expected. Furthermore, there are cases where no relationship (Sasal et al. 1999) and even positive size-density scaling relationships are reported in parasitic species (Poulin 1999). Reported departures from Damuth’s Rule are not unusual, and have also been observed in several free-living systems (Marquet et al. 1990, Gaston et al. 1997, Smallwood 2001,
Generally, deviations from such macroecological patterns can be a product of sampling extent, phylogeny and spatial scale of the analysis (Hayward et al. 2010, Isaac et al. 2013, Pedersen et al. 2017).

Two apparent issues arise when comparing results from previous parasite population scaling analyses: (1) the definition of a parasite population is not consistent across studies and (2) the spatial extent of studies vary considerably (reviewed further in Table 2-1). As a result, this makes comparisons across studies trivial, and it remains unclear as to whether parasites are not fitting into Damuth’s Rule because of the parasitic lifestyle or methodological issues.

(1) **Spatial grain.** The metrics used to describe parasite population density are not consistent across studies. For example, density is described as mean intensity of parasites (Arneberg et al. 1998), number of parasites per unit (usually grams or volume) of host (George-Nascimento et al. 2004, Muñoz et al. 2015), or the total parasites per hectare or meter within an ecosystem sampled (Hechinger et al. 2011, Lagrue et al. 2015). A traditional view of a parasite population is nested within an individual host, and this provides clear-cut boundaries to census parasitic populations. Nonetheless, this does not allow for direct comparisons to their free-living counterparts, which is why some studies represent populations in a conventional sampling unit of square meters or hectares of an ecosystem. While each measure of a parasite population has its merits, they represent fundamentally different spatial scales of a host-parasite interaction.

(2) **Focus.** Debates over proposed universal patterns in metabolic theory are frequent, but the merits of some of these criticisms are masked by fundamental differences of scale (Loeuille and Loreau 2006, White et al. 2007). Macroecological
questions should be addressed using macroecological data, spanning a large diversity of taxa from various geographic regions (Damuth 1981, Marquet et al. 1990). Many of these analyses on parasite populations use local data from a single ecosystem to address macroecological questions (Hechinger et al. 2011a, Lagrue et al. 2015). At the local scale, these patterns predicted by metabolic theory are not the most relevant expectation. Consequently, the apparent diversity of patterns, specifically the scaling exponents, across ecosystems is not surprising. Overall, this makes interpreting results from past size-density relationships on parasites problematic because these analyses are conducted at either local or global scales (White et al. 2007).

The aim of my study is to highlight the influence of spatial scales, in relation to both spatial grain and focus, in macroecological patterns in parasite ecology, and to provide a framework for future studies on the macroecology of parasites. In this study, I describe the scaling between parasite population density and parasite body size by using two spatial grains to quantify parasite populations: within host and within ecosystem density. I also extend this to explore the influence of focus using local and global datasets when describing parasite size-density relationships. To do this, I constructed scaling relationships at both the local (data from one ecosystem) and global scale (data aggregated across ecosystems). These two general issues of scale bring into question whether parasites are not following ecological ‘rules’ merely because the wrong spatial scale is being used to answer a macroecological question.

METHODS
I used field-collected data from two rivers sampled in Chapter 1 (Raritan and Passaic Rivers), along with the following datasets: Paseka (2017) and Lagrue et al. (2015). This yielded data from 7 freshwater ecosystems: Raritan, Passaic and Mullica Rivers (Paseka 2017) from New Jersey, and Tomahawk, Hayes, Waihola and Tuakitoto Lakes from New Zealand (Lagrue et al. 2015). I used these datasets because they provided information on both parasite intensity (# parasites/host) and parasite density per unit of aquatic ecosystem sampled. This was necessary for this study, because I aimed to compare the effects of how parasite populations are delineated within a dataset on observed size-density patterns. Thus, parasite population densities are represented using two spatial grains: **within hosts** (# parasites/host) and **within ecosystems** (# parasites/m² of aquatic ecosystem sampled). Consequently, the within host infection intensity describes a discrete parasite population, while the within ecosystem measurement reflects a portion of the metapopulation of parasites (Figure 2-1).

All analyses were conducted in R v. 3.5.1 (R Core Team, 2018). I analyzed relationships between parasite density and parasite body size using multiple regressions on log-transformed data. I refer to different levels of the focus of analysis using the terms **local analyses** when comparing size-density relationships within a single ecosystem and **global analyses** when comparing size-density relationships with data aggregated across multiple ecosystems. For the local analysis, I constructed ecosystem specific scaling relationships using maximum observed parasite density data from one of the seven aquatic ecosystems. I then visually inspected whether the mass range (maximum/minimum body size) and density range (maximum/minimum population density) influenced scaling exponents. This is an important step because scaling
relationships are sensitive to mass range (Sibley et al. 2011). Then I aggregated data across all seven ecosystems to create a ‘global’ analysis based on multiple ecosystems. In the global dataset I used the maximum parasite density observed across all ecosystems for a given parasite species (e.g., cross-system maximum), and the size-density relationship was then analyzed across all parasite species inhabiting all seven ecosystems.

I assessed the scaling relationship of parasite population density to parasite body size and their host resource using the general form of Eqn. 1. A host resource term was included to account for differences in resources (Hechinger 2013).

\[ N_p \propto M_p \times R_h \quad \text{(Eqn. 1)} \]

Here \( M \) is the average body size, \( N \) in the population density, \( R \) is the resource pool, and subscripts \( p \) and \( h \) denote parasite and host, respectively.

Variation in temperature can explain variation in abundance, metabolism and other biological processes (Gillooly et al. 2001, 2005, Hechinger et al. 2011a). Within ecosystems, temperature does not vary much but across the seven ecosystems used in the global comparison there can be considerable differences in temperature between the New Jersey and New Zealand samples. To account for this, I incorporated variation in temperature by adding a temperature dependence (e.g. Arrhenius function) term \((E/kT)\) to my general model (Eqn. 2).

\[ N_p \propto M_p \times R_h \times e^{-E/kT} \quad \text{(Eqn. 2)} \]

Where \( E \) is the activation energy, \( k \) is the Boltzmann’s constant \((8.62 \times 10^{-5} \text{ eV} \text{K}^{-1})\), and \( T \) is the absolute temperature in Kelvin (Gillooly et al. 2001, Brown et al. 2004). All
hosts sampled were ectothermic fish, so I assumed host body temperature was that of the average water temperature reported within that site.

The host resource term (R) may differ when delineating parasites within their hosts or within ecosystems, because the spatial grain of the resource pool changes. I chose to represent host resource (R) as the average host body size ($M_h$) for the within host model. For the within ecosystem model, the resource is represented as host biomass density ($B_h$). This results in Eqn. 3 for the within host model, where parasite density is expected to scale negatively with parasite body size (expected slope = -0.75) and positively with host body size (expected slope = 0.25) (Hechinger 2013).

$$N_p (within_{host}) \propto M_p^{-0.75} \times M_h^{0.25} \times e^{-E/kt} \quad (Eqn \ 3.)$$

In Eqn. 4, the within ecosystem model, parasite density is expected to also scale negatively with parasite body size (expected slope = -0.75) and positively with host biomass density (expected slope = 0.75) (Carbone and Gittleman 2002). Note that the expectation for the host resource term (R) differs between Eqn. 3 and 4.

$$N_p (within_{ecosystem}) \propto M_p^{-0.75} \times B_h^{0.75} \times e^{-E/kt} \quad (Eqn \ 4.)$$

To reflect parasites within the ecosystems sampled, $N_p$ is represent as $\frac{N_p}{m^2}$ and R is replaced with B, which is biomass density (g/m$^2$).

To control for phylogenetic non-independence I used a phylogenetic generalized least squares (PGLS) model. Phylogenetic effects are incorporated by the construction of the expected phylogenetic variance-covariance matrix, which was established assuming a
Brownian motion of trait evolution. To do this, a phylogeny and associated tree of all parasite species sampled was created with data from the Open Tree of Life (http://www.opentreeoflife.org) using the r package ‘rotl’ (Michonneau et al. 2016). I set branch lengths equal to 1 with the package ‘ape’ (Paradis et al. 2004), because the Open Tree of Life does not report branch lengths and parasites phylogenies are not well resolved. Finally, PGLS models were implemented using the package ‘nlme’ (Pinheiro et al. 2014). To assess the importance of phylogenetic effects I compared models with a fixed $\lambda$ at 0 (comparable to OLS model) and 1 (strong phylogenetic signal) and used likelihood ratio tests to compare the fit of the models. I also used maximum likelihood to estimate the value of $\lambda$ in PGLS models.

RESULTS

Spatial scale, whether it pertained to focus: local (within a single ecosystem) or global analysis (across multiple ecosystems) and/or spatial grain: delineating parasite populations, influenced the observed slope values and whether parasites fit Damuth’s Rule (Figure 2-3 and 2-4). When analysing local size-density data within a single ecosystem, I found variable scaling exponents for each ecosystem. Also, the relative importance of parasite body size and host resources differed when using different metrics of parasite population density (Figure 2-3 and 2-4). Nevertheless, the global analysis showed some support for Damuth’s Rule, but this was ultimately contingent again on how the spatial grain used to define parasite populations (Figure 2-5).
1. Local scale analysis

**Parasite populations within ecosystems:** When parasite populations are delineated within their respective aquatic habitat (n/m²), parasite body size was a significant predictor variable in five of the seven ecosystems at the local scale. All significant parasite exponents were negative, but their values varied across systems (Sup. Table 2-1). Moreover, all values tended to be steeper than predicted by Damuth’s Rule, although their associated 95% CIs did overlap with -0.75: Tuakitoto (slope = -1.31 (95% CI: -1.87, -0.75)), Waihola (slope = -1.00 (95% CI: -1.55, -0.45)), Hayes (slope = -0.99 (CI -1.43, -0.54)), Tomahawk (slope = -1.23 (CI -2.16, -0.30)) and Mullica (slope = -0.88 (CI -1.64, -0.07)). Parasite body size was not significantly related to parasite density in both the Raritan (p=0.20) and Passaic (p=0.18) Rivers. Host biomass density was a significant predictor of parasite density in four of the seven ecosystems: Tuakitoto (slope = 0.77 (95% CI: 0.09, 1.46)), Waihola (slope = 0.82 (95% CI: 0.07, 1.56)), Raritan (slope = 0.81 (95% CI: 0.39, 1.23)), and Passaic(slope = 0.40 (95% CI: 0.02, 0.77)). However, in Hayes (p=0.14), Tomahawk (p=0.17) and the Mullica (p=0.77) host biomass density was not statistically significant.

**Parasite populations within hosts:** Generally, in the local scale analysis, the parasite within host models (# parasite/host) were poorer fits relative to the models that quantified parasites within ecosystems (individuals/m²) (Sup Table 2-2). Surprisingly, the only ecosystem with a significant relationship between parasite body size and parasite abundance within their host was the Mullica river (slope = -0.94 (95% CI: -1.80, -0.07)). Otherwise, parasite body size was not a significant predictor of parasite abundance within hosts. Two ecosystems had a significant relationship between parasite abundance and
host body mass: Tuakitoto (slope = 0.22 (95% CI: 0.06, 0.39)) and Hayes (slope = 0.25, (95% CI: 0.05, 0.45)). Again, all other ecosystems showed no clear relationship with host body mass. Consequently, neither host or parasite body size explained variation in parasite within host density in the following systems: Waihola, Tomahawk, Raritan and Passaic.

2. Global scale analysis

In both global models, temperature was not significant, so it was excluded from subsequent models (p = 0.9 parasites within ecosystems; p = 0.13 parasites within host). There was also no effect of parasite phylogeny on these results (Sub. Table 2-3, 2-4). The outcomes of the global model (e.g., analysis occurring across ecosystems) differed when delineating parasite populations either within ecosystems or within hosts. Nonetheless, relationships between parasite density and both host resources and parasite body size were observed.

**Parasite populations within ecosystems:** When considering parasite density nested within ecosystems, parasite population density scaled negatively with parasite body size and positively with host biomass density (full model: p <0.0001, R² = 0.39) (Figure 2-5A-B). This yielded the following equation:

\[
N_p \propto M_p^{-0.66} \times B_h^{0.66}
\]

Specifically, the scaling exponent for parasite body (\(M_p\)) size overlapped with the expected value from Damuth’s Rule (p = slope = -0.66 (95% CI: -0.88, -0.43)). The
scaling exponent associated with host biomass density \((B_h)\) was the inverse of the parasite body size relationship (slope = 0.66 (95% CI: 0.35, 0.96)) and overlapped with the hypothesized value (Carbone and Gittleman 2002).

**Parasite populations within hosts:** For the within host model, parasite abundance was not related to parasite body size, but it was positively related to host body size (full model: \(p = 0.001, R^2 = 0.16\) (Figure 2-5C-D).

\[
N_p(\text{within host}) \propto M_h^{0.33}
\]

The parasite body size exponent \((M_p)\) did not significantly differ from 0 \((p = 0.17, \text{slope} = -0.16 (95\% \text{ CI: } -0.39, 0.07))\). However, the host body size scaling exponent \((M_h)\) overlapped with the predicted value from Hechinger (2013) \((p = 0.003, \text{slope} = 0.33 (95\% \text{ CI: } 0.15, 0.50))\).

**DISCUSSION**

Despite its claim to generality, metabolic theory has been subject to intense scrutiny due to increasing numbers of substantial deviations from its predictions (Heusner 1991, Capellini et al. 2010, Kolokotrones et al. 2010). For example, at level of a specific taxon and even between different body size ranges within taxonomic groups, there is great deal of variation in estimated scaling relationships (Hayssen and Lacy 1985, Elgar and Harvey 1987). Parasites appear to be no exception to this pattern. I found a wide diversity of scaling relationships between parasite body size and population density. Yet, this wide variation among ecosystems is not surprising because I was using local
data to fit what is essentially a large scale macroecological pattern. Still, in many cases I failed to find statistically significant relationships with parasite body size. Nevertheless, when conducting my analysis at the larger ‘global’ scale I did observe a relationship between parasite body size and population density. Notably, the slope of this relationship and the importance of parasite body size was contingent on how parasite populations were delineated. I contend that the expectations for how parasites are predicted to conform to macroecological rules will depend on the type of data used in the analysis, and emphasis on spatial grain and focus of the analysis used should be discussed. Importantly, the spatial scale of the data used needs to reflect the spatial scale of the processes proposed to generate that pattern.

In my analysis describing local size-density relationships, I compared the densities of parasite species within a single ecosystem. This is a relatively narrow focus of investigation. Alas, it might be expected that the concepts described in Damuth’s Rule should be readily applicable at the local scale. However, this is usually not the case. The scaling exponents from local size-density relationships tend to be a great deal shallower than the predicted value from Damuth’s Rule, and body size explains less variation in population density locally (Blackburn and Gaston 1997). Generally, these discrepancies in local patterns may be due to changes in the relative importance of certain interactions such as interspecific competition (Nee et al. 1991) and resource heterogeneity (Ernest 2005). Other important local factors specific to parasitic organisms are host immunity and parasite transmission. For example, there are cases where the host’s immune response is able to suppress parasite growth, mediating its relationship with parasite body size directly, and also a strong immune response can reduce parasite population sizes.
through parasite mortality (Weber et al. 2017). Variation in host immune function can be location specific (Bolnick et al. 2016, Weber et al. 2017) and thus the relative importance of immunity in impacting parasite size-density patterns may vary considerably across ecosystems. Additionally, the transmission biology of parasites may be a dominant factor regulating their population density. Several parasite species used in this study possess complex life cycles. Parasites have presumably evolved complex life cycles to facilitate transmission and increase their overall fitness (Parker et al. 2003). However, complex life cycles also limit parasite populations because they incorporate multiple host species inhabiting different ecosystems and trophic levels (Thompson et al. 2005, Benesh et al. 2014, Poulin and Lagrue 2015). The difficulties of transmission are often reflected in the smaller population sizes of parasites as they travel up the food chain to their final hosts (Poulin and Lagrue 2015). This suggests that constraints postulated to occur based on Damuth’s rule may not be applicable to parasites at local scales. Further, alternate factors should be considered when looking at this pattern at small spatial scales.

At broader spatial scales, the strong negative relationship between population density and body size is proposed to be a product of pervasive energetic constraints acting upon all species (Damuth 1981, Brown et al. 2004). Global size density relationships are proposed to be robust to the effects of local factors (e.g. host immunity and parasite transmission), which may mask evidence for energetic constraints. This is because the data are aggregated at much broader spatio-temporal scales in global analyses, reducing the importance of local interactions. Furthermore, the metabolic theory of ecology assumes steady state and globally aggregated data are more likely to meet this assumption. As expected, in my global analysis parasites did align with some
predictions from Damuth’ Rule. When parasite density was represented within ecosystems (n/m²), parasite population density scaled negative with parasite body size and positively with host biomass density. Both exponents overlapped with their hypothesized values. This finding agrees with other analyses that represented parasite density within ecosystems (Hechinger et al. 2011a). However, the prior analysis on this topic (Hechinger et al. 2011a) accounted for differences in resources by correcting for parasite trophic level rather than host biomass density. This can result in error in the analysis. It is still not clear what trophic level parasites reside on (Sabadel et al. 2018), so this assumption needs to be further validated. Therefore, I suggest using a more precise measure of resource availability, via host metrics (e.g., host body size or biomass density), should be utilized in the future.

It is also important to note that in the original synthesis of Damuth’s Rule, variation in resource availability across taxa were not incorporated. There are recent studies describing the scaling of predator density with their body sizes in which they did account for differences in resources through incorporating their prey density (Carbone and Gittleman 2002, Carbone et al. 2007). In this case, strong relationships were observed but this relationship was isometric (i.e. slope = 1), not allometric as shown in my study. However, when excluding prey density from their model, the scaling of predator density and predator body size did fit Damuth’s predictions (Carbone and Gittleman 2002). Clearly, accounting for resource availability should be further examined to determine its broader significance in these ecological patterns. Fortunately, host-parasite interactions provide a tractable system to test such hypotheses, because variation in resources are easily quantified through measurements of host body size. Thus, there is
great promise in the utility of parasites to test macroecology patterns and this avenue should be further pursued.

Ultimately, the decision on how to delineate and quantify a parasite population clearly influences the outcome of these analyses. For example, in the global analysis the relationship observed for the within ecosystem model was not equivalent to the model that represented parasites within hosts. Surprisingly, parasite body size was not a useful predictor of parasite abundance within their hosts, while host body size did explain some variation in parasite populations. This general finding was consistent when analysing data at the local scale; most local models did not find support for parasite body size as a significant predictor of parasite abundance within their host. Contrary to my results, another analysis that assessed the importance of both parasite and host body size on parasite abundance within their host did show parasite body size to be a significant predictor in their model (Hechinger 2013). However, they represented parasite density differently (e.g., n/gram of host) and this assumption may have influenced their results due to spurious correlations. Nonetheless, these contrasting results are puzzling. A host is effectively a stage specific habitat for its parasites, and I expected to find stronger relationships at this spatial grain of investigation because parasites are directly taking resources for their host.

A potential explanation for this lack of relationship with parasite body size maybe a product of energy limitation within a host. Parasites are unique in the fact that they are relatively small, and are capable of feeding on larger sized organisms, and thus invert traditional consumer-resource body size ratios (Hechinger et al. 2011a). Also, parasites can infect top consumers in a food web, meaning they feed on the highest trophic levels,
leading to higher assimilation efficiencies (Kozlovsky 1968, Sanders et al. 2016). Given these basic attributes of parasite biology, I predicted much higher abundances of parasites than I observed. Thus, I propose this absence of a pattern between parasite population abundance and parasite body size within their host occurs because resource or energetic limitations are not a driving force structuring parasite population at this level. Notably, smaller sized parasites did not occur at higher densities relative to larger parasites in same-sized hosts in some systems, supporting the view of constraint by factors other than their energetic metabolism.

Application of macroecological analyses across a large diversity of parasitic taxa and along a large geographic range is necessary to synthesize the factors constraining parasite species. The lack of robust patterns between parasite density and parasite body size are likely related to the spatial scales used across studies. Yet, valid comparisons are challenging because prior investigations lack consistency. I advocate for a consistent framework and methodology when fitting parasites into macroecological patterns. Foremost, it is clear that global data should be used to answer global questions. My analysis contrasting local and global analyses revealed a diversity of weak patterns at the local scale, but stronger patterns emerged when using global data. Moreover, the definition of a parasite assemblage should also be evaluated critically prior to the analysis and reflect an appropriate spatial grain for the question. This issue is less clear cut and should reflect the current goal of the study. Regardless, it should be acknowledged that the definition of a parasite assemblage may influence the pattern being described and subsequently the expectations for the relationship. Lastly, accounting for differences in host resources explains more variation in population density across parasitic taxa and
should be incorporated. Given the sensitivity of these analyses, it seems necessary to readdress the notion whether parasites follow ecological rules with transparent and consistent metrics.
REFERENCES:


Paseka, R. E. 2017. Low parasite biomass in oligotrophic streams differs from previous estimates in aquatic ecosystems. - Freshw. Sci. in press.


Table 2-1. Summary of size density relationships reported in the literature. Many of these papers were not explicitly testing DR, so they did not report the slope of the relationship and instead I only report the direction of the relationship and $R^2$ value.

<table>
<thead>
<tr>
<th>Study</th>
<th>Relationship</th>
<th>$R^2$</th>
<th>Parasite</th>
<th>Metric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arneberg et al., 1998</td>
<td>Neg.</td>
<td>0.30</td>
<td>Nematodes</td>
<td>Intensity</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Trem, Acanths</td>
<td></td>
</tr>
<tr>
<td>Poulin, 1999</td>
<td>Neg.</td>
<td>0.51</td>
<td></td>
<td>Intensity</td>
</tr>
<tr>
<td>Morand and Poulin, 2002</td>
<td>Neg.</td>
<td>0.17</td>
<td>Nematode n/g host</td>
<td></td>
</tr>
<tr>
<td>Hechinger et al., 2011</td>
<td>Neg.</td>
<td>0.71, 0.80*</td>
<td>Endo n/ hectare</td>
<td></td>
</tr>
<tr>
<td>Lagreue et al., 2015</td>
<td>Neg.</td>
<td>0.34</td>
<td>Endo</td>
<td>n/m$^2$</td>
</tr>
<tr>
<td>Randhawa and Poulin, 2009</td>
<td>Neg.</td>
<td>0.28</td>
<td>Cestodes</td>
<td>Intensity</td>
</tr>
<tr>
<td>Sasal et al., 1999</td>
<td>NR</td>
<td>NA</td>
<td>Monogenean</td>
<td>Prevalence</td>
</tr>
<tr>
<td>Morand and Guegan, 2000</td>
<td>NA</td>
<td>NA</td>
<td>Nematode</td>
<td>Abundance</td>
</tr>
<tr>
<td>Poulin, 1999</td>
<td>Pos.</td>
<td>0.41</td>
<td>Copepods</td>
<td>Intensity</td>
</tr>
<tr>
<td>George-Nascimento et al., 2004</td>
<td>Pos.</td>
<td>0.09</td>
<td>Endo</td>
<td>n/vol host</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poulin and Justine, 2008</td>
<td>Pos. &amp; NR</td>
<td>0.51, 0.40</td>
<td>Monogenean</td>
<td>Intensity</td>
</tr>
</tbody>
</table>

NR = no significant relationship reported; * $R^2$ value derived from model including both free-living and parasitic organisms
Figure 2-1. Differences in delineating parasite populations can result in different measurements of parasite density.
**Figure 2-2.** Hypothetical expectations of size-density relationships using local and global data. When an analysis occurs at a local scale, within a single ecosystem, body size is expected to explain less variation in population density. Conversely, a global analysis should yield a steeper slope and body size explains a large amount of variation in population density across species.
Figure 2-3. Scaling exponents associated with parasite (A) and host body (B) size and their corresponding 95% confidence intervals. These linear models describe the relationship between parasite density within an ecosystem (n/m²) and parasite body size and host biomass density (g/m²). Red dashed line is drawn at -0.75 for the parasite and 0.75 for host exponent, which are the hypothesized values. Solid line is placed at zero, if the 95% CI overlaps with the solid line, then this exponent does not differ from zero.
Figure 2-4. Scaling exponents associated with parasite (A) and host body (B) size and their corresponding 95% confidence intervals. These linear models describe the relationship between parasite abundance within their host (e.g. intensity) and parasite and host body size. Red dashed line is drawn at -0.75 for the parasite and – 0.25 for host exponent, which are the hypothesized values. Solid line is placed at zero, if the 95% CI overlaps with the solid line, then this exponent does not differ from zero.
Figure 2-5: ‘Global’ size density relationships for maximum parasite density and parasite and host body mass from data aggregated across New Zealand and New Jersey freshwater ecosystems. Plotted are partial residuals after accounting for the effects of each predictor variable. A and B are models based off parasite density within ecosystems (n/m²) and C and D represent parasite abundance within their host (intensity).
APPENDIX:

**Sup Table 2-1.** Ecosystem specific scaling parameters: $M_p$ (parasite body size) and $R_h$ (host biomass density). Values are based on parasite density being represented within ecosystems (n/m²). Bolded values indicate significant coefficients in the model.

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Intercept</th>
<th>$M_p$</th>
<th>$R_h$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuakitoto</td>
<td>-5.41</td>
<td><strong>-1.32</strong></td>
<td>0.78</td>
<td>0.73</td>
</tr>
<tr>
<td>Waihola</td>
<td>-3.80</td>
<td><strong>-1.00</strong></td>
<td>0.82</td>
<td>0.58</td>
</tr>
<tr>
<td>Hayes</td>
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<td>0.81</td>
</tr>
<tr>
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</tr>
<tr>
<td>Mullica</td>
<td>-2.57</td>
<td><strong>-0.86</strong></td>
<td>-0.15</td>
<td>0.45</td>
</tr>
<tr>
<td>Passaic</td>
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<td>-0.17</td>
<td><strong>0.40</strong></td>
<td>0.24</td>
</tr>
<tr>
<td>Raritan</td>
<td>0.33</td>
<td>-0.15</td>
<td><strong>0.82</strong></td>
<td>0.33</td>
</tr>
</tbody>
</table>
**Sup Table 2-2.** Ecosystem specific scaling parameters: $M_p$ (parasite body size) and $M_h$ (host body size). Values are based on parasite density being represented within host (n/host). Bolded values indicate significant coefficients in the model.

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Intercept</th>
<th>$M_p$</th>
<th>$M_h$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tuakitoto</td>
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<td>-0.49</td>
<td><strong>0.22</strong></td>
<td>0.41</td>
</tr>
<tr>
<td>Waihola</td>
<td>-1.51</td>
<td>-0.42</td>
<td>0.25</td>
<td>0.27</td>
</tr>
<tr>
<td>Hayes</td>
<td>-0.71</td>
<td>-0.35</td>
<td><strong>0.25</strong></td>
<td>0.52</td>
</tr>
<tr>
<td>Tomahawk</td>
<td>-2.31</td>
<td>-0.67</td>
<td>0.22</td>
<td>0.26</td>
</tr>
<tr>
<td>Mullica</td>
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<td><strong>-0.94</strong></td>
<td>-0.06</td>
<td>0.45</td>
</tr>
<tr>
<td>Passaic</td>
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<td>-0.17</td>
<td>0.14</td>
<td>0.12</td>
</tr>
<tr>
<td>Raritan</td>
<td>0.57</td>
<td>-0.10</td>
<td>0.16</td>
<td>0.07</td>
</tr>
</tbody>
</table>
**Sup Table 2-3.** Comparison of models fits for PGLS models describing the relationship between parasite abundance within their host (#/host) and both parasite and host body size. When using the maximum likelihood (ML) estimate for \( \lambda \) (ML estimate = 0.32, weak phylogenetic signal) the OLS model was the most parsimonious model relative to ML-PGLS (\( \Delta \text{AIC} < 2 \)).

<table>
<thead>
<tr>
<th>Model</th>
<th>( \lambda )</th>
<th>AIC</th>
<th>BIC</th>
<th>logLik</th>
</tr>
</thead>
<tbody>
<tr>
<td>PGLS (fixed)</td>
<td>1</td>
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<td>122.09</td>
<td>-53.82</td>
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<td>PGLS (fixed)</td>
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<td>109.65</td>
<td>-47.61</td>
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<tr>
<td>PGLS (maximum likelihood)</td>
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<td>110.45</td>
<td>-46.20</td>
</tr>
<tr>
<td>OLS model</td>
<td>NA</td>
<td>103.21</td>
<td>109.65</td>
<td>-47.61</td>
</tr>
</tbody>
</table>
**Sup Table 2-4.** Comparison of models fits for PGLS models describing the relationship between parasite abundance within their ecosystems (n/m²) and both parasite and host biomass density. When using the maximum likelihood (ML) estimate for \( \lambda \) (ML estimate = 0.32, weak phylogenetic signal) the OLS model was the most parsimonious model relative to ML-PGLS (\( \Delta \text{AIC} < 2 \)).

<table>
<thead>
<tr>
<th>Model</th>
<th>( \lambda )</th>
<th>AIC</th>
<th>BIC</th>
<th>logLik</th>
</tr>
</thead>
<tbody>
<tr>
<td>PGLS (fixed)</td>
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</tr>
<tr>
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</tr>
<tr>
<td>PGLS (maximum likelihood)</td>
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<td>125.85</td>
<td>-53.90</td>
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<tr>
<td>OLS model</td>
<td>NA</td>
<td>116.99</td>
<td>123.44</td>
<td>-54.50</td>
</tr>
</tbody>
</table>
**Figure 2-1.** The effects of (A) mass range sampled (maximum/minimum body size of parasites reported from within an ecosystem) and (B) density range sampled (maximum/minimum population density size of parasites reported from within an ecosystem) on reported scaling exponent for parasite body size [within ecosystem model shown here]. Red dashed line is drawn at -0.75 to represent Damuth’s Rule.
SFigure 2-2. The effects of (A) mass range sampled (maximum/minimum body size of parasites reported from within an ecosystem) and (B) density range sampled (maximum/minimum population density size of parasites reported from within an ecosystem) on reported scaling exponent for parasite body size [within host model shown here]. Red dashed line is drawn at -0.75 to represent Damuth’s Rule.
Figure 2-3. Map of New Jersey river sites from Chapter 1 (Raritan and Passaic) and the Mullica river sites taken by Paseka 2017.
SFigure 2-4. Map of New Zealand lakes used in this analysis taken from Lagrue et al. 2015.
SFigure 2-5. Scatterplots showing the relationship between log transformed maximum parasite density within a host and parasite body mass (mg).
**Figure 2-6.** Scatterplots showing the relationship between log transformed maximum parasite density within an ecosystem and parasite body mass (mg).
**Figure 2-7.** Do parasites and their host differ follow the same general scaling rules?

Based on ANCOVA results, a common slope describes this relationship, but each group differs with respect to their intercept value (ANCOVA: F\(_{2,174}\) = 67.16, p < 0.0001, R\(^2\) = 0.43). The scaling exponent describing the relationship between body size and population density among parasites and their fish host agrees with Damuth’s Rule (slope = -0.75 (CI -0.89, -0.60)). Note the above ANCOVA does not account for differences in resources, because I could not accurately describe the resource pool for fish hosts (e.g. their prey biomass density).
**SFigure 2-8.** Frequency distribution of log transformed consumer resource body size ratios for all sampled host parasite interactions.
SFigure 2-9. Tree representing a subset of the species used for the PGLS model (accounting for the effects of phylogeny). Note: not all parasites could be used because species identity wasn’t resolved for several taxa and some taxa were represented as both larval and adult forms. When various life cycle stages were represented I include the adult form in this analysis. While it is clear the PGSL is flawed, it was use to get a coarse indication if phylogeny was driving these size-density patterns.
**Figure 2-10.** Negative log likelihood profile of $\lambda$ in PGLS model.
CHAPTER 3
THE SCALING OF THE ENERGETIC COST OF PARSITISM FROM HOSTS TO ECOSYSTEMS

ABSTRACT: Parasites are thought to play a significant role in ecosystem energy flow, but the amount of energy used by parasite communities, and the relationship of parasite communities to host energetics, remain unclear. Here, we extend key ideas in the metabolic theory of ecology to describe the energetic cost of parasitism across hosts and ecosystems. First, we develop and test theory that links host metabolism to the energy flux of parasitic communities spanning 28 host taxa. We test whether the fraction of a host’s energy budget that is allocated to parasitism is invariant with respect to host metabolic rate, and based on this prediction parasites will use a constant proportion of a host’s metabolism across host taxa. Our data affirm an allometric relationship between host metabolic rate and parasite community energy flux, although the slope of the relationship was shallower than the expected isometric relationship. This relationship suggests the fraction of energy taken by parasites declines with host metabolic rate. Finally, we extend this framework to explain the scaling of host and parasite community energetics at the ecosystem scale. Across three riverine ecosystems, we found a strong relationship between the energy flux of parasites infecting fish communities and the energy flux of those fish communities. A common scaling exponent describes host and parasite energy flux with all three ecosystems, but intercept values varied based on ecosystem identity. Overall, energetic-based models outperformed those using biomass when describing parasite community energetics within hosts and ecosystems.
INTRODUCTION

Parasites are omnipresent in nature, a fact that has propagated a plea to include parasites into food web ecology (Marcogliese and Cone 1997). Traditionally the importance of parasitic organisms has been emphasized by documenting their contribution to total biomass and trophic links within ecosystems (Lafferty et al. 2006, 2008, Kuris et al. 2008, Dunne et al. 2013, Selakovic et al. 2014). Yet, the extent to which parasites mediate energy flow within ecosystems is unclear because the processes that determine parasite biomass within ecosystems, and the relationship between biomass pools and ecosystem energetics, remain unexplored. A better understanding of these processes will help explain the wide variation in parasite productivity amongst systems (Kuris et al. 2008; Preston et al. 2013; Lagrue and Poulin 2015; Paseka 2017). For example, parasite biomass is reported to be orders of magnitude higher in certain estuaries (Kuris et al. 2008) relative to a less productive riverine ecosystem (Paseka 2017). These measures of standing stock biomass are useful, but they lack a mechanistic explanation of the processes generating these contrasting patterns in parasite biomass. This makes formulating general hypotheses about parasite energetics and productivity across systems a difficult task.

Generally, the total biomass supported by ecosystems is constrained by: 1) energy and material inputs and 2) the rate at which individuals use energy and materials for respiration and accumulate them as biomass (Brown and Gillooly 2003, Brown et al. 2004). In turn, parasite biomass ultimately will be limited by the energy and materials supplied by host and the rate at which individual parasites use host resources (Hechinger 2013). To understand the drivers of parasite energetics and productivity, it is first
necessary to examine variability in sizes of parasite communities (numbers or biomass) supported by individual hosts. Hosts represent a tractable, well-replicated ecosystem (Goater et al. 1987) because parasite assemblages form spatially explicit populations and communities nested within their host (Bush et al. 1997). Previous studies examining variation in parasite community abundances have identified host body size as an important factor effecting parasite abundance (George-Nascimento et al. 2004; Poulin and George-Nascimento 2007; Muñoz et al. 2015). However, the processes which ultimately determine the relationships between parasite community abundance and host body size are not well understood (Hechinger 2013).

Testable predictions for the relationship of parasite community abundance to host body size can be developed based on the “Energetic Equivalence Rule” (Damuth 1981, 1987). This ‘rule’ predicts parasite infection intensity, the number of parasites per host \((N_p\), # parasites/host), is limited by the rate at which energy is provided by the host \((R_h\), Watts/host) and the average rate of energy use by an individual parasite \((R_p\), Watts/parasite) (Hechinger 2013):

\[
N_p \propto \frac{R_h}{R_p} \quad \text{(Eqn. 1)}
\]

A dependence of parasite infection intensity on host and/or parasite energetics may be inferred from relationships with host and parasite body mass, since data on individual metabolic rates are typically scarce. Whole organism metabolic rate, \(R\), has been shown to vary as a power law with body mass, \(M\) (grams), and exponentially, with temperature, \(T\) (kelvin) (Gillooly et al. 2001):

\[
R \propto M^b \cdot e^{\frac{E}{kT}} \quad \text{(Eqn. 2)}
\]
Where $b$ is the scaling exponent, $E$ is the apparent average activation energy of the respiratory complex, and $k$ is Boltzmann’s constant (8.62e-5 eV/K). Substituting Eqn. 2 into Eqn. 1 gives:

$$N_p \propto \frac{M_h^{b_h} e^{-\frac{E_h}{kT}}}{M_p^{b_p} e^{-\frac{E_p}{kT}}}$$  \hspace{1cm} \text{(Eqn. 3)}$$

Where subscripts $h$ and $p$ denote parameters for hosts and parasites, respectively.

If parasite communities are energy-limited, then Eqn. 3 makes two predictions with respect to the scaling of parasite community infection intensity. First, estimates of $b_h$ and $b_p$ should be near those for whole organism metabolic rate, 0.6-0.9 (Glazier 2005). Second, since parasites within hosts should share host body temperature, infection intensity should be invariant with respect to temperature if $E_p \approx E_h$.

Initial tests for energetic equivalence in parasite communities did not account for variation in the rates at which individual parasites used energy ($R_p$ in Eqn 1) (George-Nascimento et al. 2004, Poulin and George-Nascimento 2007, Hechinger 2013). Rather, they assumed parasites utilize energy at a rate proportional to host mass-specific metabolic rate. This assumes parasite species with different body sizes have similar mass-specific metabolic rates both to each other and to their host, which is inconsistent with available evidence (e.g. Vernberg and Hunter 1959, 1961; von Brand and Alling 1962; von Brand 1973). As such, it is important to reconsider potential energetic constraints on parasite community sizes, by explicitly considering potential effects of interspecific differences in parasite energy use.
Here we examine the relationship of host energetics to that of their parasite communities. To do so, we collected data on parasite communities infecting 28 host species: fish, crustaceans, mollusk and mammals. We use these data to test three hypotheses. (1) Maximum parasite community abundance increases with host body mass as a power law with an exponent of ~0.6 to 0.9, decreases with parasite body mass as a power law with an exponent of ~0.6 to 0.9, and is invariant with respect to temperature (Eqn. 3). In addition, we examine whether parasite community abundance covaries with parasite species richness. (2) We test whether the energy flux through parasite communities is directly proportional to host metabolic rate. This hypothesis stems from Eqn 1. Note that $R_p$, the rate at which energy is used by an individual parasite (Watts/parasite), is equivalent to the total energy used by the parasite community ($F_p$, Watts), divided by community abundance ($N_p$, # parasites). Then substituting $R_p = F_p/N_p$ into Eqn. 1 and rearranging yields:

$$F_p = \delta * R_h,$$

(Eqn. 4)

where $\delta$ is the fraction of host metabolism utilized by parasites. To test this hypothesis, we use metabolic scaling parameters for hosts and parasites to estimate total energy use by parasite communities ($F_p$) and the energy provided by hosts ($R_h$).

Lastly, for hypothesis (3) we assess whether this energetic scaling framework helps explain variation in parasite productivity within and across three freshwater ecosystems. We hypothesize that, if energetics constrains parasite abundance at the level of individual hosts, then such constraints should operate at the level of host communities and ecosystems. We have three general predictions for the relationship between parasite
and host productivity: (i) within ecosystems, the energy flux of all parasite individuals within a community should increase with the energy flux of host communities, (ii) within and across ecosystems, the relationship of parasite energy flux to that of hosts should be stronger than the relationship of parasite biomass to host biomass (e.g., higher $R^2$), and (iii) differences in energy availability contributes to variation in parasite productivity observed between ecosystems. To test this hypothesis, we sum the total flux of energy and standing stock of biomass of all parasites and fish host individuals sampled within eight communities along three riverine ecosystems (methods described in Paseka 2017; Chapter 1).

METHODS

1. Parasite community data

Parasite community abundance (total number of parasites within an individual host) was quantified for a wide range of host species including: snails, insects, crustaceans, fish and mammals (Sup Table 1). For each host species, the minimum sample size of host individuals examined for endoparasites was 15 individuals; otherwise those host species were excluded from this analysis. Fish were collected from the field using a seine net or hook and line. Upon collection, fish were euthanized with an overdose of MS-222 and frozen for later parasitological necropsy. Macroinvertebrates were collected with a dip-net and dissected immediately after collection. All endoparasites were removed, counted and their associated infection sites were recorded. A subset of parasite specimens were fixed, stained and identified to the lowest taxonomic level possible based on morphological descriptions: using Schell (1985), Schmidt (1970) and Hoffman (1999). These field data were supplemented with published data on parasite
community abundances (Grunberg and Sukhdeo 2017; Paseka 2017; Grunberg in prep). In subsequent analyses, maximum parasite community abundance and community flux were used in statistical models. We chose to examine maximum parasite abundance because these communities are more likely to reflect carrying capacity, and thus be energy-limited.

Experimental parasite community abundance data were taken from Holmes 1962a, 1962b. Briefly, Holmes infected both rats (1962a) and hamsters (1962b) with two species of intestinal parasites (*Hymenolepis diminuta* and *Moniliformis dubius*) to evaluate the effects of interspecific competition on parasite growth rates. Data on parasite body mass (mg of wet weight) were collected at 10-weeks post infection for the concurrent treatment group. *Moniliformis dubius* (phylum Acathephala) are dioecious, with the females being larger than the males, and for the parasite intensity data we assumed an equal sex ratio (e.g. 5 females and 5 males) because it was not noted in the study.

2. **Body mass**

Parasite mass was quantified by pooling parasites of a single species onto pre-weighed filters (Whatman GF/F), which were stored in a drying oven set at 60° C for <2 days and later weighed on a microbalance (0.01 µg). Larger parasites were oven-dried in microcentrifuge tubes and then measured individually. The mass for parasites that were too small to directly weigh (e.g. gregarines from macroinvertebrates) were estimated using mean volumetric measurements of the parasite and assuming parasite density is that
of water. For fish mass measurements, all hosts were individually oven-dried at 60° C for <5 days after parasitological necropsy, and then weighed on a microbalance (0.0001g). The lengths of all macroinvertebrates were measured, and these data were used to estimate dry weight using published length-mass regressions (Benke et al. 1999).

3. Estimating within host energy flux

For hosts, individual-level rates of energy use were estimated based on published metabolic scaling relationships. While direct estimates of energy use would be preferred, these data are difficult or impossible to collect. Moreover, estimates of energy use based on scaling relationships have been successfully employed in the past (e.g., Barneche et al. 2014). Within a taxonomic group, whole organism metabolic rate, \( R \) (watts), generally varies with body mass, \( m \) (kilograms), as:

\[
R = a \times m^b \quad \text{(Eqn. 5)}
\]

where \( a \) (Watts/kg\(^b\)) is a normalization constant and \( b \) is the scaling exponent. Data for \( a \) and \( b \) were compiled for each taxonomic group considered here-fishes, mammals, crustaceans, and molluscs (Table 1). The ideal estimate for individual energy use would be energy ingestion rate, however scaling estimates for this parameter are sparse. Thus, we used relationships for resting metabolic rate; the available data suggest that resting metabolic rate is proportional to field metabolic rate (Nagy 1987, Koteja 1991) and ingestion rate (Peters 1983). When field temperatures differed from the temperature at which normalization constants were estimated, we used temperature-corrected metabolic
rates with the taxon-specific $Q_{10}$ values given in Table 1. In cases where $Q_{10}$ values were not available for a taxonomic group, we assumed a $Q_{10}$ of 2.

For parasite communities, community-level rates of energy use were calculated by summing individual parasite metabolic rate across all parasite individuals in the community. Specifically, the energy flux through parasite infracommunities is estimated as the sum of metabolic rate, $R$, times abundance, $N$, across all $n$ species in the community:

$$F_p = \sum_{i=1}^{n} R_i \ast N_i = \sum_{i=1}^{n} a_i \ast m_i^b \ast N_i \quad \text{(Eqn. 6)}$$

When appropriate, different values for $a$ and $b$ were used for different taxonomic groups (Table 1). Since there are few estimates of metabolic scaling parameters for parasitic species, we used parameters estimated for closely related free-living taxa.

4. Estimating within ecosystem energy flux

Host and parasite community flux (watts/m$^2$) and biomass (g/m$^2$) within ecosystems were compiled from three riverine systems in New Jersey: the Raritan, Passaic and Mullica Rivers (Paseka 2017; Grunberg in prep). In both studies, total parasite and fish numerical and biomass density were quantified across seasons and sites within each of the three rivers. Fish-host and parasite density values were converted to energy flux using the previously described community flux equation (Eqn. 6), where abundance (N) was replaced with the numerical density (N/m$^2$) of each species, yielding community flux within the river system (watts/m$^2$). Each parameter was estimated for the
entire host and parasite community at each time point (N=4 seasons) for each sampling
sites within each river (N=3 sites in Raritan, N=3 Passaic, N=2 Mullica).

Statistical analysis

All statistical tests and graphics were produced using R v. 3.3.3 (R Core Team, 2017). We first compared the fit of non-linear regression and log-transformed regressions
using a likelihood analysis to assess the validity of additive and multiplicative error
assumptions, respectively (Xiao et al. 2011). We used AIC to evaluate whether the
assumption of normal error (non-linear) or lognormal error (log linear model) are
favoured by our model. If $\Delta \text{AIC} | \text{AIC}_{\text{non-linear}} - \text{AIC}_{\text{lognormal}} | < 2$ then normal error is
preferred and $< 2$ then log-normal error is appropriate. Our models were best-fit by
lognormal error, so we proceeded with log-transformed data (SFig. 3-1, SFig. 3-2).

To test model predictions (Eqn. 3 & 4), we performed least-squares regression
analyses on natural-log transformed data. For Eqn. 3, we estimated the relationship of
log10 transformed parasite maximum community abundance, $\log_{10}(N_p)$, to host body
mass ($\log_{10}(M_h)$), average parasite body mass ($\log_{10}(M_p)$), inverse absolute
temperature ($\frac{1}{kT}$), parasite species richness, $R$:

$$
\log_{10}(N_p) = \text{Int} + b_h \times \log_{10}(M_h) + b_p \times \log_{10}(M_p) + E \times \frac{1}{kT} + b_r \times R
$$

The scaling exponents from Eqn. 3 ($b_h$, $b_p$ and $E$) are given by the slopes of this
statistical model. We also examined interactions among predictor variables.
Similarly, for Eqn. 4 we estimated the relationship of log transformed maximum parasite community flux ($\log_{10}(F_p)$) to log transformed host metabolic rate ($\log_{10}(R_h)$) AND species richness $R$; ultimately, however, $R$ was excluded from this model as it was not a significant covariate:

$$\log_{10}(F_p) = Int + b_1 * \log_{10}(R_h)$$

Note that $10^{(Int)} = \delta$, the fraction of host metabolism used by the parasite community.

Within ecosystem scaling of parasite and host productivity were analysed using log transformed biomass density and community flux data. Each observation in this analysis is taken from a specific season by site combination that occurs within each system (N= 36 observations total). In this specific analysis ecosystem identity can be contributing to variation in scaling relationships, so we used an ANCOVA adding ecosystem identity as a term in our model

$$\log_{10}(E_p) = Int + b_2 * \log_{10}(E_h) + \text{ecosystem}$$

RESULTS

The relationship of maximum parasite infracommunity abundance (# parasites/host) to host body mass, average parasite body mass, temperature, and parasite species richness provided varying support for model predictions (Eqn. 3). Maximum parasite community abundance increased with host body size to the 0.34 power ($p < 0.01$; 95%CI: 0.11, 0.58; Fig. 1A), and decreased with average parasite body mass to the -0.92
power ($p < 0.01$; 95%CI: -1.3, -0.57; Fig. 1B). As expected, community abundance was not related to temperature ($p = 0.80$). Parasite community abundance increased with parasite species richness (exponent = 1.5; $p < 0.01$; 95%CI: 0.74, 2.3; Fig. 1C).

Somewhat unexpectedly, there was a strong interaction between average parasite body mass and species richness ($\text{exp} = 0.34$; $p < 0.01$; 95%CI: 0.15, 0.59; Fig. 1D). This means that an increase in species richness by one increases the slope of the relationship of log$_{10}$(Np) to log$_{10}$(Mp) by a factor of 0.34. No other interactions among predictors were significant ($p > 0.05$). Together, host mass, parasite mass, temperature, richness, and the richness x parasite mass interaction explained 74% of the variation in infracommunity size.

Next, the relationship of parasite community energy flux to host metabolic rate and parasite species richness was not consistent with model predictions (Eqn. 4). Unlike results for community abundance, parasite species richness did not significantly influence parasite community energy flux ($p = 0.3$). Host metabolic rate strongly influenced parasite community flux ($p < 0.01$, $R^2=0.83$), although the slope of the relationship was lower than the expected isometric relationship (observed exponent: 0.83; 95%CI: 0.68, 0.97). This allometric relationship suggests that the fraction of energy used by parasites declines with host metabolic rate. The empirical equation was: $F_p = 0.006 \times R_h^{0.83}$. So, the fraction of host energy a parasite community uses, $\delta$, varies with host metabolic rate as:

$$\delta = \frac{F_p}{R_h} = 0.006 \times R_h^{-0.18}.$$
Within each ecosystem, we found a strong relationship between the estimated energy flux of all parasites infecting the entire fish community and the energy flux of those corresponding fish communities ($R^2 = 0.93$, $p<0.0001$). Specifically, we found a common scaling exponent across all three ecosystems ($\text{exp} = 0.41$; 95% CI: 0.35, 0.48) with varying intercept values based on ecosystem identity (Figure 3; Table 2). The lowest intercept value was found for the Mullica river system, followed by the Passaic and Raritan Rivers (Table 2). We also found a common scaling exponent ($\text{exp} = 0.73$; 95% CI: 0.34, 1.13) for the relationship between parasite and host biomass density across three ecosystems ($R^2 = 0.43$, $p=0.001$), but again intercepts that vary based on each ecosystem (Figure 3A, Table 2).

**DISCUSSION**

We have shown here that host energetics constrain both the abundance and energy use of parasites at the level of host individuals and ecosystems. First, at the level of hosts, we found that much of the variation in maximum parasite community abundance was explained by parasite body mass, host body mass and parasite species richness. Importantly, our results extend previous work on parasite infracommunities (George-Nascimento et al., Poulin & George-Nascimento) to show that accounting for differences in parasite body mass is necessary to assess energetic equivalence in parasite communities, as was originally pointed out by Hechinger (2013). Still, our results only partially supported predictions of energetic equivalence – in particular, the functional relationship of parasite community abundance was significantly shallower than expected.
(observed = 0.34, expected = 0.6 to 0.9). Second, we found a positive, but allometric, relationship between parasite community energy flux and host metabolic rate. This was inconsistent with model predictions based on energetic equivalence (i.e. an isometric relationship; Eqn. 4), suggesting that the fraction of host energy that parasite communities use decreases with host metabolic rate. Finally, we showed that host energetics constrains that of parasites at the level of whole ecosystems. Within each ecosystem, parasite energy flux increased with host energy flux (e.g. common slope), although ecosystems varied in the magnitude of parasite energy flux (e.g. different intercepts). Moreover, the energy flux of parasites and hosts appeared to be better correlated than standing stock biomass.

Unlike previous analyses of energy equivalence in parasite communities (George-Nascimento et al. 2004; Poulin and George-Nascimento 2007; Hechinger 2013; Muñoz et al. 2015), we explicitly considered effects of species richness. Intuitively, more speciose parasite communities had higher abundance after accounting for differences in parasite and host body mass. Perhaps less intuitively, we observed an interaction between richness and parasite body size such that, as parasite species richness increases, the relationship of parasite abundance to body size becomes shallower. We hypothesize that this interaction may be related to immunological mechanisms. Some parasite assemblages show evidence of immune-mediated priority effects and immune priming (Hoverman et al. 2013, Halliday et al. 2018), where in some cases infection by one parasite species facilitates or inhibits additional parasite taxa to colonize their host. Thus, exposure to a wide diversity of parasite species may make hosts more or less susceptible to sustaining parasite infections. As a result, the importance of parasite body size in
constraining parasite abundance may diminish and host immune state may be a more relevant constraint. Whether these small-scale interactions between parasites and hosts’ immune systems occurring within host individuals are contributing to this potential broad interspecific pattern is not clear and remains an open question for future investigation. Nonetheless, prior models did not incorporate the effects of parasite richness (George-Nascimento et al. 2004; Poulin and George-Nascimento 2007; Hechinger 2013; Muñoz et al. 2015), and our analysis suggests richness should be considered in future studies.

The relationship observed between parasite community energy flux to host metabolic rate showed that smaller sized hosts are disproportionately affected by parasites. In particular, hosts with lower metabolic rates have a greater fraction of energy stolen by parasites (Fig. 2). Parasite community density (measured as parasite individuals/gram of host) has also been shown to scale negatively with host body mass across taxa (George-Nascimento et al., 2004). While this analysis was based on numerical density, they arrived at a similar conclusion and proposed that the per capita effect of parasitism is greater on smaller sized organisms. If parasites are generally taking proportionally more energy from smaller organisms, this can have implications for energy flow within ecosystems. These smaller sized hosts are typically placed at lower trophic levels, implying that parasites may take more energy from lower trophic levels, thus altering energy flow (e.g., reducing energy available to higher order consumers). Still, it is worth noting that the allometric relationship between parasite community energy flux and host metabolic rate does not necessarily mean that the total energetic cost of parasite infection declines with host metabolic rate. Our model only accounted for the direct energetic cost of parasitism. There are many potential indirect energetic costs of
parasite infection, such as that of mounting and maintaining an immune response (Little and Killick 2007; Allen and Little 2011). However, estimating the precise metabolic cost of the immune function is difficult (Lochmiller and Deerenberg 2000), and the extent to which these costs vary across species is unclear. There may be potential to develop a scaling framework that incorporates both the energetic cost of parasitism, immune function and host energetics as a potentially fruitful extension of our present work.

We recognize that individual parasite energy use was estimated coarsely for our analyses. Ideally, this analysis would have used direct estimates of energy use, or a finer taxonomic resolution for the metabolic parameters, but these data do not readily exist. We argue that using the metabolic scaling relationships at the phylum level for parasites is a better approximation than: 1) assuming all parasitic taxa metabolize resources at the same rate, or 2) excluding this variable entirely. It is also important to note that we used metabolic scaling parameters based on aerobic respiration, whereas parasites in oxygen-depleted environments (e.g. intestine) primarily use anaerobic respiration (von Brand 1966, 1973). As a result, the normalization constant will likely be underestimated for some parasite species (von Brand and Alling 1962). Nonetheless, if the normalization constant is consistently underestimated across parasitic groups, then it is unlikely this will influence the slope of the relationship of parasite community flux to host metabolic rate. While our estimates of parasite metabolism can introduce error into our analysis, including parasite metabolism nonetheless provides a more reasonable measure of parasite energetics that highlights the differences among parasites species within a host and ecosystem.
In our ecosystem scale analysis, we report a common slope describing the relationship between host and parasite productivity within river systems, suggesting a common mechanism producing this pattern. We argue the amount of energy flowing within a host community ultimately produces this scaling relationship and parasites are constrained by host productivity. While we found evidence for a common scaling relationship, we also report different intercepts for each ecosystem. These differences in intercepts are due to variation in productivity across ecosystems. For example, the Mullica River is an oligotrophic aquatic ecosystem, in which there is low levels of parasite biomass (Paseka 2017). This system also had the lowest intercept value in our model indicating overall lower levels of host and parasite productivity in that system. In contrast, the Raritan River, with the highest model intercept, is characterized by a history of pollution, higher fish biomass and higher productivity. Therefore, we suggest the documented variation in parasite biomass across previous studies (Kuris et al. 2008; Paseka 2017) may largely be attributed to variation in productivity across systems.

Our results also have broader implications for our understanding of constraints on community abundance and energetics. The relationships between abundance and body size informs how resources are divided among species within communities (White et al. 2007) and has implications for biodiversity patterns and energy flow within ecosystems. Yet, few studies of natural communities can explicitly measure total resource availability for these communities. Parasites provide a novel system for assessing relationships between community abundance and individual body size while explicitly accounting for differences in total resource availability (via host body size).
It is clear that parasites have the potential to mediate energy flow and here we provide evidence that supports the use of a metabolic-based framework to address such topics. Prior attempts to link parasitism to ecosystems have used biomass (Kuris et al. 2008; Preston et al. 2013; Lagrue and Poulin 2015; Paseka 2017), a surrogate for energy, but as shown here biomass patterns within ecosystems do not necessarily reflect energetic patterns. We contend that not accounting for metabolic differences that occur among parasite taxonomic groups may under- or overestimate their importance in ecosystem energetics. Furthermore, excluding differences in parasitism energy usage can make comparison across systems more difficult, as parasite community composition varies considerably among hosts and ecosystems. This is evident by the robust patterns emerging from our metabolic scaling analysis.
REFERENCES:


Hernandez, A. D. and Sukhdeo, M. V. K. 2008. Parasites alter the topology of a stream...


Lagrué, C. and Poulin, R. 2015. The scaling of parasite biomass with host biomass in lake ecosystems: are parasites limited by host resources? - Ecography (Cop.): n/a-n/a.


Paseka, R. E. 2017. Low parasite biomass in oligotrophic streams differs from previous estimates in aquatic ecosystems. - Freshw. Sci. in press.


Table 3-1: Taxon-specific metabolic scaling parameters (a: normalization constant, b: scaling exponent) for parasites and their hosts.

<table>
<thead>
<tr>
<th>Group</th>
<th>(a (W/kg^b))</th>
<th>(b)</th>
<th>Temp</th>
<th>Q₁₀</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hosts</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fishes</td>
<td>0.220</td>
<td>0.88</td>
<td>20</td>
<td>1.7</td>
<td>[1]</td>
</tr>
<tr>
<td>Mammals</td>
<td>2.806</td>
<td>0.68</td>
<td>38</td>
<td>2.8</td>
<td>[1]</td>
</tr>
<tr>
<td>Crustaceans</td>
<td>0.265</td>
<td>0.78</td>
<td>20</td>
<td>2</td>
<td>[2]</td>
</tr>
<tr>
<td>Mollusks</td>
<td>0.159</td>
<td>0.78</td>
<td>20</td>
<td>2</td>
<td>[3]</td>
</tr>
<tr>
<td>Insects</td>
<td>0.479</td>
<td>0.76</td>
<td>20</td>
<td>2.6</td>
<td>[4]</td>
</tr>
<tr>
<td><strong>Parasites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematodes</td>
<td>0.0236</td>
<td>0.72</td>
<td>20</td>
<td>2</td>
<td>[2]</td>
</tr>
<tr>
<td>Protozoa</td>
<td>0.0170</td>
<td>0.68</td>
<td>22</td>
<td>2</td>
<td>[2]</td>
</tr>
<tr>
<td>Acanthocephalan</td>
<td>0.0158</td>
<td>0.66</td>
<td>20</td>
<td>2</td>
<td>[5]</td>
</tr>
<tr>
<td>Platyhelminthes</td>
<td>0.1670</td>
<td>0.92</td>
<td>20</td>
<td>1.95</td>
<td>[6]</td>
</tr>
</tbody>
</table>

**Figure 3-1.** Effects of host body mass (A), parasite body mass (B), and parasite species richness (C) on parasite community abundance. Data are plotted as partial residuals of the statistical model:  
\[
\log_{10}(N_p) = -1.7 + 0.34 \times \log_{10}(M_h) - 0.87 \times \log_{10}(M_p) + 1.4 \times R + 0.35 \times [R \times \log_{10}(M_p)]
\]
Figure 3-2. Interaction plot for the effect of parasite species richness on the relationship between parasite body mass and parasite community abundance. Data are plotted as partial residuals of the statistical model.
Figure 3-3. The relationship of host metabolic rate to maximum parasite infracommunity energy flux. Both parasite community flux and host metabolic rate are Q10 transformed to account for differences in temperature.
**Figure 3-4.** Within ecosystem scaling of parasite and host biomass density and energy flux within the Mullica, Passaic and Raritan rivers. (A) The relationship between parasite and host biomass density is described by the following equation: $\log_{10}\left(\frac{B_p}{m^2}\right) = \text{Int}_{eco} + 0.73 \times \log_{10}\left(\frac{B_h}{m^2}\right)$, where the intercept values differ for each ecosystem:

- $\text{Int}_{eco} = -3.11$ (Mullica), -3.38 (Passaic) and 2.51 (Raritan).

(B) The relationship between parasite and host community flux is described by the following equation:

$\log_{10}\left(\frac{F_p}{m^2}\right) = \text{Int}_{eco} + 0.41 \times \log_{10}\left(\frac{F_h}{m^2}\right)$, where the intercept values differ for each ecosystem: $\text{Int}_{eco} = -1.18$ (Mullica), -0.27 (Passaic) and 0.03 (Raritan).
## APPENDIX

**Sup. Table 3-1.** List of host species analyzed and their associated sample sizes and taxonomic groups.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size</th>
<th>Taxonomic group</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aphredoderus sayanus</em></td>
<td>75</td>
<td>fish</td>
</tr>
<tr>
<td><em>Armadillium vulgare</em></td>
<td>199</td>
<td>crustacean</td>
</tr>
<tr>
<td><em>Caecidotea communis</em></td>
<td>15</td>
<td>crustacean</td>
</tr>
<tr>
<td><em>Catostomus commersonii</em></td>
<td>48</td>
<td>fish</td>
</tr>
<tr>
<td><em>Cyprinella spiloptera</em></td>
<td>190</td>
<td>fish</td>
</tr>
<tr>
<td><em>Enneacanthus obesus</em></td>
<td>124</td>
<td>fish</td>
</tr>
<tr>
<td><em>Esox americanus</em></td>
<td>25</td>
<td>fish</td>
</tr>
<tr>
<td><em>Etheostoma fusiiforme</em></td>
<td>17</td>
<td>fish</td>
</tr>
<tr>
<td><em>Etheostoma olmstedii</em></td>
<td>187</td>
<td>fish</td>
</tr>
<tr>
<td><em>Fundulus diaphanus</em></td>
<td>396</td>
<td>fish</td>
</tr>
<tr>
<td><em>Gammarus fasciatus</em></td>
<td>2095</td>
<td>crustacean</td>
</tr>
<tr>
<td><em>Helisoma trivolvis</em></td>
<td>38</td>
<td>mollusk</td>
</tr>
<tr>
<td><em>Lepomis auritus</em></td>
<td>110</td>
<td>fish</td>
</tr>
<tr>
<td><em>Lepomis gibbosus</em></td>
<td>37</td>
<td>fish</td>
</tr>
<tr>
<td><em>Lepomis macrochirus</em></td>
<td>73</td>
<td>fish</td>
</tr>
<tr>
<td><em>Libellulidae</em></td>
<td>22</td>
<td>insect</td>
</tr>
<tr>
<td><em>Micropterus dolomieu</em></td>
<td>21</td>
<td>fish</td>
</tr>
<tr>
<td><em>Micropterus salmoides</em></td>
<td>38</td>
<td>fish</td>
</tr>
<tr>
<td><em>Notropis amoenus</em></td>
<td>21</td>
<td>fish</td>
</tr>
<tr>
<td><em>Notropis bifrenatus</em></td>
<td>221</td>
<td>fish</td>
</tr>
<tr>
<td><em>Physa acuta</em></td>
<td>92</td>
<td>mollusk</td>
</tr>
<tr>
<td><em>Pleurocera virginica</em></td>
<td>100</td>
<td>mollusk</td>
</tr>
<tr>
<td><em>Porcellio scaber</em></td>
<td>180</td>
<td>crustacean</td>
</tr>
<tr>
<td><em>Rhinichthys atratulus</em></td>
<td>75</td>
<td>fish</td>
</tr>
<tr>
<td><em>Rhinichthys cataractae</em></td>
<td>23</td>
<td>fish</td>
</tr>
<tr>
<td><em>Semotilus atromaculatus</em></td>
<td>29</td>
<td>fish</td>
</tr>
<tr>
<td><em>Umbra pygmaea</em></td>
<td>302</td>
<td>fish</td>
</tr>
<tr>
<td>Hamster</td>
<td>10</td>
<td>mammal</td>
</tr>
<tr>
<td>Rat</td>
<td>10</td>
<td>mammal</td>
</tr>
</tbody>
</table>
SFigure 3-1. Comparison of the normality and homoscedasticity of residuals for the log-linear (LR) and non-linear relationships (NLR) describing the relationship between parasite community flux and host metabolic rate.
**SFigure 3-2.** Model fit for LR and NLR analysis describing the relationship between parasite community flux and host metabolic rate. The assumption of multiplicative error used in log-linear relationships was supported by our data ($\Delta$AIC $>$ 2; $AIC_{c\text{-norm}} - AIC_{c\text{-logn}} = 170.23$).
SFigure 3-3. The relationship of host metabolic rate to maximum parasite infracommunity energy flux prior to Q10 transformation, which is correcting for differences in temperature.
SFigures 3-4. The above relationship yielded platyhelminth metabolic scaling parameters. Plotted: (A) body mass and metabolic rate (natural log-transformed), (B) temperature and mass-corrected metabolic rate, (C) body mass and temperature corrected metabolic rate (after Q10 transformation at 20°C).
References for metabolic scaling parameters used in this study:


CONCLUSION

A common goal throughout this dissertation was to establish the role of space and energy in mediating patterns in parasite ecology. When considering spatial scales, I considered the role of local and global data, while also incorporating different spatial grains of host-parasite interactions (e.g. within host and within ecosystems). It is well known space and can influence many patterns in ecology and not surprisingly this also applies to those observed in parasite ecology. Moreover, I stepped away from using standing stock currencies such as biomass to quantify the energetic relationship between parasites and their hosts. Instead I used estimates of energy, based on published metabolic scaling relationships, to give a more complete picture of parasites, hosts and their potential to mediate energy flow. The field of parasite and disease ecology is growing and before proceeding further it is important to validate some assumptions and methodology being frequently used.

In my first chapter, I showed how spatial gradients in rivers can influence parasite community structure. I evaluated whether change in environmental factors can result in concordance between parasites, hosts and their river habitat. Overall, I observed no concordance between parasites and their hosts suggesting that parasites and their hosts are not responding similarly to changes that occur within ecosystems. Moreover, patterns in concordance among groups were different between the two river ecosystems sampled. From this I propose that at finer spatial scales (e.g. within ecosystems) strong concordance between host and parasites assemblages may not be evident. However, I suggest that at broader scales, regional filters may produce a stronger degree of concordance than observed in the present study.
In my second chapter, I contrasted patterns observed for Damuth’s Rule when using data manipulated at varying spatial scales. Here, I varied the focus of the analysis (e.g. local and global) and spatial grain of the data (e.g. parasite populations nested within their host or within aquatic ecosystems). At local scales I found wide variation in the relationship between parasite density and body size, while the global analysis generally fit the pattern posited by Damuth’s Rule. However, this result was also contingent on how parasite populations were defined. Given the results of these analyses, I advocate for a consistent use of spatial scales that also reflect the processes generating the pattern being tested.

In my last chapter, I extended a metabolic-scaling framework to describe parasite community level energetics across hosts and ecosystems. Across host taxa, I found variation in host energetics produces an allometric relationship with parasite community energetics, and this relationship rejects the concept of energetic equivalence in parasite communities. At the ecosystem scale host energetics better explained parasite productivity rather than host biomass measures, suggesting that accounting for variation in how hosts and parasite use energy need to be considered in the future. I propose reevaluating our understanding of parasites and energy flow through the lens of metabolic ecology to generate generalizable hypotheses relating parasites to ecosystems energetics.

There are many ways in which the present work can be expanded and perfected. One striking gap I noticed was an absence of macroecological data on parasites from freshwater ecosystems. It is difficult to synthesis generalizable patterns in parasite ecology without data from a diversity of parasites inhabiting a diversity of ecosystem types. Future attempts to gather this data should consider the relevant metrics needed to answer these questions: parasite body size, host body size, parasite infection intensity, location,
temperature etc. Furthermore, metabolic scaling relationships for parasitic taxa should be revisited to improve energetic models focusing on host-parasite interactions. Put simply, we currently lack the data to assess properly whether parasites fit into general ecological rules. I also predict a novel connection between host life history theory (specifically pace of life and variation in investment to immune function) and the energetic scaling of parasite infections can be pursued based on the work presented here. Moving forward, I expect the forefront of metabolic theory and disease ecology can be used to scale up the consequences of individual infections to ecosystem processes and will be a fruitful field of study.