

IMPACTS OF SPACE, ABUNDANCE AND FOOD WEB STRUCTURE ON
PARASITE LIFE CYCLES

by

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ABSTRACT OF THE DISSERTATION
IMPACTS OF SPACE, ABUNDANCE AND FOOD WEB STRUCTURE ON
PARASITE LIFE CYCLES
by WAYNE DAVID ROSSITER

Dissertation Director:

Prof. Michael V.K. Sukhdeo

The search for fundamental patterns or rules by which parasites establish and persist in free-living species is a rapidly expanding area of interest for both parasitologists and ecologists. Though host-parasite interactions are fairly well understood at the population level, little is known about parasitism at the community level, nor why some free-living species harbor many parasite taxa while others are seemingly resistant to parasite establishment. The purpose of this dissertation was to explore several species and community attributes that could be important to parasite establishment and persistence in both a marine saltmarsh (Tuckerton, NJ) and a freshwater riverine system (Raritan River, NJ). This study specifically emphasized feeding interactions, abundance and spatial distributions of free-living species and their respective helminth parasites. In Tuckerton saltmarsh, I observed a strong spatial patterning in trematode infections of the mudsnail, *Ilyanassa obsoleta*, and this pattern is strongly correlated with habitat type and host quality. At the community level (along with data from four previously published systems), trophically transmitted parasites were

found to utilize asymmetric predator-prey interactions, in which predator hosts have many prey items and prey hosts have relatively few predators. In a pristine site along the Raritan River high resolution abundance data revealed that predator-prey interactions are spatially constrained by habitat and that this pattern was even stronger for host-host and parasite-host interactions. Finally, I found a decrease in efficiency of biomass transfer up trophic levels across a perturbation gradient in this river system. This pattern correlated with losses in both free-living and parasite diversity. However, the relationship between these factors and human impact was not linear, suggesting a threshold at which community structure becomes less invasible by parasites. Collectively, this study suggests that spatial context, in combination with community structure, can greatly affect parasite establishment and persistence and can be used to explain or predict which free-living species are more hospitable hosts.

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"In prosperity, our friends know us; in adversity, we know our friends."

-John Churton Collins

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CHAPTER 1

Introduction

The search for fundamental patterns or rules by which parasites establish and persist in free-living species is a rapidly expanding area of interest for parasitologists and ecologists (reviewed in Guegan et al., 2005; Poulin, 2007). At the population level, much is known about the nature of host-parasite interactions of both pattern and process (e.g., Anderson and May, 1978; Rollinson and Anderson, 1985). For example, numerous studies have demonstrated the ability for parasites to regulate oscillations in host populations in much the same way as predators regulate prey populations (Dobson and Hudson, 1992). Parasites are known to rapidly adapt to locally prevalent host genotypes (Lively and Dybdahl 2000), and almost universally establish aggregated distributions in host populations, where few host individuals harbor the majority of the parasite “component” population (Crofton, 1971, Shaw et al. 1998). However, many fundamental problems (like the causal mechanisms for the aggregated distribution of parasites in host populations) remain unresolved, and the putative answers often point to processes at the meta-population and community levels. On the horizon of this area of research are the broad questions of whether or not there are species (or functional groups of species) that are more likely to harbor parasites (e.g., Poulin, 1997; Hugot et al., 2001; Benesh et al., 2011), whether certain types of trophic interactions are more likely to transmit parasites (Marcogliese, 2007; Lafferty, 2010; Rossiter and Sukhdeo, 2011), or whether any community-level characteristics are good indicators of the presence, absence or abundance of parasites (Chen et al., 2008). Consequently, many of the assumptions

about the relationships between free-living and parasite populations and communities remain tenuous and largely unverified.

While poorly understood, parasitism at the community level is an area of enquiry that has rapidly developed over the past two decades. A survey of peer-reviewed articles that contain the words 'parasite', 'community' and/or 'food web' in their titles reveals a nearly exponential rate of increase (Figure 1), and numerous books and reviews now exist on the topic (e.g., Marcogliese, 2002; Dobson et al., 2005; Byers, 2007; Sukhdeo, 2010; Poulin, 2010). While many studies have described the parasite fauna of particular species or animal groups, few have defined the distribution of parasites across entire free-living communities, and still fewer have addressed how the structure or dynamics of a free-living community forms or constrains the parasite community embedded within it (Pedersen and Fenton, 2006). It is assumed that parasite communities are tightly bound to, and therefore reflect, host communities, but the nature of this relationship is almost completely unknown. In the search for clear relationships between the structure of free-living communities and their respective parasite fauna, several community-based attributes have been identified as potentially important.

For example, it is intuitive that increasing the number of potential host species would necessarily increase the diversity of parasites. This has been termed the 'diversity begets diversity' hypothesis (e.g., Hechinger and Lafferty 2005), and the idea extends well beyond parasite ecology (e.g., Mayer and Pimm, 1997; Sugden, 2001; Janz et al., 2006). By extension, it has been argued that, if healthy ecosystems are more speciose than their embattled counterparts, an ecosystem rich in parasites is actually a healthy one (Hudson et al., 2006). However, some studies have found counter evidence suggesting

that, at least within a narrow range of diversity, changes in the free-living community have no impact the diversity of parasites (Anderson and Sukhdeo, 2011). Others have demonstrated that parasite species richness can increase with perturbation (Hernandez and Sukhdeo, 2008). While counterintuitive, this finding would make sense if, as evidence seems to demonstrate, rare and ‘peripheral’ species are the first to disappear during extinction events, having little effect on the overall topology or global stability of a community network (e.g., Davies et al., 2004; Jonsson et al., 2006; Srinivasan et al., 2007; Petchey et al., 2008). Consequently, such species would not provide parasites with evolutionarily stable interactions, a necessary component of parasitism (Price 1980). Thus, community structure and energetics may have a more profound effect on the presence or absence of parasites than does the number of free-living species available to parasites.

It is clear that parasite presence, absence, abundance and location in communities must be dictated by selective pressures that constrain parasite establishment (e.g. Combes, 2001), and that these pressures are linked to the energetics of the system (Hernandez and Sukhdeo, 2005; Poulin, 2010). Therefore, the elucidation of general patterns will likely require the stripping down of food web and community ecology to its bare bones, viewing ecological networks and species’ interactions (namely trophic) as energy flows upon which parasites establish (Sukhdeo, 2010). Here I explore population and community level patterns of parasitism in both salt-marsh and freshwater riverine communities. I also evaluate the relationship between the dynamics of energy transfer in food webs and the characteristics of their respective parasite communities, with particular emphasis on trophically transmitted macroparasites. Specifically, I focus on how energy

flows might dictate the distribution of parasite biomass in ecological communities, operating under the null prediction that the attributes of the free living community (namely species diversity, biomass and network structure) are energetically mirrored by the parasite communities they house. Finally, I examine whether or not parasites might be able to resist relatively small perturbations to host communities, because they are concentrated in hosts that are of higher relative abundance, have mild population oscillations, and are thus more evolutionary and ecologically stable (Price, 1980; de Castro and Bolker, 2005).

Background

In his book, *Animal Ecology* (1927), Charles Elton introduced a powerful and cogent understanding of community ecology and food web theory. In many ways, his work founded the field of community ecology (Leibold and Wootton, 2001), and among other things, offered the observation that all ecological communities could be described in terms of trophic pyramids, with a wide base of primary producers (autotrophs), and an ever diminishing quantity of heterotrophs at each subsequent trophic level. Explicit in Elton's understanding of trophic interactions was parasitism and the cycling of parasites through food webs (Sukhdeo, 2010). Since that time, many advances, both conceptual and methodological, have augmented, expanded, and in some cases corrected Elton's ideas (e.g., Lindemann, 1942; Odum, 1953; Yodzis, 1984; Brown, 2004). Starting in the mid-20th century, ecologists began trying to understand the fundamental properties of ecological communities in terms of energy (e.g., Lindemann, 1942; Odum, 1959), largely because energy was held to be the essential currency of all biological interactions (e.g.,

Winiwarter and Cempel, 1996; Brown, 2004; Rooney and McCann, 2007). If energy can be used to explain overarching properties in free-living communities, it would follow that the parasite communities that are imbedded in host communities will be constrained by the same energetic laws. Given this broad observation, we are yet to draw any clear lines linking host and parasite community patterns (Lindenfors et al., 2007; but see Hall, 2009 for more speculative treatments of the subject). However, gains in this area of enquiry would substantially enhance the unification of ecological patterns and processes with our understanding (and predictions) of the dynamics of parasite communities.

Incorporating parasites into community ecology

For well over a century, parasitologists have been collecting detailed accounts of the parasite fauna present in both individual species and communities at large (reviewed in Price, 1980; Bell and Burt, 1991; Poulin, 1995; Poulin and Morand, 2000; Lindenfors et al., 2007). As data sufficient for meta-analyses became available, some surprising patterns emerged. Few would have guessed that parasites are represented in nearly every animal group and may make up as much as 75% of the interactions observed in biological systems (Lafferty et al., 2006). By some estimates, four parasite species are lost with the extinction of each free living host species (Whiteman and Parker, 2005). Given their ubiquity and abundance, it follows that parasites could have dramatic impacts on free living communities (Thomas et al., 2000; Mouritsen and Poulin, 2005; Wood et al., 2007), and while there is debate about how to incorporate parasites into the existing theoretical frameworks, there are clear patterns about the way parasites exist in host populations, as well as entire communities of free-living species. Parasite faunas are

more diverse in larger host species (Morand and Poulin, 1998; Lindenfors, 2007), as well as hosts of higher relative abundance (Arneberg et al., 1998; Vazquez et al., 2005), or wider distributions (Barger and Esch, 2002; Morand and Krasnov, 2010). Likewise, older (and/or larger) individuals in a host population display more diverse assemblages of parasites than do younger (and/or smaller) individuals (Dorovskikh and Stepanov, 2008). Parasite species richness (particularly trophically transmitted parasites) increases with host species trophic breadth, as well as trophic level (Poulin, 1997), and parasite species tend to be larger in larger hosts (Morand et al., 1996). While the ‘diversity-begets-diversity’ argument predicted that an increase in the biomass of a free living community would be mirrored by its respective parasite fauna, a recent study of three salt marsh systems in California found no clear relationship between host or system biomass and the biomass of their parasite communities (Kuris et al., 2008). An additional surprising discovery has been that parasite species richness does not obey the latitudinal rules of free-living communities, likely because host specificity decreases as one approaches the equator (Rohde, 1978; Blaylock et al., 1998; Poulin, 1999). That is, parasite species diversity remains high in both high and low latitudes because parasites are more specialized (i.e. have smaller host spectra) as one moves away from the equator. Some parasite taxa are closely associated with particular taxonomic groups of hosts, suggesting phylogenetic constraints on parasite speciation (Mouillot et al., 2008; Rossiter and Sukhdeo, 2011, Benesh et al. 2011), and some parasite taxa exhibit strong associations with particular types of ecosystems (reviewed in Bush, 2001). However, these patterns are not shared across parasite groups.

In terms of incorporating parasites into existing theory in community ecology, there are a handful of different ideas in play. In many ways, parasites are functionally equivalent to predators (Raffel et al., 2008), and many have argued that they should be placed in host communities as top predators (e.g., Sukhdeo and Hernandez, 2005), both in terms of their trophic interactions and their relative biomass in the system (a surrogate for energy). In some ways this is intuitive because even top predators have parasites, and those parasites would feed a level above top predators. However, there are also convincing arguments against this view. For example, not all parasites feed on top predators, but instead are sewn into the free living community at multiple trophic levels (e.g., Chen et al. 2008, Rossiter and Sukhdeo 2011), though the autotroph level is often excluded. More damaging to this argument is the observation that, at least in some systems, parasites represent more biomass than do top predators (e.g., Kuris et al. 2008), suggesting that it is inappropriate to place them atop any trophic pyramid. Finally, stable isotope techniques have permitted the first empirical determinations of both parasite and host trophic positions (e.g., Pinnegar et al., 2001; Power and Klein, 2004; Stapp and Salkeld, 2009), and these studies have largely undercut the placing of parasites as top predators in ecological communities. These studies demonstrate that some parasites (for example trematodes and nematodes) should be placed above their hosts, while others (cestodes and acanthocephalans) fed on the same trophic level as their hosts. Further, it is speculated that the consideration of specific stages of parasites with complex life cycles would reveal that parasites are spread throughout nearly all trophic levels of a given community.

Others have attempted to treat parasite communities as a side-loop, similar to the microbial loops found in aquatic systems, largely because they can be viewed as a kind of energetic ‘tax’ on free living organisms (Raffaelli, 2002). This ideological framework led to parasites being grouped both as nodes in a larger community network, but also within ‘sub-webs’ in which parasites are confined to a partition of the food web matrix (Lafferty et al., 2005). Still other groups have applied plant-pollinator theory to host-parasite interactions, in the form of bipartite interaction networks (Vazquez et al., 2007; Poulin et al., 2010). Finally, some have elected to completely remove them as unique nodes in an interaction web, and simply overlay them onto free-living food webs (Chen et al. 2008; Rossiter and Sukhdeo, 2011; Sukhdeo, 2010). The logic behind this move was simply that parasites are not free-living organisms. While plants and animals interact across some habitat, the host *is* the habitat for a parasite, and thus the parasite’s fitness and survival is intimately linked to the survival of an individual host (Lafferty and Kuris 2002; Rossiter and Sukhdeo, 2012).

Parasites and Food Web Matrices

Currently, most of our analyses of the structure and dynamics of ecological communities are grounded in models that display communities in terms matrices of species interactions. In the case of food webs, predator species are listed along the top row, while prey species are listed along the first column, and trophic interactions are indicated by binary code, where 1 indicates an interaction and zeros appear where no interaction occurs (though it is possible to incorporate a more specific value of interaction strength; Figure 2a). This matrix is converted into a graphical depiction of an

‘ecological network,’ in which each node is a species (or trophospecies) and edges are simply lines (in some cases directional) that indicate a trophic link between some predator node and a prey node (Figure 3b). There are many advantages to using trophic networks (food webs) to describe communities. First, every species eats something and/or is eaten by something. Thus, every member of an ecological community can be captured in a food web. Second, the central currency represented in any trophic interaction is energy, though other surrogate measures may be used (e.g., Zanden and Rasmussen, 1996; Vázquez et al., 2005), and this nests nicely within the growing field of ecological energetics (e.g., Yodzis, 1984, Brown et al., 2004, etc). Third, in relative terms, feeding interactions are easy to measure or observe both in the field and in laboratory settings (reviewed in Laska and Wootton, 1998; Abrams, 2001; Berlow et al., 2004; Wootton and Emmerson, 2005). Other community dynamics like competition, indirect effects, and mutualisms are often much harder to observe and quantify for entire communities (and are less emphasized in existing literature). Finally, because these networks lend themselves to classical graph theory (Bersier et al., 2002, Allesina et al., 2005), many topological properties of the network are easily calculable (though their utility remains an area of debate; Pimm, 1988; Paine, 1988; Polis, 1991; Byers, 2009; Sukhdeo, 2010). That is, these networks can be searched for universal or transcendent patterns (e.g., Camacho et al., 2002; Garlaschelli, 2004; Poulin, 2010), and even modeled with dynamism (e.g., de Ruiter et al., 2005). In principle, the matrix can be modeled as energy or biomass flows along directional edges when nodes are ascribed some quantity (again, biomass or population sizes; e.g., Jordán and Molnár, 1999). But how parasites

should be incorporated into these matrices and subsequent analyses remains a point of debate.

The first real inclusion of parasites in food webs was that of Roughgarden et al. (1993), though some of the implications had already been considered by Dobson and Hudson (1986). This food web centered around the *Anolis* lizards of the Caribbean, and contained only 44 taxa (free-living and parasitic). However, it did include two nematode parasites, treating them as nodes, functionally equivalent to free living species. The authors also made modest efforts to calibrate interaction strengths for all predator-prey interactions, largely based on and extrapolated from predation frequencies and gut contents. In the final analysis, the authors readily admitted that these calibrations (aside from direct observations) were ‘more or less arbitrary decisions.’ The problem was that the entire life cycles of these parasites were not incorporated into the web, but only the adult worms. Still, it was discovered that the inclusion of parasites into the food web produced trophic chains of up to eight species. In some ways, the parasites represented energetic loops in the system when any parasite stage is eaten by non-host predators, as has been more recently described by Thielges et al. (2008). It would not be until the early 1990s that robust food webs would come to include parasites. One of the most well studied and broadly published food webs to emphasize parasites was that of Ythan Estuary (as well as Loch Leven; Huxham et al., 1995). This is a much larger data set, containing 88 free living species and 42 parasites. It comes as no surprise that the inclusion of parasites as nodes in the matrix resulted in an increase in the number of top predators. As was seen previously, the study also demonstrated that the addition of parasites substantially increased food chain lengths. In a subsequent paper, parasites of

the Ythan Estuary food web were broken into trophospecies, according to their life history stages, effectively adding these stages as independent nodes (Huxham et al., 1996). This resulted in no significant change in the observed values for intervality (a measure of predator overlap), but did draw attention to the inherent problems with small predators (parasites and micropredators) being organized in food webs that tend to be ordered by body mass or size (Cohen, 1990; Memmot et al., 2000).

Concurrent with the work of Huxham and colleagues, interest in parasites and food webs began to emerge elsewhere. In the article 'Food webs: A plea for parasites' (1997), Marcogliese argued that parasites could be used to track energy flows in a food web network, that they could potentially regulate food web dynamics, and even act as 'keystone parasites.' Others speculated that parasites could redirect energy in food webs by altering predator-prey interaction strengths, via parasite induced behavioral modification (Morand and Gonzalez, 1997). The Carpinteria marsh food web represented another large (83 free living species) matrix, containing 40 parasite species (Lafferty et al., 2005). Like most food webs, many of the predator-prey links were putative or inferred. So too were many of the parasite-host links, which composed a 'sub-web' for analysis. The first observation was that the inclusion of parasites led to a pattern that did not conform to the assumption that diversity declines as you move up trophic levels. Oddly, the average host spectrum for parasites (analogous to trophic breadth) was substantially larger than the average trophic breadth of predators in the matrix. This contradicted the existing belief that the fitness of a parasite decreased as additional host species were added at any one stage of development, leading to parasites that are host-specific and narrow in their host spectrum (reviewed in Combes, 2001).

This also led to higher than expected linkage densities values across the entire food web. Because parasites were overrepresented in terms of links (there were more host-parasite links than predator-prey links in the system), the authors would later conclude that ‘parasites dominate food web links’ (Lafferty et al., 2006), and that contrary to existing theory, mid-trophic level species are most vulnerable to predation (in this case parasitism).

The location of parasites in food webs has also become a topic of interest, both in terms of the empirical patterns and the mechanisms responsible. Chen and colleagues (2008) analyzed host and non-host characteristics in species from three existing food webs that contain parasites, using an array of species-specific network indices. Broadly, the authors discovered that parasites were not randomly distributed in free-living food webs, but rather, parasites occur disproportionately in species in higher trophic levels. Parasites were also more likely to show up at the end of any given food chain, and parasite diversity increased with increasing values of centrality and trophic breadth. Rossiter and Sukhdeo (2011) found that the type of predator-prey interaction can have profound effects on the presence or absence of trophically transmitted parasites. Again, parasites were not randomly distributed across predator-prey links, but instead the same predator-prey interactions were utilized repeatedly by many parasite species. Predator-prey interactions utilized in parasite trophic transmission were also asymmetric, in that predator hosts had more prey items than the prey hosts had predators. This suggested that some interactions among free-living species are more stable for parasites than others (Rossiter and Sukhdeo, 2011).

In keeping with the well established literature describing the differences between terrestrial, freshwater and marine communities (e.g., Chase, 2000; Shurin, 2006), empirical data on parasites in food webs has revealed that parasite strategies (and their placement in trophic networks) vary with system type. For example, the helminth parasites of marine systems tend to be much more generalist (i.e., display greater trophic breadth) than their terrestrial or freshwater counterparts (Marcogliese, 2002). This seems to be best explained by the frequency with which larval stages of helminths arrive (and survive) in non-host species, often using them as paratenic hosts (Marcogliese, 2007). This is enhanced by the fact that core predators of marine food webs also have wide trophic breadths and core prey species have more predators (Carr et al., 2003). Thus, multiple hosts are incorporated into the same energy channels in food webs. From the parasite's perspective, these core interaction modules are functionally the same as single predator-prey interactions (Rossiter and Sukhdeo 2011). Additionally, there is a propensity for the larval stages of these parasites to be longer lived and able to utilize repeated transfers up food chains, which tend to be longer in aquatic systems in general (Marcogliese, 2002).

Dynamic food webs

So far, I have only discussed static models of communities (with great emphasis on food web approaches). However, in the absence of replicated, well-controlled, long-term experimental systems, dynamic models are our best bet for examination of the mechanisms responsible for the structure of ecological communities and the establishment of parasites within them. The parameterization of dynamic food web

models has proven to be very difficult (Berlow et al., 2004). The major difficulty has been that food web matrices implicitly track populations of interacting predator and prey species, which in themselves necessitate both abundances and interaction strengths when evaluating network dynamics. That is, the effect of any one species on another is determined by the size of the population and the per capita impact of that species. In many cases, abundance data exist, and it is the interaction strengths that are missing. This shortcoming has been addressed in several ways. For instance, abundance data have been used to estimate interaction strengths (e.g., Wootton, 1997), as has the frequency of interaction (Dietl, 2003). Gut contents, when applicable, are very reliable measures of interaction strength for timed feeding periods (Wootton, 2005). In the realm of modeling, most have simply populated the food web with interaction strengths that are randomly drawn from some distribution (e.g., May, 1973, Wilmers et al., 2002; Melián and Bascompte, 2004; Quince et al., 2005). These values are usually applied to simple Lotka-Volterra population models (e.g., Chen and Cohen, 2001; Wilson et al., 2003) for each species in the network, extracting metrics like stability (the speed with which perturbations to a system dampen or amplify over time; May, 1974), fragility (a measure of network fracturing as species are deleted; Sole and Montoya, 2001; reviewed in Pimm, 2002 and Verhoef and Morin, 2010) or community robustness (Dunne et al., 2004). Lotka-Volterra predator-prey models remain the primary means for adding dynamism to trophic interactions, and numerous authors have expanded these multi-species-species models to accommodate expansions of both the predator's trophic breadth and prey species' vulnerability. The nature of equations that are simultaneously dependent on linked instantaneous change rates prevents us from being able to solve for

exact values of population sizes in the system, but this does not prevent us from evaluating the system. Solving for the real parts of each population eigenvalue allows one to determine whether the perturbation will amplify or dampen for a respective species in the matrix (Dunne et al., 2005). This process can be iterated so as to determine the importance of changes to the interaction strengths or the population sizes of given species.

The *a priori* assumptions that go into any given model of food web dynamics are dubious at best. The first, and unavoidable, assumption is that the dynamics of a network of trophic interactions are somehow descriptive of the dynamics actually observed in ecological communities. That is, we assume that the fluctuations in species populations are determined by the nature of their trophic links. Clearly, this ignores the impact of other interactions like mutualisms, competition or commensalism. Another debatable assumption that exists in all models of community dynamics is that the observed presences, absences or abundances depict a community at equilibrium (May, 1973; Wootton, 2005), and there are some concerns about whether or not the observed predator and prey abundances represent stable values (i.e., they produce change rates that equilibrate or oscillate at or around zero). Of course, there are also assumptions associated with the description of predator-prey interactions via Lotka-Volterra models. It is possible that the predation rates are density-dependent and non-linear, both of which can be built into any differential equation, but which seldom are, due to the dramatic increase in the complexity of the model. In short, we must assume that our chosen equations accurately describe the mechanistic nature of each trophic interaction. In the end, it is not difficult to produce a dynamic model of one's food web, but the utility and

realism of its dynamics may leave many skeptical about its application to describing real systems (e.g., Peters, 1988; Steele, 2009).

With respect to parasites in dynamic food web models, there are other concerns. First, parasites are very small, and the per capita interaction strengths for parasitic species are probably very different from those of predator-prey interactions (Lafferty, 2010). However, this concern also exists for any micropredator or grazing microherbivore. More so than free living species, linking parasite stages represents a serious problem. For free living taxa (such as young of the year fish compared to adults or nymphal/larval insects vs adults), different stages are often treated as separate nodes in the network. This problem is amplified in parasites with complex life cycles. First, as previously mentioned, parasites live in or on their hosts, meaning that the death of the host leads to the death of the parasite. Not only does it result in the death of the parasite, but in all likelihood, the death of many parasite individuals at once. It is difficult to determine how to capture the dynamics of parasite prevalence and intensity in models that are designed to explain whole system dynamics. The abundance of each stage of the parasite is largely determined by the prior stage in the life cycle, and any parasites in the next time step represents a parasite individual at a prior time step, until the life cycle is complete. But, in many larval stages of the parasite life cycle there is asexual amplification, another unique problem when dealing with parasites.

Even given these limitations, the consideration of parasites in dynamic food webs, as in other areas of community ecology, is gaining momentum. One recent attempt to model parasites in dynamic food webs revealed that non-host species were more sensitive to perturbation and extinction than host species (de Castro and Bolker, 2005). However,

Chen and colleagues (2011) have discovered that parasites themselves are much more susceptible to secondary extinction with the removal (both random and directed) of host species. This incongruence is likely because Chen and colleagues incorporated linked stages in the complex life cycles of parasites, meaning that, for a parasite with a three host life cycle, there is an increased chance that at least one of these host species will be extirpated. Because parasites are obligate to all hosts in the life cycle, but predators are not usually obligate to any given food source, parasites are apparently more sensitive to changes in the free-living community. This was the same conclusion suggested by a modeled salt marsh food web in which invasive species were allowed to replace native species (Lafferty and Kuris, 2009). The authors of this study concluded that the inclusion of parasites in dynamic food web models yield communities that are more prone to perturbation and species loss.

Parasites, Scaling Laws and Ecological Communities

Aside from the matrix-based models of ecological networks (such as food webs), there are other areas of community ecology where parasites might profitably be considered. One of the most fruitful lines of research that emerged from Elton's original work was the formal extension of his observation that food webs tend to take on a 'pyramidal' shape, in which biomass decreases at each subsequent trophic level. These conceptual models lack the resolution of matrices that contain individual species, but offer energetically-based insights into the overarching constraints on community structure. Now a mainstay in any discussion of food web dynamics, biomass pyramids have been augmented by similar and related pyramids for abundance, species richness

and body size. What Elton (and later Lindemann, 1942) achieved was a consequential description of the energetic constraints on community structure. Subsequent studies have suggested that the shape of a trophic pyramid can be described in terms of allometric and isometric relationships between predators and their prey (e.g., Reuman et al. 2008).

These draw upon fundamental relationships between body mass and various other characteristics like trophic level, metabolic rate, abundance, species diversity, population density and the total biomass of each trophic level (Marquet et al., 2005). That is, the pyramid is a consequence of underlying regularities regarding predators and prey.

Ultimately, these arise as a consequence of metabolic rate and tend to conform to a universal power law relationship, $Y=aX^b$, in which Y is a given parameter (for example population density), X is body mass of the average individual, b is some constant and is always roughly equal to $-3/4$ (e.g. Griffiths, 1992; Brown et al., 2004). This $-3/4$ scaling law (as well as its reciprocal $1/4$ scaling law) are ubiquitous properties of animals (studies suggest that autotrophs operate under $b = -2/3$ scaling rule; Niklas et al., 2003), and these constraints ultimately tell us something about the energetic constraints of energy moving through ecological communities (Griffiths, 1992).

Unfortunately, as with ecological networks and trophic pyramids, parasites (as well as micropredators) seemed to defy these rules, or at least do not fit free-living patterns. For example, the size of a predator is usually one to three orders of magnitude greater than its prey (Cohen et al., 1993; Woodward et al., 2005; figure 3). While there is much scatter (largely system-dependent) around the log-log linear relationship between predator and prey size, parasites demonstrate a nearly opposite pattern (i.e. they are orders of magnitude smaller than their hosts; Memmott et al., 2000; Leaper and Huxham,

2002). Likewise, the species diversity of predator guilds or trophic levels can be expressed as a single-phase exponential decay curve, in which subsequent trophic levels have fewer species than prior levels (figure 4). It is thought that this pattern arises due to the combined effects of inefficiencies in energy conversion up food chains, and the increase in body size at higher trophic levels. If energy is limited, and the per capita mass of an organism increases, it follows that both population abundance and species diversity decline with increasing trophic level. Again, parasites defy this relationship, with parasite richness estimates suggesting that, at least for vertebrate taxa, there are perhaps four (Parker et al., 2004) to seven (Luque and Poulin 2007) times as many parasite species as host species, and parasite species richness perhaps having no relationship to trophic level (Poulin and Leung, 2011).

Even though parasites do not conform to the same trends (or more specifically, y-intercepts) as their free-living counterparts, the framework itself has allowed ecologists and parasitologists alike to consider parasites in the context of size, abundance and biomass. For example, returning to the Ythan Estuary food web, Leaper and Huxham (2002) found that, while parasites are smaller than their hosts, their size scales with host size, similarly to observed predator-prey relationships. A more recent study by Cohen (2007) found that “in a parasite chain, the ratio of parasite mass to host mass increases as the trophic level of the host increases (and the mass of the host decreases).” More impressive, but perhaps not surprising, was the observation that the slopes of log-log graphs of parasite mass to host mass and predator mass to prey mass were nearly identical. Only the y-intercept changed. This suggests that parasites are in fact constrained in the same ways as free-living species. As previously mentioned, the host is

both the prey and the habitat for parasites. Seen in this light, parasite size, abundance and species richness increases with increasing host (habitat) size. This is completely analogous to the observed scaling patterns in free-living ecological communities. Thus, the take home message is that parasites seem to be constrained by energetic laws in analogy (if not homology) to their free-living counterparts, but the exact relationship between the two groups requires further study.

In this dissertation, I explore several of the population and community-level attributes that affect parasite establishment. The results and findings presented here come from multi-year studies in both marine (estuarine) and freshwater (riverine) systems. Drawing from three years of survey data and several manipulation experiments in a nearly pristine saltmarsh, I demonstrate that, in some cases, host quality and habitat can be mechanistically implicated in determining the presence or absence of parasites (Chapter 2). Using these data, as well as other published data sets, I show that the structure of food webs (namely predator-prey asymmetry) can be used to predict the location of trophically transmitted parasites within a network (Chapter 3). Transitioning to a large freshwater river, I demonstrate that parasite life cycles are tightly bound to host species with high degrees of spatial overlap, and that free-living predators themselves tend to feed on prey items that are spatially proximal (Chapter 4). Finally, I explore the impact of human development on free-living and parasite communities, using four sites along a perturbation gradient (Chapter 5).

General methods

Tuckerton salt marsh is a 2460 hectare peninsula that juts out into the Great Bay-Little Egg Harbor complex, which is part of the Jacques Cousteau National Estuary Research Reserve. The food web matrix was constructed using a combination of survey and feeding interaction data from the NJDEP, Rutgers University Marine Field Station and three years of field collections by the authors. Some feeding interactions were assumed based on additional literature from studies conducted in other salt marshes in the region (i.e. Connecticut to Delaware/Maryland; e.g., Fell et al. 1982; Kreeger et al. 1988; James-Pirri et al. 2001).

The Raritan River is a typical lotic freshwater system (Patrick 1994). The watershed drains approximately 1,100 square miles of central New Jersey, and travels 31 miles before emptying into Raritan Bay. The four sites I have chosen represent a perturbation gradient in which human impact increases dramatically as one moves from Stanton Station (Hunterdon County) eastward to New Brunswick (Middlesex County), but are clearly freshwater, experiencing little to no mixing with the brackish conditions of the bay.

I quantified the entire community, ranging in size from bacteria to the largest top predators, and where possible, also quantified biomass. When the dry-weight biomass could not be observed, I approximated per capita masses by calculating the mean volume of organism and converting that volume to a mass value approximated by the most similar conversion value from <http://www.convert-me.com/en/convert/weight2volume> (which has more than 300 mass-volume conversion factors ranging from various forms of vegetation and animal products, to liquids, to minerals). Collections were taken at each site during each season (from Summer 2009-Summer 2011), or monthly in the case of the

Stanton Station site. In order to address patterns of parasite-host abundance at a higher resolution, the Stanton Station site was broken down into replicated habitat types (three replicates of runs, riffles and pools respectively). Primary productivity was quantified by chlorophyll density measures, phytoplankton counts, and dry mass counts of macrophyte vegetation over space. Microfauna (e.g., zooplankton) were collected using plankton nets, and quantified by preservation in sugar formalin (4% solution), stained with Rose Bengal, with subsequent counts under a compound microscope. Biomass was estimated for phytoplankton and zooplankton by calculating the volume of morphotypes, and calculating the mass of water at that volume. Meiofauna and macrofauna were quantified by replicated (three replicates) benthic core samples and Surber sampler collections respectively.

Macroinvertebrates were dried and weighed. Fishes, turtles and other aquatic vertebrates were trapped by seining, minnow traps and larger crab traps (which allow larger fish to be collected). These data were supplemented by hook-and-line collections of larger predatory fish that are underrepresented in trap collections. Initially, many fish were weighed as wet mass and then dehydrated and weighed to establish the relationship between wet mass and dry mass. Thereafter, only wet mass has been taken and those masses were converted to dry mass approximations. Macroinvertebrates, fish and ranids were evaluated for parasites by dissection. On several occasions, fish, turtle and frog blood samples were evaluated for protozoan parasites by Geimsa staining of blood smears. Ectoparasite counts were also made for all aquatic vertebrate on site, and the parasite infracommunity of turtles is estimated from fecal collection and floatation. No turtles have been euthanized for dissection. Bird counts were conducted, and riparian

mammals were quantified by point counts as well as midden counts for muskrats and raccoons. Bird feces were collected for parasite identification via fecal floatation, but raccoon and muskrat feces were not collected, and no individuals were taken for parasitological dissection. The mass of microscopic parasites (protozoans and some larval forms) were estimated in the same way that microfauna are calculated. All larger larval and adult parasites were dried and weighed directly.

Figure 1.1: Graph of the increasing rate of publications dealing with parasites and free-living communities. Increase in publications containing the terms “food web” and “parasite” is nearly logarithmic.

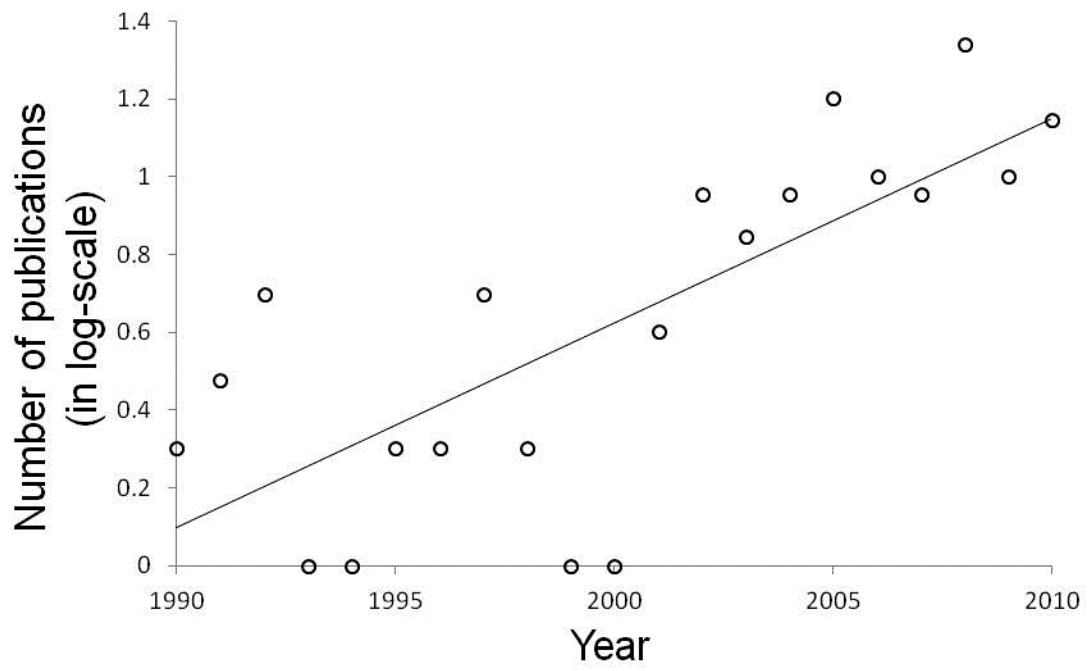


Figure 1.1

Figure 1.2: Example of the conversion of a binary food web matrix into a food web. A) a subsample of the food web matrix constructed from a Pine Barrens stream (Hernandez and Sukhdeo, 2005). AL = algae, DE = detritus, CH = chironomid, AM = amphipod, LE = *Lepomis sp.*, and WB = wading bird. B) the entire Pine Barrens food web constructed from the binary file. Node size indicates linkage values (i.e. larger nodes are species with more links).

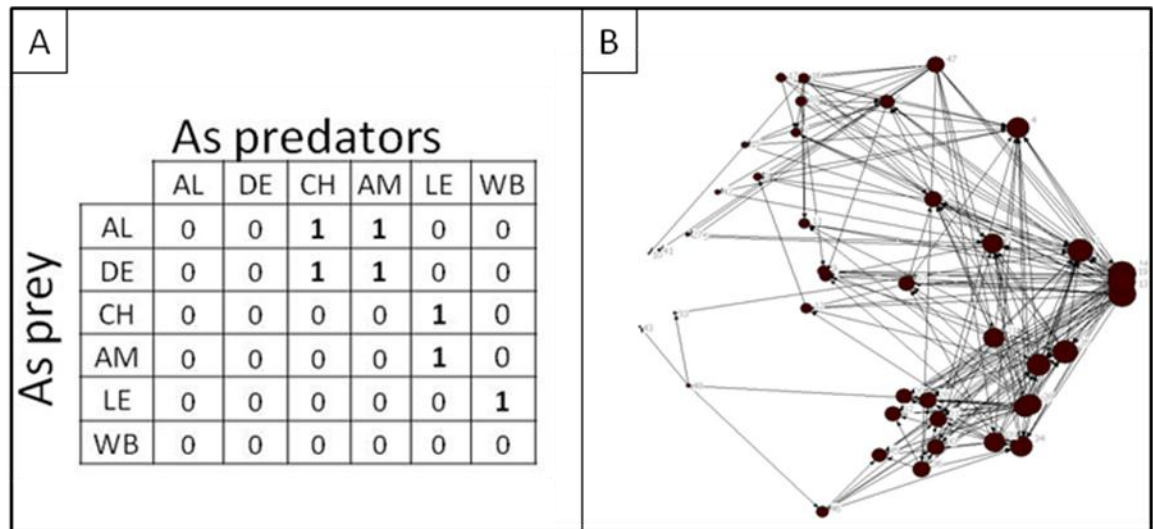


Figure 1.2

Figure 1.3: Log-log graph of the relationship between 334 predator and prey sizes (from Cohen et al. 2003). Diagonal line represents the line of isometry, along which predators and prey would be the same size. Almost all data points fall above this line, indicating that predators are almost always larger than their prey.

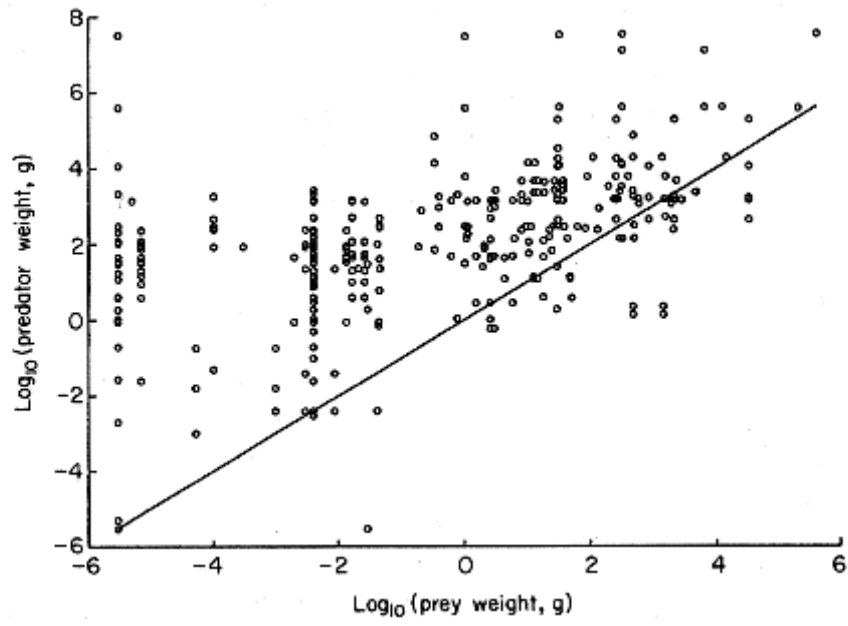


Figure 1.3

Figure 1.4: An adaptation of data taken from Tuesday lake (Cohen et al. 2003), the Bering Sea (Trites 1999) and Ythan Estuary (Huxham et al. 1995), showing the mean relative species richness of subsequent trophic levels (all relative to the producer level). The best fit is a single-phase exponential decay rate ($R^2 = 0.9497$).

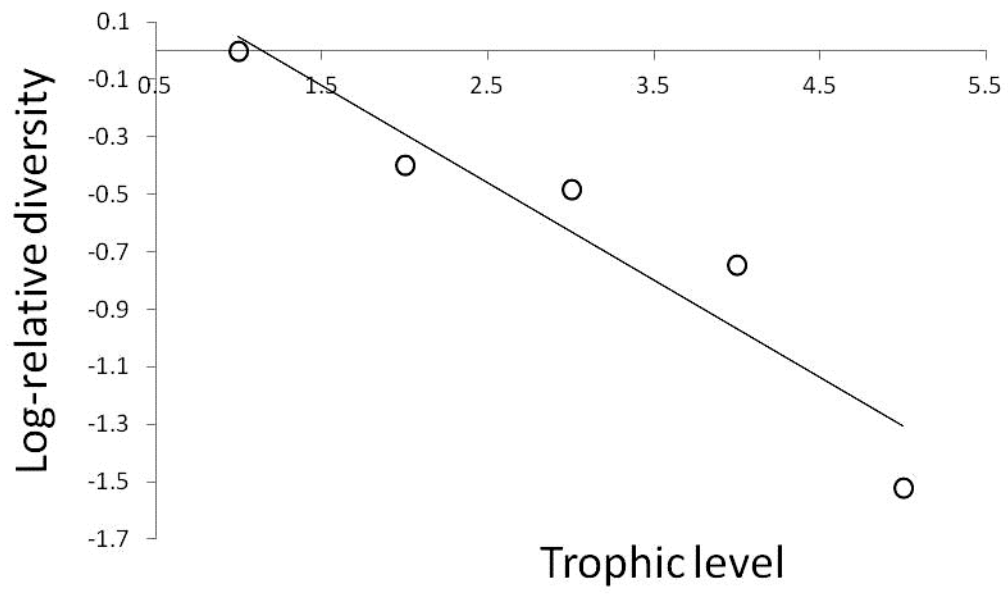


Figure 1.4

Figure 1.5: Sampling sites in the Raritan River (NJ) watershed. Dots indicate sampling locations. Gradient of human impact moves left to right. ST = Stanton Station, BM = Burnt Mills, NB = North Branch, HW = Highway 287. Stanton Station is the most pristine location, and is nearest the headwaters that feed into the Raritan River proper. Burnt Mills is also very pristine, while both North Branch Park and the Highway 287 sites demonstrate increasing environmental perturbation.

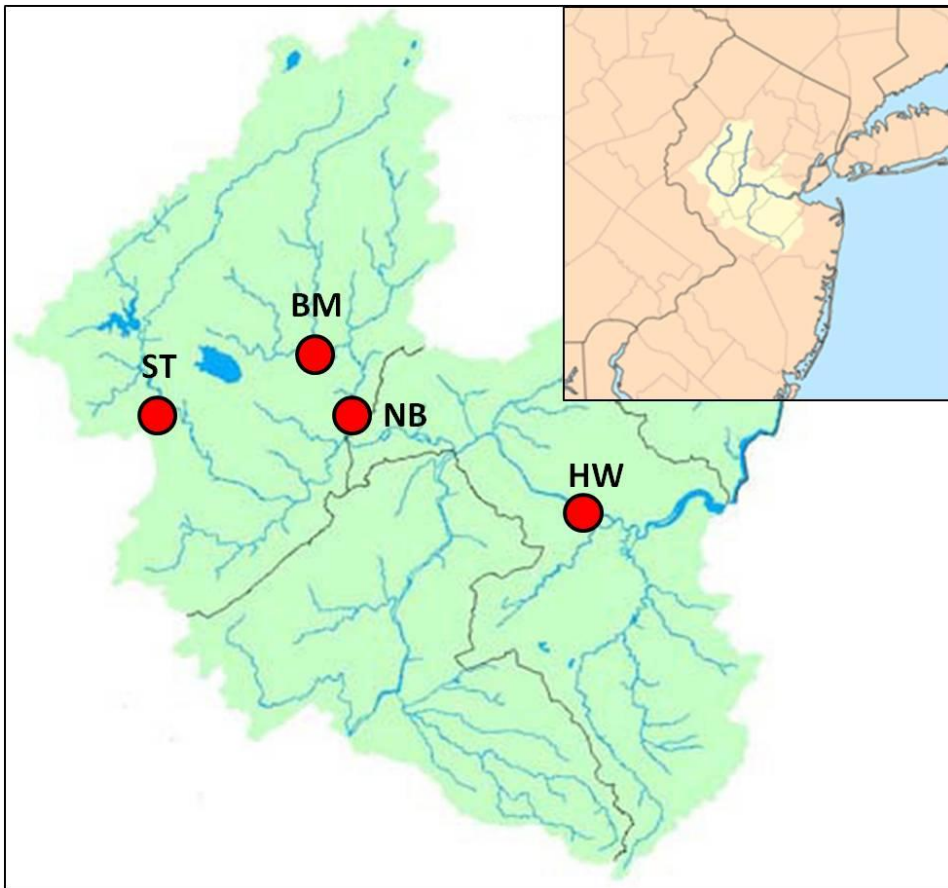


Figure 1.5

CHAPTER 2

Host quality and spatial patterning in infections of the Eastern Mudsail (*Ilyanassa obsoleta*) by two trematodes (*Himasthla quissetensis* and *Zoogonus rubellus*).

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Abstract

Several studies have suggested that the fitness of a parasite can be directly influenced by the quality of its host. In such cases, selective pressures could act to funnel parasites towards the highest quality hosts in a population. The results of this study demonstrate that snail host quality is strongly correlated with spatial patterning in trematode infections, and that habitat type is the underlying driver for both of these variables. Two trematodes (*Himasthla quissetensis* and *Zoogonus rubellus*) with very different life cycles assume the same spatial infection pattern in populations of the first intermediate host (*Ilyanassa obsoleta*) in coastal marsh habitats. Infected snails are disproportionately recovered from intertidal panne habitats which offer more hospitable environs for snails than adjacent habitats (intertidal creeks, coastal flats and subtidal creeks) in terms of protection from turbulence and wave action, as well as the availability of food stuffs. Snails in intertidal panne habitats are of higher quality when assessed in terms of average size-specific mass, growth rate, and fecundity. In mark-recapture experiments, snails frequently dispersed into intertidal pannes, but were never observed leaving them. In addition, field experiments demonstrate that snails confined to intertidal panne habitats are disproportionately infected by both trematode species, relative to conspecifics confined to adjacent habitats. Laboratory experiments show that infected snails suffer significant energetic losses, and consume more than uninfected conspecifics,

suggesting that infected snails in intertidal pannes may survive better than in adjacent habitats. We speculate that one possible mechanism for the observed patterns is that the life cycles of both trematode species allows them to contact the highest quality snails in this marsh ecosystem.

The spatial patterning of parasites in host populations remains a principle area of investigation for parasitologists (e.g. Esch and Fernandez, 1994; Guegan et al., 2005; Poulin 2006, Matthee and Krasnov, 2009), and the elucidation of the mechanisms responsible for the relationship between parasite prevalence and host distribution remains one of the most unresolved areas of parasite ecology (Wilson et al., 2002; Galvani, 2003; Poulin, 2007; Byers et al., 2008). For example, host individuals in one location might exhibit high levels of infection, while adjacent or nearby conspecifics remain relatively free of parasites. Classic explanations for this phenomenon can be broadly grouped into 3 categories of causal mechanisms. Aggregated distributions are a consequence of differential host susceptibility, of variability in parasite-host encounter rates (incidence of contact), or of parasite induced behavioral modification post infection (Crofton, 1971; Lion et al., 2006). Differences in host susceptibility may be the result of genotypic variation, phenotypically plastic responses to the environment, or as a product of age, sex, or prior infection-recovery status (Curtis and Hurd, 1983; Sheridan et al., 2000; Gervasi and Foufopoulos, 2008). Differential host susceptibility has been implicated across a range of studies that include fish-trematode (Karvonen et al., 2004), snail-trematode (Krist et al., 2000), *Daphnia*-microparasite (Schoebel, 2010), rabbit-nematode (Cattadori et al., 2007), and beetle-cestode (Yan and Norman, 1995) systems (broadly discussed in Galvani, 2003). When aggregated distributions are caused by spatially (and

temporally) dependent variation in host-parasite encounter rates, the underlying mechanisms are varied, and may include abiotic factors (Fingerhut et al., 2003), variation in exposure time or host age (Karvonen et al., 2004; Curtis, 2007), dilution effects (Curtis and Hurd, 1983; Ostfeld and Keesing, 2000; Johnson and Thielctges, 2010), differences in the relative abundance of infected hosts (Hechinger and Lafferty, 2005; Thielctges et al., 2008; Hall et al., 2009), or environmental pollutants and habitat degradation (e.g. Galli et al., 2001; Koprivnikar et al., 2007; Krause et al., 2010; reviewed in Blanar et al., 2009; Marcogliese and Pietrock, 2011). In the case of parasite induced behavioral modification post infection, the infection risk can be homogeneous with respect to space, time, host size, age, gender, or social rank, but successful infection of the parasite leads to a direct and repeatable change in the behavior of the infected host that can result in the spatial aggregation of infected hosts (Curtis, 1993; Levri and Fisher, 2000; Lefe`vre et al., 2008).

An alternative, but rarely considered, explanation for the persistence of spatial aggregation in parasites is spatial heterogeneity in host quality. In parasite-host interactions, the host represents habitat for the parasite, and it follows that the quality of that habitat (host) could greatly impact the fitness of the parasite. For example, in sexually transmitted pathogens, there is a significant reduction in net reproductive rate (R_0) when infected hosts become too ill to copulate (e.g., Ward, 2007). Strong links between host condition and parasite fitness have also been reported in ectoparasites (Tschirren et al., 2007), trematode-snail systems (Seppällä et al., 2009), and fungal-zooplankton systems (Gower and Webster, 2004; Hall et al., 2009a). Thus, in situations where host quality directly impacts parasite survival, growth, reproductive output, or

transmission opportunity, and where host quality varies over space, we would expect heterogeneities in the prevalence of a given parasite.

While the terms host ‘quality’ and host ‘fitness’ are related, they are not synonymous. Host fitness directly refers to the ability of (and the degree to which) the individual host is able to transfer its genetic information into the next generation. In parasites, host quality is analogous to habitat quality in free-living organisms, and it refers to “the ability of the environment to provide conditions appropriate for individual and population persistence” (McDermid et al., 2005). Because there is a relationship between pathogenicity, a parasite’s ability to transmit, and host condition (e.g., Massad, 1987; Day 2002; Alizon and van Baalen, 2005), it is clear that the ability of any individual host to provide conditions appropriate for the parasite to persist and transmit is important. These conditions may include host resources available to the parasite, the frequency of contact between the host and other competent hosts, host metabolic rate, host size relative to conspecifics, and the temporal stability of conditions inside the host (e.g., Harvey and Gols, 1998; Bize et al., 2008; Rigaud et al., 2010).

Here, we demonstrate that host quality is a strong correlate with the spatial patterning of infection of the eastern mudsnail (*Ilyanassa obsoleta*) by 2 trematodes with very different life cycles (*Himasthla quissetensis* and *Zoogonus rubellus*). Snail quality (as measured by size-corrected mass, feeding rate, energetic cost of infection, and reproductive output for uninfected snails) varies over space, with snails that inhabit the intertidal pannes of the marsh surface being both of higher quality and disproportionately infected by *H. quissetensis* and *Z. rubellus* relative to snails occupying adjacent habitats.

Methods

The system

Tuckerton salt marsh is a 2,460 ha peninsula that juts out into the Great Bay-Little Egg Harbor complex, which is part of the Jacques Cousteau National Estuary Research Reserve (New Jersey; 39° 30' N, 74° 19' W). The near end of the peninsula has been extensively ditched and drained for mosquito control (Lathrop et al., 2000), greatly modifying the hydrology of the marsh, as well as the biota present. This study was conducted at the far tip of the peninsula which is nearly pristine, and which represents the most contiguous, unaltered salt marsh in this region (http://www.bbep.org/char_rep.html).

Ilyanassa obsoleta is a common prosobranch snail in coastal marshes from Florida to the Bay of Fundy, and can reach densities as high as 1000/m² (Curtis, 2005). The ecology of this snail has been extensively studied (see references in Kelaher et al., 2003). It is an exceptionally long-lived species, with many wild-caught individuals being >5-yr-old (perhaps much older; Curtis et al., 2000), and those in captivity approaching 30, or more, yr in age (Curtis, 1995). *Ilyanassa obsoleta* is an opportunistic scavenger that gains most of its nutrition as an algal/biofilm grazer, but will readily feed on carrion (Scheltema, 1964). It is a model species for investigating snail-trematode interactions, and its behavior, infection, and demography for the coastal marshes of Delaware are summarized in Curtis (2002).

Himasthla quissetensis is an echinostome fluke that infects the alimentary tract of birds (namely *Larus* sp.) as an adult. Eggs are passed in host feces, from which miracidia are released and actively infect *I. obsoleta*. Rediae release cercariae that 'sink

and crawl' along benthic surfaces until they are pulled into the incurrent siphon of a molluscan 2nd intermediate host (*Mya arenaria*, *Mytilus edulis*, *Pecten irradians*, *Ensis* sp. or *Crepidula* sp.), where they encyst on the gills and mantle flaps, and wait to be eaten by the bird definitive host, thus completing the life cycle (Stunkard, 1938a; Cheng et al., 1966).

Zoogonus rubellus is a plagiurchiid digenean parasite of the digestive tract of fish definitive hosts (namely *Paralichthys* sp., *Opsanus tau* and *Anguilla* sp.). Eggs are passed in feces, and the free living miracidium infects *I. obsoleta*. Tailless cercariae actively penetrate the body wall of a polychaete 2nd intermediate host (predominantly *Nereis virens*), which are eaten by the fish host, completing the life cycle (Stunkard, 1938b).

Field survey

We surveyed each of 4 distinct habitats (3 replicates each) in which *I. obsoleta* occurs (coastal flats, subtidal creeks, intertidal creeks, and intertidal pools/pannes; Fig. 1a) on a monthly basis from 2006-2009. Whenever possible, at least 30 snails, and no more than 50, were collected from each of the 12 sites each mo. In contrast to the system described by Curtis (2005), snails often remain in the intertidal creeks and pannes through the winter, but burrowing behavior of the snails and icing over of these habitats prevented regular collections during winter mo. Snails were measured (length from the apical whorl to anterior tip of aperture and diameter at widest whorl) and dissected. After removing the shell, the wet tissue mass of the snail was also recorded. Habitat-specific data were separated by both gender and size classes. Three size classes were established based on shell volume instead of shell length, because older snails often have

broken and/or eroded apical whorls, and are much wider than younger snails of equal length. Thus, measuring length alone would distort the relationship between length and mass. Additionally, mass was predicted to increase linearly with volume, but not with body length. The 3 size classes we used roughly match those of Curtis (1995, 2009), with the smallest size class containing ~8- to 15-mm snails, the medium class containing ~16- to 22-mm snails, and the largest class containing snails ~23- to 30-mm long (no snails were larger than 30 mm). Parasite identification was aided by Shell (1970) and McDermott (1951).

Snail condition, movement, and infection across habitats

Snail infection varied drastically and predictably across marsh habitat types (see Results). One possible explanation for the strong pattern could be differential dispersal post-infection (PI). To determine dispersal patterns for snails in each habitat type, we conducted mark-recapture experiments. Initially, 800 snails were collected from coastal flat site 1, tagged by gluing 2.38-mm numbered Floy Tags[®] onto the shell, and released back into coastal flat site 1 and the adjacent intertidal panne site 1 (400 each) in the spring of 2008. These sites were chosen because of the large size of the intertidal pool and its proximity and connectedness to the open coastal flat (see Fig. 1b). Snails were recaptured during monthly collections of unmarked snails, and their precise location was recorded using GPS. Coordinates at these sites can be measured at a resolution of ~30 cm x 30 cm. Snails were recaptured during each of our monthly field surveys, and readily intermixed with unmarked conspecifics. Because pannes represent closed, relatively small areas when compared to open coast sites, and because the snails often

bury themselves during turbulent wave action, the recapture effort in coastal areas was much greater than that of panne habitats. The objective was to produce similar numbers of recaptured snails, as opposed to spending equal time searching in each habitat. It is important to note that this did not enable us to directly address migration post-infection, i.e., we did not establish infection status prior to release, but any differences in the immigration-emigration rates (which were measured here) could be important in identifying the underlying mechanism(s) for the observed infection pattern and snail habitat preference.

To establish snail growth and infection rates in respective habitat types (coastal flats, subtidal creeks, intertidal creeks, and intertidal pools/pannes), an enclosure experiment was conducted in the summer of 2008. Snails were collected from intertidal creek site 2, measured, weighed, marked, and placed into inclusion cages in each type of habitat. We collected from the intertidal creek site because: (1) snails were unlikely to be infected; (2) snails in this site show little migration, increasing the chances that multiple generations would be related (offering a partial control for genetic variation); and (3) the distribution of snail sizes was most even here (allowing us to evaluate growth rates across all size classes). The inclusion cages were each 1 m³ volume and were open on the top and bottom, allowing the snails to move, eat, and mate on a natural substratum. One hundred snails were placed in each cage. The top was bent inward at an acute angle, to prevent snails from escaping from the top, but still allow food stuffs (carrion, *Ulva sp.* etc., to enter during high tides). Three, 10 cm x 10 cm tiles were secured at the inside base of each cage (previous trials revealed that snails would actively lay eggs on this surface). The tiles were removed and egg masses were counted at the end of peak

production (late May-early June). Directly measuring individual reproduction in each cage was impractical, but per capita values were approximated, excluding infected individuals (which are castrated), and males.

Snail feeding behavior

Intertidal pannes might offer superior food resources for snails, and we predicted that infected snails would spend more time feeding, to offset the energetic cost of infection. In laboratory manipulations, we used cercariae production and host weight loss as proxies for the energetic cost of parasitism. To determine if infected snails offset the energetic cost of cercariae production by consuming more, we conducted a feeding experiment. The infection status of each snail was determined by conducting 24 hr cercariae emergence collections on individual (isolated) snails. Snails were labeled and measured as described above. We chose snails from intertidal panne sites to insure a high prevalence of infection. Thirty snails infected with *H. quissetensis* and 30 uninfected snails were weighed and placed in 45- to 50-ml clear, straight-sided jars filled with pre-mixed salt water (28 ppt) in the morning, and were covered (mesh screening) and left until the following morning. All snails received a dried pre-made food pellet containing a 1:1 mixture of macerated *Ulva* sp. and fishmeal made in-house. Each pellet was weighed prior to adding it to the jar. At the end of each 24-hr period, each snail was removed and weighed, and the water from each jar was passed through a Buchner funnel containing a Whatman ® hardened ashless filter, which collected the remaining pelleted food. The remaining food was dried, weighed, and the change in mass for both the snail and the food pellet was recorded. This process was repeated 2 additional

(nonconsecutive) days, so that each snail was subjected to the experimental treatment 3 times.

In a separate experiment, we repeated the treatments described above, and measured cercariae emergence rates for snails infected with *H. quissetensis*, to estimate the mass lost in cercariae production during any given 24-hr period. Twenty uninfected snails were used as a control group for measuring mass loss over the 24-hr collection period. These snails received a ‘fasted’ treatment, in which no food was added during the collection period. Another 20 infected snails received the same ‘fasted’ treatment. A third group of 20 snails (infected) received a food pellet as described above. At the end of each 24-hr period, snails were removed and weighed, and cercariae were filtered out by the same method as described above. The filter containing cercariae was stained using a weak dilution of Gram’s iodine, and all cercariae were counted using a dissecting scope. This program was conducted for 3 consecutive days in order to estimate the daily variation in cercariae emergence from individual infected snails. Snails were necropsied following this trial to confirm infection status.

Statistical analyses

During pilot surveys in 2006, we assessed the biotic and abiotic characteristics of the various habitats observed in the Tuckerton salt marsh. The variables recorded were pH, salinity, temperature, conductance, dissolved O₂, depth, and the presence or absence of *Fundulus heteroclitus* and *Spartina alterniflora*. We initially examined 32 collection sites (8 replicates of 4 habitat types; coastal flats, intertidal pannes, isolated pannes, and intertidal + subtidal creeks). Because data points were missing for 4 collection sites, only

28 of the original sites were used in this analysis. These data were used in an ordination analysis (Canonical Correlation Analysis) to determine the degree of similarity between habitat types.

A global null model was constructed to determine the probability of co-occurrence for each pair of trematodes in a given individual. In each pair-wise combination, infection by each species was assigned randomly to the entire data set, based on overall prevalence values. For example, if the prevalence for a given species is 0.079 (394 snails of 4980 sampled), then those 394 infections would be randomly assigned to numbers between 1 and 4980. This would be aligned with the infections randomly assigned to a second draw for another species, and the shared numbers between random draws represent concomitant infections. This was iterated 100 times (rarefaction curves demonstrated that the null model arrived at the true variation around each mean very quickly) for each parasite pair, and we evaluated whether or not the observed frequencies of co-occurrence represented outliers beyond a 95% confidence interval. This null model method is similar to the C-score index of Stone and Roberts (1990) recently used by Zimmermann et al. (2011).

Because the method used in our global null model is highly conservative and is known to underestimate the expected frequency of double infections due to intraguild (trematode-trematode) interactions (Lafferty and Kuris, 1994), we used a second type of null model that is based on the observed habitat-specific prevalence values. Again, the prevalence value for each trematode species in a particular habitat was used to seed the model, and infections were randomly assigned to individual snails. This was iterated 1000 times, and co-infections occurred each time a snail was assigned two trematode

species. This process was performed for each species pair in each habitat type. Given that prevalence values varied greatly across habitat types, this method is much more likely to detect exclusion (when a dominate species excludes or replaces a subordinate one) or facilitation (where infection by one species increases the likelihood of infection by another). However, in almost all cases, prevalence values from individual samples were insufficient to calculate mean and variance for prevalence values. Thus, observed prevalence values represent a single point of pooled data, and we simply asked if these points fall outside of the 95% confidence limits derived from each null model. Likewise, we did test for patterns of co-occurrence over time.

To evaluate the differences between timed pairs, i.e., any 2 seasons, we performed a nonparametric Wilcoxon Matched-pairs Test using the statistical package GraphPad Prism. To determine the significance of the observed differences in prevalence between habitat types, we performed a 2-way ANOVA (which asks how the response variable, prevalence, is affected by 2 factors, habitat and season), followed by pair-wise Bonferroni post-tests. While infection was strongly correlated with habitat type, the observed patterns might also be explained by snail size, sex, or collection season. To assess the roles of multiple variables in predicting infection status, we constructed a generalized linear model (GLM) for each parasite using the statistical software package JMP 8.2 ®. Our model included habitat, season, snail size, snail mass, and snail gender as predictor variables for infection (the response variable). Because snail size and mass were strongly correlated, we combined these 2 variables using PCA to create 1 composite variable. In the GLM, we assumed a binomial distribution with a logit link function.

This method is more appropriate for categorical or dichotomous predictor and response variables (Dickens, 1998).

Results

In total, 4,980 snails were collected and surveyed for larval trematodes (766, 814, 1,610 and 1,790 in subtidal creeks, intertidal creeks, coastal flats and intertidal pannes respectively), however due to missing data on some snails, only 4,532 were used for further analysis. Seven species were identified; *Himasthla quissetensis* (prevalence= 0.0877), *Zoogonus rubellus* (prev.= 0.0897), *Austrobilharzia variglandis* (prev.= 0.0060), *Stephanostomum tenue* (prev.= 0.0051), *Lepocreadium setiferoides* (prev.= 0.0014), *Gynaecotyla adunca* (prev.= 0.0028), and 1 un-identified olphthalmoxiphidiocercaria (prev.= 0.0074). *Himasthla quissetensis* and *Z. rubellus* accounted for 88.6% of all infections, and were strongly associated with intertidal panne habitats (Figure 2). While these 2 species made up the majority of observed infections, there were significantly fewer concomitant infections than predicted by our overall null model (5 co-occurring infections compared to a null prediction of 15.68 ± 9.43 ; $P = 0.014$). This was more pronounced in our habitat specific models. The expected number of co-infections by *H. quissetensis* and *Z. rubellus* based on our null model for intertidal pannes was 28.18 ± 2.43 (95% CI), whereas the observed number of co-infections by these two species was three ($P < 0.01$). The co-occurrence of *Z. rubellus* and *A. variglandis* was significantly more frequent than predicted by our null model for intertidal pannes (4 observed co-infections compared to 2.29 ± 0.38 ; $P < 0.01$). No other comparisons that included either of the two dominate species differed significantly from our null models. For most other

comparisons, the observed numbers of co-infections, combined with the rarity of each species, prevented us from determining if the co-infection values deviated from random.

In general, snail populations tended to be highly aggregated and variable, but densities of $>300/\text{m}^2$ often occurred in all 4 habitat types (though less frequently in coastal flats). Snails from intertidal pannes were overrepresented in the two largest size classes compared to those of other habitats (Table I). There was a temporal pattern in the infections by *H. quissetensis* and *Z. rubellus*, with prevalence peaking in late spring-early summer, and steeply declining during winter mo, (2-way ANOVA, $P = 0.0216$ and $P = 0.0112$, respectively). Infection prevalences for both parasites were strongly linked to habitat type ($P < 0.001$ for both), with the highest infections occurring in intertidal pannes and differing significantly from every other habitat type ($P < 0.01$ in all cases; Bonferroni post-tests). Nearly 83% of the snails from intertidal panne habitats fell into the 2 largest size categories, as opposed to 44%, 61%, and 43% in coastal flat, intertidal creek, and subtidal creek sites, respectively. A comparison of size-corrected masses (i.e. grams of snail per unit volume) for snails in each habitat type revealed that snails from intertidal pannes were 4.214% larger than conspecifics from other habitats ($P < 0.05$ in all pairwise comparisons). This pattern was more pronounced in larger snails. Conversely, intertidal pannes displayed a much lower proportion of snails in the smallest size class. While there was some tendency for males to be infected by either *H. quissetensis* or *Z. rubellus* more frequently than females, no strong pattern was detected (but see GLM results below).

The GLM constructed for each parasite revealed different drivers for infection in *H. quissetensis* and *Z. rubellus*, respectively. For both species, the full model was

significantly different from the null model ($p < 0.001$ in both cases). For *H. quissetensis*, habitat was a highly significant predictor of infection status, while season had very little predictive power (Table II). Snail gender and PC1 (size+mass) were also significant factors. A finer analysis of effect sizes suggested that intertidal pannes were the strongest driver ($p < 0.001$), and coastal flats were also highly significant ($p < 0.001$). A similar result was found in our GLM for *Z. rubellus*, where habitat ($p < 0.001$) and season ($p < 0.001$) were highly significant, while snail gender, size, and mass were not. In this case, intertidal pannes, coastal flats, and autumn seasons were the only significant predictor variables. Based on these results, even when accounting for snail size and gender, the presence or absence of infection is most strongly correlated with intertidal pannes and coastal flats, respectively.

We successfully recovered 145 snails in our mark-recapture study. The observed dispersal pattern was unidirectional, with 22 of the snails released in coastal flat 1 moving into intertidal panne 1 (Fig. 1b). However, no snails released from the intertidal panne moved out of the surface marsh and into the coastal flats, even though these sites are separated by as little as 12 m at the pool's nearest end. In general, snails did not disperse far from their release points, with the maximum dispersal being 41.7 m, and the mean being 8.4 m (assuming straight-line distances). Several marked snails were recaptured within a m of their release point, though we suspect that they meander around the general area. Additionally, many of the snails in intertidal pannes overwintered there, and were collected either during the winter mo, or the following year.

In our caged enclosure experiment, there was no significant relationship between habitat type and mass added for snails up to ~18 mm (680 mm^3). However, snails caged

in intertidal pannes that were 18 mm, and larger, were significantly heavier at the time of recollection than those from coastal flat 1 as determined by a 2-way ANOVA ($P = 0.002$; Figs. 4a, b). Additionally, 23 new infections (13 *Z. rubellus* and 10 *H. quissetensis*) occurred in the intertidal panne, while only 1 new infection (*Z. rubellus*) occurred in the coastal flat, and there were no new infections in either the intertidal creek or subtidal creek sites (Fig. 4c). Finally, per female egg mass production in intertidal panne sites was significantly higher than either intertidal creek sites or coastal flat sites (2-tailed t -test, $P = 0.0017$ and $P = 0.0001$ respectively; Fig. 4d). Egg production in intertidal creeks was also higher than in coastal flats ($P = 0.0011$). Because several tiles were lost from subtidal creek sites, the sample size was too low to detect any significant pattern for comparisons to other habitat types.

Our feeding experiment demonstrated that, per capita, infected snails tended to consume a larger proportion of their body mass ($9.606\% \pm 1.623$) than those that were uninfected ($8.519\% \pm 0.667$). Cercariae emergence varied dramatically over the 3-day measuring period, with an average variation (change in cercariae production between any 2 days for the same snail) of 323.76 ± 288.37 , and total daily production ranging from 0-1208 cercariae. There were no differences in daily cercariae production per snail between those that were fasted and those that were fed (399.94 ± 263.42 and 369.78 ± 206.20 , respectively). There was a significant difference between the average mass lost per 24-hr period for snails that were infected and fasted compared to those that were uninfected and fasted ($P = 0.0258$; Fig. 3), but not those that were infected and fed ($P = 0.1269$). There was no correlation between the mass of the snail and the number of cercariae it produced. Using a simple multiplicative scaling up of cercariae mass

calculated for *H. elongata* in Thieltges et al. (2008), the average cercariae biomass leaving infected snails was $0.012 \text{ g/day} \pm 0.007$ (approx 1.9% of the snails body mass).

Discussion

This study demonstrates that heavy infections and high prevalence values of both *H. quissetensis* and *Z. rubellus* in the mudsnail (*I. obsoleta*) are spatially restricted to intertidal pannes where the quality of the snail hosts is high. Snail hosts in these habitats are larger and more fecund than snails recovered from adjacent creeks or coastal flats, and snails relocated to these sites did not disperse to other sites. The pattern is likely a consequence of each parasite's life cycle, as caged snails in the intertidal pannes are more likely to be infected when compared to conspecifics confined to other habitats. Habitat was the best predictor of infection status, even when simultaneously considering other potential variables like snail size, gender, or collection season; this is in agreement with several other reports (Wullschleger, and Jokela, 1999; Smith, 2001; Knudsen et al., 2004; Durieux et al., 2010). However, our study also demonstrates that the quality of the host snails is tightly linked to the spatial heterogeneity of these parasite infections. Host quality is known to be important to parasites (e.g., Vinson, 1976; Tschirren et al., 2007; Hall et al., 2009b), and our study demonstrates measurable differences in snail quality across habitats. The size-corrected masses of snails (one surrogate for host quality) in intertidal pannes are greater than those of snails in other habitats and the pannes are populated with a greater proportion of snails from the largest size class. Additionally, snails also add mass more rapidly, and the per capita egg production of snails was much greater in intertidal pannes.

The observed differences in host quality across habitat types may be strongly linked to the abiotic and biotic characteristics specific to each habitat. Intertidal pannes are shallow depressions in the marsh surface that are tidally flushed by ocean water from the open coast. During our pilot study of the various habitats within the marsh, we found that the pH, salinity, conductance, and temperature of the intertidal pannes are roughly the same as coastal flats, but markedly different from the stagnant conditions of isolated pannes, in which few animals survive. Thus, the intertidal pannes are very hospitable to snails but, in contrast to coastal flats, are protected from wave action, largely because of the massive stands of tall-form *Spartina alterniflora* that grow around these depressions. Wave action and turbulence are known to induce burrowing behavior in these snails (Levinton et al., 1995), and this would reduce feeding/scavenging and mating opportunities in coastal flats and subtidal creeks. Evidence also suggests that intertidal pannes provide significantly better habitat in terms of nutrition. As tides come in, *Ulva* sp. and carrion (two high quality staples of the mudsnail diet; Curtis and Hurd, 1979; Hurd, 1985; Giannotti and McGlathery, 2001) get washed into these depressions, and are left behind as the tide goes out. Our mark-recapture study indicates that snails disperse into intertidal pannes from adjacent habitats, but seldom leave (in contrast to the migrations described by Cranford, 1986 and Curtis, 2005, where snails move into deeper subtidal areas for the winter). We have observed several marked snails near their original release point on the marsh surface for 3 consecutive yr. Nevertheless, no pattern of genetic isolation has ever been reported from populations of *I. obsoleta* because the species is able to disperse as planktonic veliger larvae (Gooch et al., 1973; Diaz-Ferguson

et al., 2010), and it is unlikely that any habitat is populated as a result of intentional movements of adult snails.

From the perspective of the parasite, the observed differences in host quality (as well as habitat characteristics) appear to be important. Our feeding experiment suggested that there are significant energetic costs to parasitism for these snails. Cercariae production did not vary between fed and fasted snails, meaning that a significant amount of energy is being derived from the snail host regardless of host condition. On average, daily cercariae production was 1.9 percent of the snail's total mass (excluding shell mass), and snails that were fasted lost a larger proportion of their body mass than those that were fed during the experiment. This finding, taken with the observation that snails in intertidal pannes are heavier and add mass more rapidly, suggests that infected snails are much more likely to meet the increase in nutritional requirements while in intertidal pannes. While we did not directly measure parasite induced mortality in situ, numerous studies have argued that trematode infection is the greatest source of adult snail mortality (Brenchley 1982, and references therein), further suggesting that host quality is an important feature of intertidal pannes.

Our caged experiments show that test snails were infected by *H. quissetensis* and *Z. rubellus* more frequently when confined to intertidal pannes than when confined to coastal flats. This is strong evidence for increased host-parasite encounter rates in intertidal pannes (though we cannot rule out the possibility that habitat characteristics in intertidal pannes could modify host defenses or physiology such that host susceptibility is lowered). This interpretation is reinforced by the fact that definitive host species may be disproportionately present in these habitats (see below), and by a putative reduction in

encounter rates in the coastal flats. Most of the snails collected in coastal flats during mid-high tide were buried in the sediment, and this could reduce the contact rate between active miracidia and competent snail hosts (Fingerut et al., 2003; and argued in Curtis, 2009).

The spatial and temporal overlap with downstream hosts in intertidal pannes may also be a significant factor in producing aggregation in parasite infective stages. With both parasites, the downstream hosts are strongly associated with the intertidal pannes. For example, in *H. quissetensis*, 2nd intermediate hosts *Geukensia demissa* (Atlantic Ribbed Mussel) and *Mytilus edulis* (Blue Mussel) aggregate in large clumps around emergent patches of *Spartina* sp. that are associated with these habitats (Bertness and Grosholtz, 1985; particularly in the Tuckerton salt marsh [Sherwood and Petraitis, 1998]). In addition, the most common definitive hosts, gulls (specifically *Larus argentatus*), are frequently associated with uppertidal habitats of salt marshes, including intertidal pannes (Erwin et al. 1981), and the spatial distribution of definitive hosts (especially birds) is known to be an important predictor of infection pattern of intermediate hosts (Bustnes and Galaktionov, 1999; Skirnisson et al., 2004; Hechinger and Lafferty, 2005; Fredensborg et al., 2006). Similarly, for *Z. rubellus*, the predominant 2nd intermediate host, *Nereis diversicolor*, is strongly associated with *Spartina* sp. stands in intertidal pannes (Paramor and Hughes 2007), and the definitive hosts, *Opsanus tau* (toadfish), *Anguilla rostrata* (American eel) and *Paralichthys dentatus* (summer flounder) spend much of their time in intertidal creeks and pannes (Shenker and Dean, 1979; Burke et al., 1991). This means that the requisite hosts (and, consequently, the

parasite infective stages) may be both abundant and spatially overlapping in intertidal panne habitats.

Here, we identify a strong correlation between habitat type and the spatial patterning of infection by *H. quissetenis* and *Z. rubellus*. Additionally, we show that snails from intertidal pannes are larger, more fecund, grow more rapidly, and are more likely to be infected by either parasite when compared to conspecifics from other habitats. These findings support the idea that spatial heterogeneity in parasite prevalence could be explained by a scenario in which the life cycle of each trematode species leads to increased contact of miracidia with high quality snail hosts (which is itself driven by habitat). Several other studies have discovered positive relationships between host condition and parasite fitness (e.g. Gower and Webster, 2004; Tschirren et al., 2007; Hall et al., 2009; Seppällä et al. 2008), but have not considered these as mechanisms that could promote spatial patterns in parasite infection. Our study provides evidence that heterogeneities in the prevalence of a parasite can arise in situations where host quality varies over space.

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Figure 2.1: (a) Map of the tip of Tuckerton Peninsula indicating the location of all collection sites for the 4 habitat types. Inset – site of mark recapture studies. (b) Expanded image of inset in Figure 1a of adjacent sites used in the mark-recapture study (intertidal panne 1 and coastal flat 1). Dots indicate recollection points for individual snails at a resolution of ~30cm x30cm. Black dots = released into intertidal panne snails; white dots = released into coastal flat snails. Of the 800 individuals released (400 per site), 145 were recaptured. Snails released in the intertidal pannes did not migrate into adjacent habitats.

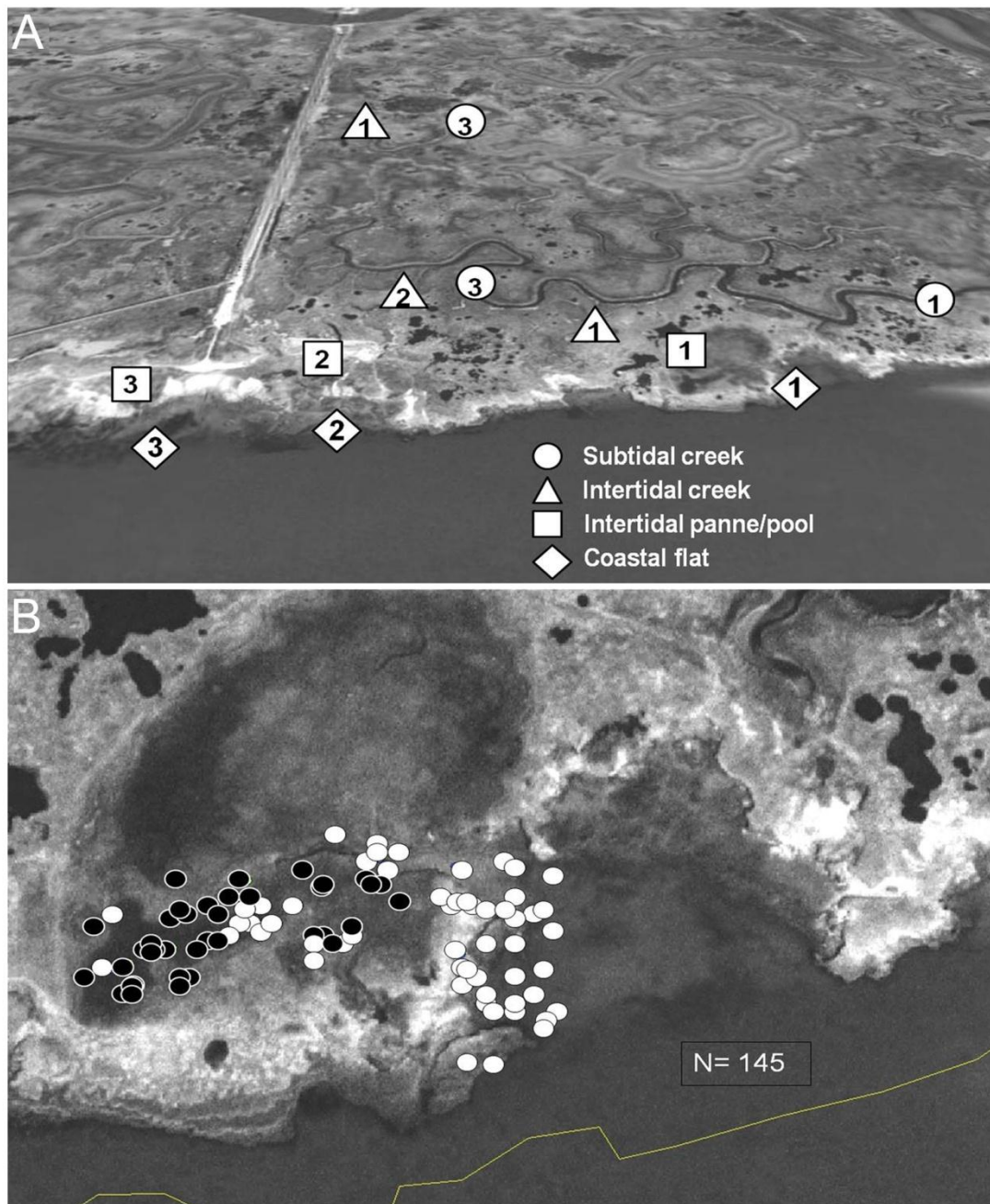


Figure 2.1

Figure 2.2: Seasonal patterns of prevalence for *H. quissetensis* (a) and *Z. rubellus* (b) in four habitat types (intertidal pannes, intertidal creeks, coastal flats and subtidal creek). Monthly data has been collapsed into 3-mo periods (e.g. Spring= March, April and May; Summer = June, July and August; etc.). Snails from intertidal pannes have significantly higher prevalence of both trematode parasites relative to snails from other habitat types, across all seasons. All habitats show significant decreases in infection prevalence in the fall seasons of 2007 and 2008.

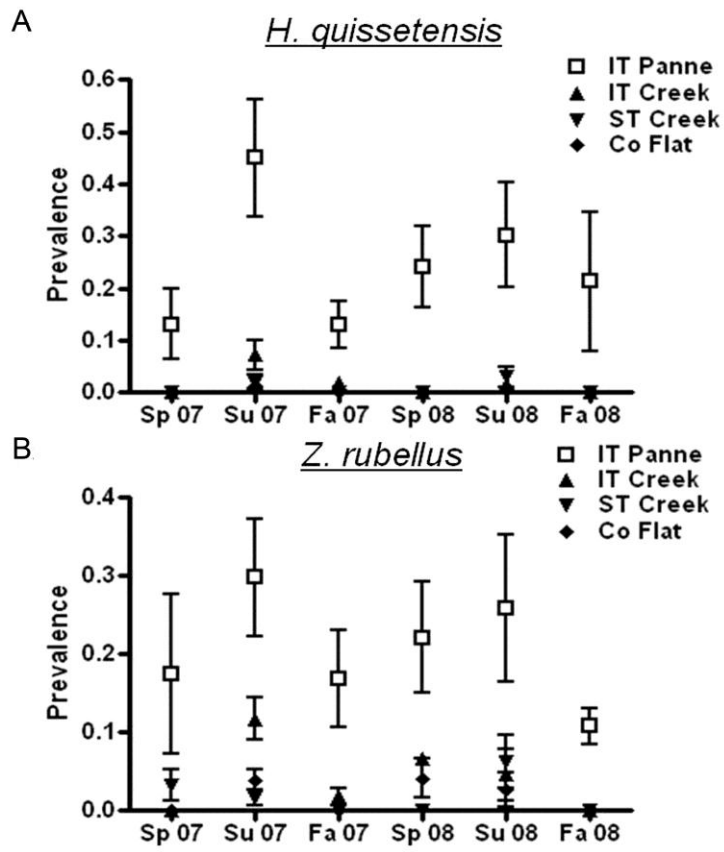


Figure 2.2

Figure 2.3: Graphical presentation of our Canonical Correlation Analysis (CCA).

Variables included normalized data for salinity, depth, temperature, pH, conductance, and the presence of *Fundulus* sp. and *Spartina* sp. Canonical transformations (axes) attempt to maximize the separation between the dependent variable, in this case habitat type.

While intertidal pannes and open coastal flats can be clearly separated, they are more similar to each other than to isolated pannes, with tidal and subtidal creeks representing transitional habitats across Canonical 1.

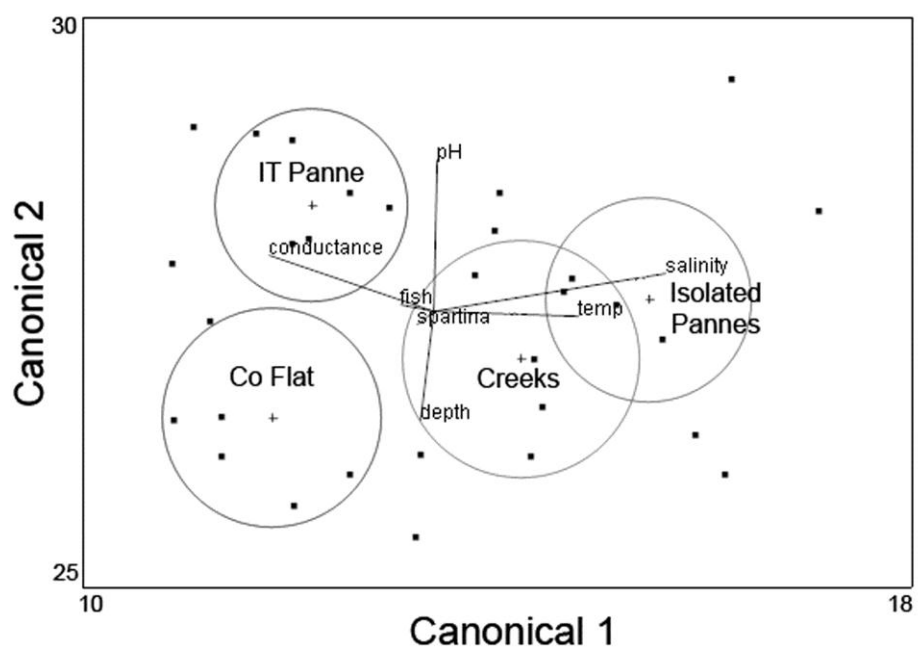


Figure 2.3

Figure 2.4: (a) Mean mass of snails in the medium size class following our enclosure experiment. Tukey's Multiple Comparison Test revealed that the mean value for intertidal pannes was not significantly different from the coastal flat, but did differ from intertidal and subtidal creeks ($P < 0.01$ in both cases). (b) Mean mass of snails in the large size class following our enclosure experiment. In this case, the mean for intertidal pannes differed significantly from all other habitats ($p < 0.05$ for all). (c) Incidence of new infections during the enclosure experiment. New infections were almost entirely confined to intertidal pannes. (d) Per capita egg production in each habitat during the enclosure experiment. Subtidal creeks were excluded due to missing data (resulting from destroyed tiles during the experiment). Per capita production was statistically higher in intertidal pannes.

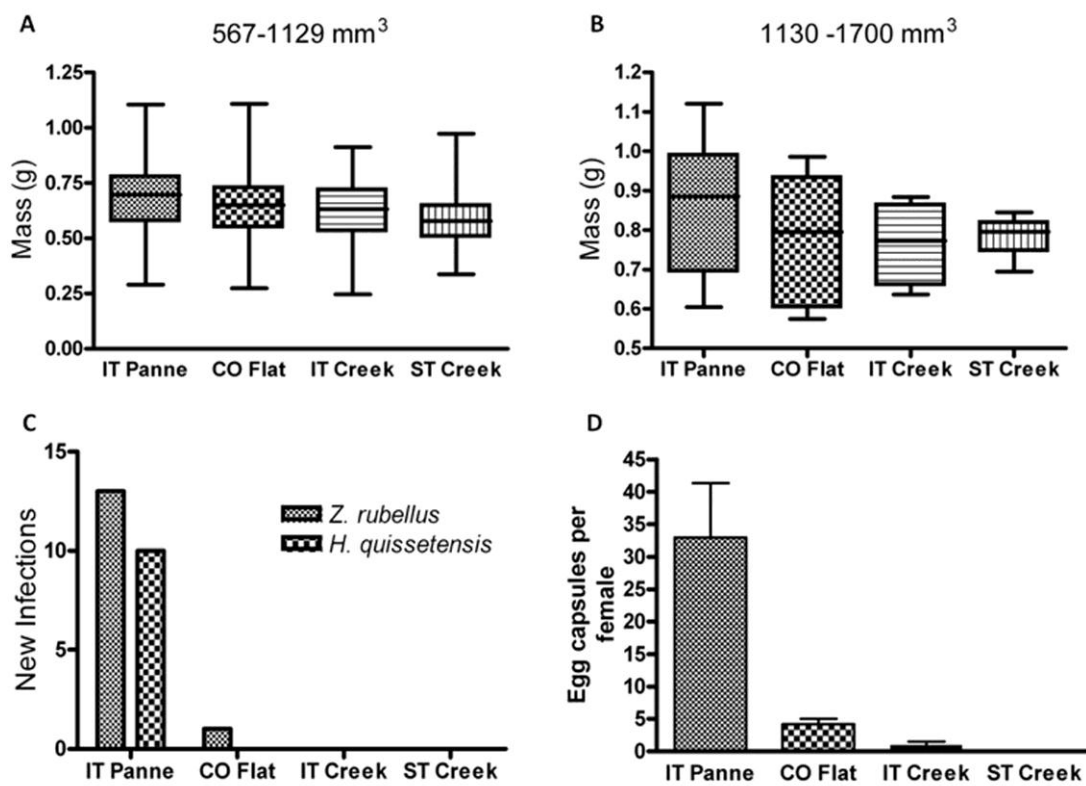


Figure 2.4

Table 2.1: The infection prevalence and average mass of the 3 snail size classes in each habitat. The mean mass of snails in intertidal panne habitats is greater than other habitat types. Additionally, a larger proportion of snails in intertidal pannes are in the largest size class, suggesting increased growth rates, or higher survivorship in these sites, or both.

| | 0-566 mm³ | | | | 567-1129 mm³ | | | | 1130-1700 mm³ | | | |
|----------|---------------------------------|-----------------|--------------------------|------------------------|------------------------------------|-----------------|--------------------------|------------------------|-------------------------------------|-----------------|--------------------------|------------------------|
| | prop. | mean mass(g) | <i>H. quiss</i> prev. | <i>Z.rub.</i> prev. | prop. | mean mass(g) | <i>H. quiss</i> prev. | <i>Z.rub.</i> prev. | prop. | mean mass(g) | <i>H. quiss</i> prev. | <i>Z.rub.</i> prev. |
| IT Panne | 17.3 | 0.445 | 0.101 | 0.134 | 71.2 | 0.695 | 0.268 | 0.192 | 11.5 | 0.977 | 0.42 | 0.089 |
| CO Flat | 55.3 | 0.477 | 0.011 | 0.019 | 40.6 | 0.642 | 0.016 | 0.037 | 4.1 | 0.778 | 0 | 0.063 |
| IT Creek | 38.1 | 0.437 | 0.034 | 0.027 | 57.5 | 0.669 | 0.018 | 0.045 | 4.4 | 0.823 | 0.006 | 0.03 |
| ST Creek | 56.6 | 0.420 | 0.015 | 0.044 | 41.0 | 0.616 | 0.070 | 0.028 | 2.9 | 0.794 | 0 | 0 |

Table 2.2: Output of our Generalized Linear Models (GLM) for both parasites. Overall significance values of each predictor variable indicate that habitat type was the most powerful predictor of infection status for both parasite species. For *Himathsla quissetensis*, both snail gender and size+volume (PC1) were also significant. Within the habitat variable, intertidal panne (ITP) and coastal flats (COF) were the most significant terms. For *Zoogonus rubellus*, habitat and season were the only significant predictor variables, and intertidal panne (ITP), coastal flats (COF) and the Fall season were the most significant terms. DF = degrees of freedom, L-R ChiSq = Likelihood Ratio Chi-Square, prob>ChiSq = the probability under the null hypothesis of observing a Chi-square statistic as large, or larger, than the actual value, i.e., the *P*-value.

| <i>H. quissetensis</i> | | | | <i>Z. rubellus</i> | | |
|------------------------|-----------|------------|------------|--------------------|-----------|------------|
| Source | DF | L-R ChiSq | prop>ChiSq | DF | L-R ChiSq | prob>ChiSq |
| Habitat | 3 | 242.5226 | 2.71E-52 | 3 | 122.2468 | 2.53E-26 |
| Season | 3 | 1.249 | 0.7413 | 3 | 35.9145 | 7.81E-08 |
| Sex | 1 | 4.5927 | 0.0321 | 1 | 1.493 | 0.2218 |
| PC1 | 1 | 12.1568 | 0.0004 | 1 | 0.9289 | 0.3351 |
| Term | L-R ChiSq | prop>ChiSq | L-R ChiSq | prob>ChiSq | | |
| Intercept | 283.8924 | 1.07E-63 | 309.0995 | 3.43E-69 | | |
| Habitat[COF] | 25.303 | 4.90E-07 | 13.9804 | 0.0002 | | |
| Habitat[ITC] | 5.8775 | 0.01533 | 1.929 | 0.1649 | | |
| Habitat[ITP] | 194.8185 | 2.82E-44 | 113.5825 | 1.61E-26 | | |
| Season(fa) | 0.7155 | 0.3976 | 19.7429 | 8.86E-06 | | |
| Season(sp) | 0.4908 | 0.4836 | 0.4127 | 0.5206 | | |
| Season(su) | 0.8052 | 0.3976 | 0.6495 | 0.4203 | | |
| Sex[f] | 4.6827 | 0.0305 | 1.493 | 0.2218 | | |
| PC1 | 43.457 | 4.33E-11 | 0.9289 | 0.3351 | | |

CHAPTER 3

Exploitation of asymmetric predator-prey interactions by trophically transmitted parasites

[Oikos. 2011. 120(4): 607-614]

Abstract

The directionality of asymmetric interactions between predators (definitive hosts) and prey (intermediate hosts) should impact trophic transmission in parasites. This study tests the prediction that trophically transmitted parasites are funneled towards asymmetric predator-prey interactions where intermediate hosts have few predators and definitive hosts feed upon many prey ('downward asymmetry'). The distribution of trophically transmitted parasites was examined in four published food webs in relation to mismatch asymmetry of predator-prey interactions. We found that trophically transmitted parasites exploit downwardly asymmetric interactions in a nonrandom manner, and particular predator-prey pairs contain more trophically transmitted parasites than would be expected by random chance alone. These findings suggest that food web topology has great bearing on the ecology of trophically transmitted parasites, and that consideration of parasite life cycles in the context of food web organization can provide insights into the forces affecting the evolution of trophic transmission.

Introduction

In parasites with complex life cycles, trophic transmission represents a unique situation in which the parasite's survival and transmission is completely dependent upon predation of one smaller intermediate prey host by a larger predatory definitive host

(Lafferty 1999; Kuris 2003; Parker et al. 2003; Choisy et al. 2003; Gandon 2004). The way in which this single predator-prey link is integrated into the larger community may greatly influence the stability of the interaction (Allesina and Pascual 2008; Dambacher et al. 2002), and simple predictions can be made regarding the types of predator-prey interactions that will favor the trophic transmission of parasites. We argue that parasites should preferentially exploit predator-prey interactions that are downwardly asymmetric (i.e. one predator species feeding on many prey species) because highly linked generalist predator hosts would be more resistant to dynamic cycling and would be less likely to have dramatic impacts on any one prey host (Purvis et al. 2000, Layman et al. 2007). As an evolutionary response, this would be consistent with the idea that trophic transmission is favored when interactions between predator and prey hosts are stable and predictable over evolutionary time (Price 1980, Thompson 1982; Combes 2001). Parasites would also benefit from these interactions because they reduce the dilution effect of propagules wasted on non-host predators. In this paper, we use data from published foodwebs (and one unpublished) to test the prediction that trophically transmitted parasites tend to exploit downwardly asymmetric predator prey interactions.

From the perspective of the parasite, four basic types of predator-prey interactions are available for trophic transmission; strongly symmetric, upwardly asymmetric, downwardly asymmetric, and weakly symmetric (Fig. 1). Because the trophic transmission of parasites is contingent upon the predation success of the downstream definitive host, one might (incorrectly) predict that parasites would tend to settle into predator-prey interactions that are symmetrically strong in both directions (Fig 1a). When the predator and prey are strongly interdependent, it presents the parasite with a

guaranteed transmission path in which the prey host will always be eaten by the appropriate predatory host. This assumption is implicit in many studies of the evolution and dynamics of parasite transmission which focus on specific predator-prey interactions among competent host species. However, recent evidence from network theory (and some empirical studies) suggests that strong interactions between specialists may act to destabilize food webs, often leading to highly cyclic “boom-bust” dynamics for each population, and may represent a significant extinction risk for the species involved (e.g. Inuoye 1980; Nachman 1988; Post 2000). Thus, for parasites, strong interdependent interactions are potentially less stable over time.

Weakly symmetrical and upwardly asymmetric interactions should also be inhospitable links for trophically transmitted parasites. Both are likely to be nested in food webs, and are thought to be less susceptible to perturbation (Montoya et al. 2009; O’Gorman and Emmerson 2009). However, prey (intermediate host) with many non-host predators can produce a dilution effect (‘wasted effort’) on parasite propagules, because many infective stage larvae will be transferred to non-host predators (figure 1b). The addition of a noncompetent predator that feeds on an intermediate host will result in a decrease in the probability of successful transmission at a rate of $1/N_p$, where N_p is the number of predators feeding on the focal prey host. Decreased transmission correlates directly with decreased parasite fitness (Lafferty, 1999), and being eaten by non-host predators results in failed transmission (Barber et al. 2000; Keesing et al. 2006).

By this logic, interactions that are downwardly asymmetric should present the best situation for successful transmission of the parasites. These interactions should offer a higher probability of successful transfer from the intermediate host to the appropriate

predatory host, as well as predator-prey interactions that are dependable and stable. The purpose of this study was to test this prediction.

Methods

Asymmetry can be measured as the degree of ‘mismatch’ between two focal species and their associated interactions (Vazquez et al. 2007). In a predator-prey interaction utilized by a parasite, the mismatch would represent the difference between the number of prey species the focal predator feeds on and the number of predators feeding on a focal prey species. The degree of linkage is relevant to the potential dilution effect of infective stage larvae (i.e. having three predators is better than having fifteen regardless of the number of prey the predator has), therefore the number of interaction links for each focal species is made proportional to the total number of links in the network matrix, and is defined as $s_i = 1 - \left(\frac{l_i}{l_t}\right)$ where l_i is the number of feeding links that predator i has and l_t is the total number of predatory links in the matrix. This is the ‘down’ strength or predatory impact of a given species. Conversely, the ‘up’ strength of each prey species can be defined as $s_j = -\left(1 - \left(\frac{l_j}{l_t}\right)\right)$, where l_j represents the number of predators feeding on prey species j and l_t again denotes the total number of predatory links in the matrix. The up strength is made negative so that it mirrors the down strength such that $-1 > (S_i + S_j) > 1$. These species (node) specific values are similar to those evaluated in Chen *et al.*, (2008) wherein degree (the number of nodes directly linked to a given node) is decomposed into the degree in (~diet breadth) and degree out (~the

number of predators a species has). If the sum of the two values is negative, the interaction between the two focal species demonstrates downward asymmetry (the predator has more prey than the prey has predators), whereas a positive value indicates upward asymmetry, and a value of zero will always indicate a symmetrical relationship. The mismatch value was calculated for every predator-prey interaction in each food web matrix.

From the perspective of the parasite, a problem arises with this calculation because a larval parasite may utilize multiple hosts at a given stage of its life cycle. For this reason, treating each mismatch value for predator-prey interactions as independent biases the analysis against detecting any relationship between patterns of mismatch and selection against the dilution effect. We introduced a correction in which multiple downstream hosts (predators) for a given parasite are collapsed into one, because, assuming equal interaction strengths among relevant (linked) host predators, they will function additively with respect to parasite transmission. For example, if a given intermediate host has seven equally effective predators, and only one of these is a competent host for the parasite, the probability of successful transmission is 0.14. On the other hand, if four of the seven predators act as a downstream host for the parasite, the probability of successful transmission will be 0.57 (instead of 4 independent values of 0.14), and this additive property must be accounted for. A similar correction was introduced for parasites that utilize multiple intermediate hosts that are all prey for a definitive host.

We evaluated the position of trophically transmitted parasites relative to predator-prey asymmetry in three published food webs that contain parasites; a Pinebarrens

blackwater stream in NJ (Hernandez and Sukhdeo 2008), the Carpinteria salt marsh (Lafferty et al. 2006a) and Ythan estuary (Huxham et al. 1995). The Carpinteria Salt Marsh food web was divided into two separate matrices; the less complex matrix of known interactions (Carpinteria) and a larger matrix of known and putative interactions (Carpinteria KP). Also included in these analyses is a foodweb of a salt marsh in Tuckerton, NJ that was produced as part of this study. Tuckerton salt marsh is a 2460 hectare peninsula that juts out into the Great Bay-Little Egg Harbor complex, which is part of the Jacques Cousteau National Estuary Research Reserve. The food web matrix was constructed using a combination of survey and feeding interaction data from the NJDEP, Rutgers University Marine Field Station and three years of field collections by the authors (data and references are available upon request). Some feeding interactions were assumed based on additional literature from studies conducted in other salt marshes in the region (i.e. Connecticut to Delaware/Maryland; e.g. Fell et al. 1982; Kreeger et al. 1988; James-Pirri et al. 2001). Together these five matrices present a gradient of increasing species richness; 48-112 free living taxa, 216-1300 predator-prey links and 30-517 links being exploited by trophically transmitted parasites.

The interaction asymmetry measures were not normally distributed, and we used MATLAB to construct a null model to determine if the mean asymmetry value for interactions exploited by trophically transmitted parasites differed from the mean of randomly selected interactions in the matrix. In the null model, a defined number of observed predator-prey interactions being exploited by parasites (the number of exploited links in the original matrix) were randomly assigned to each matrix, and this process was iterated 1000 times for each matrix. Trophic level could also potentially be a

confounding factor in the placement of trophically transmitted parasites (for example, no parasites are transmitted from autotrophs to herbivorous heterotrophs), and thus, the trophic level of each predatory species was determined, and the distribution of asymmetry values for each trophic level were evaluated. Trophic level is traditionally determined by adding one to the mean value of all trophic levels a particular species feeds upon, but this can lead to artifacts that might obscure the actual predatory role of some species. For example, a generalist top predator may feed on many trophic levels, and thus assigned to a lower trophic level than a specialist top predator. In this study, we simply assigned predators to the level above the level of their highest prey item. Intraguild predation on juveniles was excluded from this determination.

Different parasite species may come to exploit the same predator-prey links in a nonrandom manner if trophically transmitted parasites were being funneled towards particular predator-prey interactions. Thus, a second null model was used to predict the probability distribution of any given link acting as a transmission path for more than one parasite species. The total number of links utilized in parasite transmission were randomly re-assigned to the matrix (1000 iterations) where predator-prey links were allowed to be repeatedly sampled. The distribution of links utilized and the number of parasites using any given link were compared to the observed patterns in each web.

The random assignment of trophically transmitted parasites (the null model) using the entire matrix of interactions makes several assumptions that are biologically unrealistic. First, it neglects the role of parasite-host taxonomy in constraining the trophic interactions available to any given parasite species. However, subgroups of interactions specific to parasite or host taxa were too few to perform any meaningful

resampling procedures. The second assumption in our global null model is that the trophic level of the host does not constrain parasite exploitation. However, our results suggested that trophic level does influence the presence or absence of trophically transmitted parasites. In order to disentangle the roles of these factors, and to determine the power with which each is able to predict parasite location in each food web, we reconfigured each matrix and extracted the following interaction-specific data: parasite type (trematode, cestode, etc.), definitive host type (fish, bird, mammal, etc.), intermediate host type (fish, amphipod, decapods, bivalve, etc.), the mismatch (asymmetry) value, definitive host trophic level and intermediate host trophic level. The mismatch value summarizes the relative degree of linkage for a predator-prey couplet (i.e. the number of prey a predator has relative to the number of predators a prey has). We then performed a classification and regression tree (CART) analysis on these data using JMP Version 8.0 (2008 SAS Institute), with parasite presence/absence as the dependent variable. This was a single analysis, incorporating all predator-prey interactions for all webs. While the number of predators eating a given prey species (and vice versa) increases as the total number of links in the system increases, this relationship is not linear. Instead, any given prey or predator contributes represents a smaller proportion of the links relative to the total system. Thus, the magnitude and variation around asymmetry values for the smallest food web (Pinebarrens) were larger than those of the largest food web (Tuckerton). A simple standardization procedure was used to make all link values proportional to the smallest system. We used CART analysis because 1) it easily combines continuous and categorical data and 2) it allows us to ask which variable (host taxonomy, host trophic level or interaction asymmetry) more

strongly determines the presence or absence of trophically transmitted parasites (see De'Ath and Fabricius 2000). We used the 'maximize significance' criterion for determining splits, and the k-fold cross-validation procedure to determine the optimal number of splits in the decision tree, and we quantified the predictive power of the decision tree based on the Receiver Operating Characteristic (ROC) curves.

Results

Key network statistics varied across systems, but the distributions of asymmetry values for those predator/prey interactions that were exploited by parasites were all right skewed towards mean asymmetry values greater than one (Figure 2). The mean asymmetry value for links exploited by trophically transmitted parasites differed from the null predictions in each system (Figure 2; T-test p-values for all systems demonstrated means of the null models and observed values were statistically different beyond the 95% C.I.). Because this pattern was confirmed across all systems, it appears robust to changes in species richness, connectance, and the relative number of parasites in each system. For example, the complete Carpinteria KP food web contains 83 free living species and 517 parasite trophic transmission links that demonstrate downward asymmetry. The Tuckerton food web has 112 free living species with only 32 links transmitting parasites, but those links are also downwardly asymmetric. In the case of systems that contain many trophically transmitted parasites (e.g. Ythan and Carpinteria KP), the diversity of utilized links does not increase proportionally with the total number of transmission links (analysis of co-variance indicates that the slopes of the two linear regressions are significantly different; null model slope= 0.57 and s.e.= 0.02, observed slope = 1.61 and

s.e.= 0.26). Instead, the same asymmetric links are repeatedly targeted as the number of trophically transmitted parasites increases, and the proportion of repeatedly utilized links increases at a rate three-fold faster than predicted by our null model (Figure 3). This means that an increase in the number of trophically transmitted parasites in a given system will not result in a reciprocal increase in the number of predator-prey links utilized for trophic transmission, but rather, the same interactions are used by many parasites. Consistent with this pattern, there is a weak but positive relationship (statistically significant in all but the Tuckerton food web) between the number of parasites infecting individual host species and the host's trophic breadth (the number of prey species it feeds on; Figure 4). Parasite exploitation of intermediate hosts did not correlate with number of predators (data not shown). However, there was a significant relationship between the number of predators that fed on an intermediate host and the proportion of those predators utilized by parasites (slope = 0.37, $R^2 = 0.274$, $p = <0.0001$). Asymmetry values varied predictably with trophic level in all systems (Figure 5), with lower trophic levels containing predator-prey interactions that are upwardly asymmetric, and higher trophic levels being downwardly asymmetric.

Classification and regression tree analysis provided an optimum decision tree that had a true positive assignment rate of 98.3%. The first primary splitter detected was the asymmetry metric at either <0.006 or >0.006 (with and without parasites respectively; figure 6). This split accounted for 68.4% of the data, and asymmetry in general made up 48.5% of all decisions in the tree. Predator taxonomy was the second predictor variable, and it was able to exclude 96.5% of the remaining false positive assignments.

Discussion

There has been recent increased interest in questions regarding how parasites might influence the structure and dynamics of host food webs (e.g. Thompson et al. 2005; Sukhdeo and Hernandez 2005; Hernandez and Sukhdeo 2008; Huxham et al. 1995; reviewed in Dobson et al. 2006; Lafferty et al. 2006b, 2008). This study asks how the structure and dynamics of food webs might influence the ecology and evolution of parasite life cycles and parasite-host interactions (see also Chen et al. 2008 which focuses on host species network indices, as opposed to interaction-specific metrics). We provide evidence that the asymmetry of predator-prey interactions influences colonization by trophically-transmitted parasites. Specifically, our findings support the thesis that trophically transmitted parasites are funneled towards downwardly asymmetric interactions as a potential evolutionary response to the fitness risks involved in parasite consumption by non-host predators (dilution effect). Empirical evidence demonstrates that parasites are more sensitive to secondary extinction risks than free living species (Lafferty and Kuris 2009), and supports the idea that highly linked predators are stable and dependable hosts for trophically transmitted parasites. The “boom-and-bust” dynamics of strongly interacting predator-prey pairs can represent a significant extinction risk for the species involved (e.g. Nachman 1988; Inuoye 1980; Post 2000), and this risk would be amplified for parasites that utilize these interactions for transmission, because the bulk of parasite component populations are restricted to a small proportion of heavily infected hosts. That is, for the parasites, these interactions may not be stable or predictable over evolutionary time. Downward asymmetry offers increased stability and

reduced extinction risk, while maintaining a high probability of successful transmission (reduced dilution effect) for parasites.

Our results also suggest that the degree of asymmetry in a predator-prey interaction can be a powerful predictor of the presence or absence of trophically transmitted parasites. This does not imply that there are no other strong forces molding the evolution of trophic transmission. Clearly host-parasite co-evolution, host size and longevity, or physiological and taxonomic constraints are important, but it seems that asymmetry works concomitantly with these other factors to determine the establishment and persistence of trophically transmitted parasites in predator-prey interactions. While four of the food webs in this study were too depauperate of trophically transmitted parasites to directly address the play between host taxonomy, trophic level and asymmetry, the full Carpinteria food web was robust enough to perform a more detailed breakdown each parasite-host interaction type. For example, the distribution of asymmetry values for trophic interactions that do or do not transmit parasites were significantly different in bird-fish, bird-bivalve and bird-annelid interactions ($p = <0.0001$ in all cases). This, along with the dominance of asymmetry values in predicting the presence of parasites in our CART analysis, suggests that predator-prey interaction asymmetry acts concurrently with taxonomic or phylogenetic or other ecological constraints on parasites.

The inference that parasites may be under selective pressures to exploit predator-prey interactions that are downwardly asymmetric fits well with the observed pattern that generalist predators tend to have more parasites than specialists (e.g. Price 1980; Marcogliese 2002; Vasquez et al. 2005; Chen et al. 2008). It is intuitive that increasing

the number of prey items increases the probability of feeding on a prey item that harbors parasites. However, our findings demonstrate that generalist predators harbor more parasites than would be predicted by increasing trophic breadth alone. Thus, the funneling of parasites towards asymmetric predator-prey interactions offers an explanation for the nonrandom way in which different species of trophically transmitted parasites repeatedly utilize the same asymmetric interactions.

In all of the food webs examined in this study, the degree of asymmetry is correlated with the trophic level of the focal predator, a pattern identified previously in other studies (e.g. Lafferty et al. 2006b; Chen et al. 2008). Trophic transmission typically occurs at higher trophic levels, and these are more likely to be downwardly asymmetric. One concern could be that the pattern of parasites settling in asymmetric interactions is an artifact of poor taxonomic resolution. Taxonomic groups representing the autotrophs and the first and second level heterotrophs tend to be much more poorly resolved than the taxa of subsequent trophic levels (Martinez, 1991). However, this would not alter the basic conclusions of this study because increasing the resolution of the first and second heterotrophic levels would increase the total number of prey items for higher level predators, and this would increase the degree of asymmetry in those interactions.

The food webs in the present analyses all used a predator-prey matrix that records species presence and interactions in binary code (i.e. presence or absence of a interactions), but this simplistic assumption may not adequately represent the real topology of natural webs (Paine 1988; Lafferty et al. 2008; Byers 2008; Sukhdeo 2010). Because interaction strengths (or the incidence of contact) between two hosts influences parasite transmission, binary datasets may obscure additional pressures acting to mold

parasite life cycles. For example, consider an intermediate host that is consumed by many predator species. The frequency of predatory interactions could favor the parasite *if* requisite definitive host(s) preferentially prey on the focal intermediate host and/or the definitive host(s) are hyper abundant relative to other relevant predators. These effects cannot be determined with our current dataset. Clearly, the resolution and inferences of food web studies will be enhanced if measures of species abundance, biomass and interaction strength are included (Brown and Gillooly 2003; Raffaelli 2007; Kuris et al. 2008; Sukhdeo 2010). Nevertheless, we find a pattern of nonrandom exploitation of asymmetric predator-prey links by trophically transmitted parasites in spite of the simplicity of the binary food web matrices used.

Finally, there are predator-prey interactions which are not downwardly asymmetric, but which are still utilized by trophically transmitted parasites. In all cases, these are intermediate host species which are very abundant, generalist in niche, and widely distributed (e.g. *Fundulus sp.*, *Nereis sp.*, or *Gammarus sp.*). These hosts represent large compartments of energy for the parasite, and these intermediate hosts are embedded into the cores of their respective communities (e.g. Kneib 1986; Ronn et al. 1988 and Waters and Hokenstrom 1980 respectively). This perspective suggests that a fundamental vantage point for further exploring the way in which parasites are embedded into free-living food webs would be to explore parasite-preferred asymmetric predator-prey interactions using energy flow and quantitative interaction parameters within systems (Hairston and Hairston 1993; Lettini and Sukhdeo 2010; Sukhdeo 2010).

Figure 3.1: Four basic interaction types (a-d). Shaded boxes represent focal predator (squares)-prey (circles) interactions utilized in parasite trophic transmission, with associated non-host predator-prey links represented in hatch-marked lines. All lines (edges) are assumed to be of equal weight in the absence of measured abundance or interaction strength.

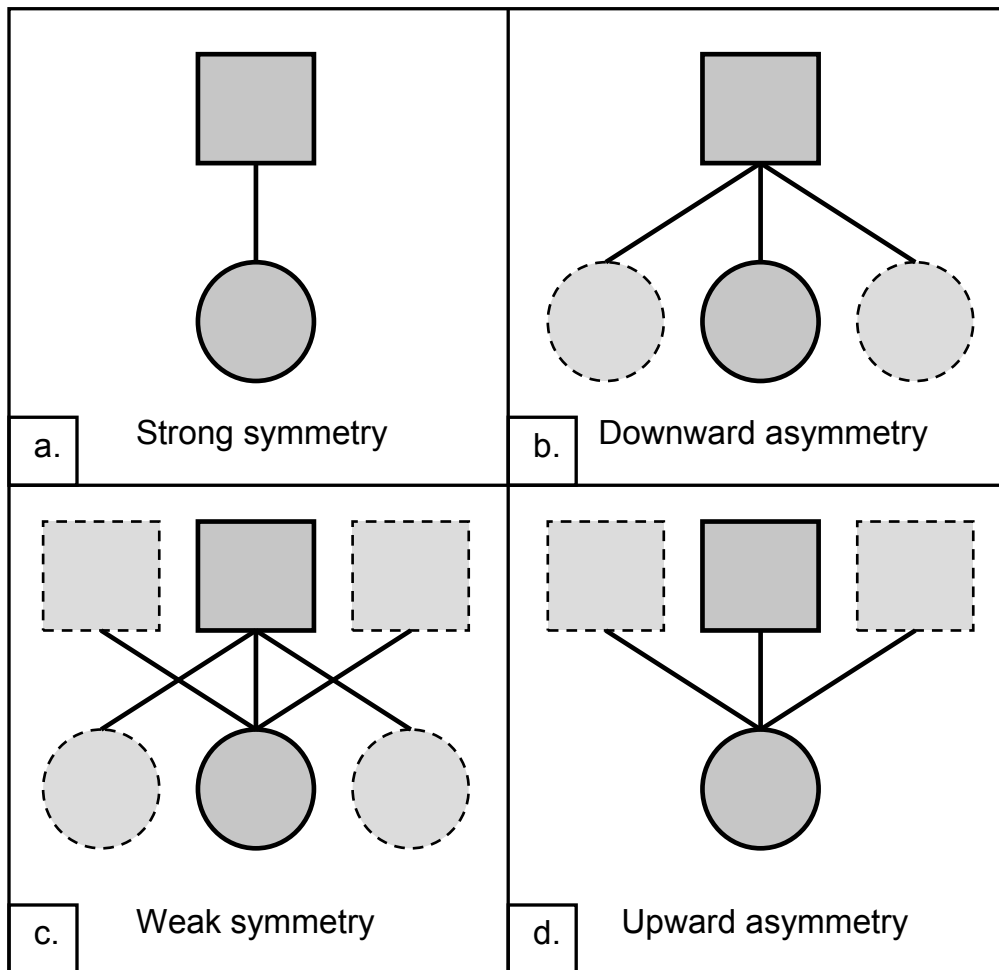


Figure 3.1

Figure 3.2: Observed measures of mismatch asymmetry (triangles) in predator-prey links that are utilized for parasite transmission compared to null model predictions (open squares) for each system, with error bars representing standard deviation from the mean. Mean values below the zero line indicate downwardly asymmetric interactions, indicating that predators have more prey than prey have predators. Those values above the zero line denote the reciprocal situation. In all systems, parasites preferentially exploit downward asymmetries. All differences between null and observed means were statistically significant ($p < 0.05$).

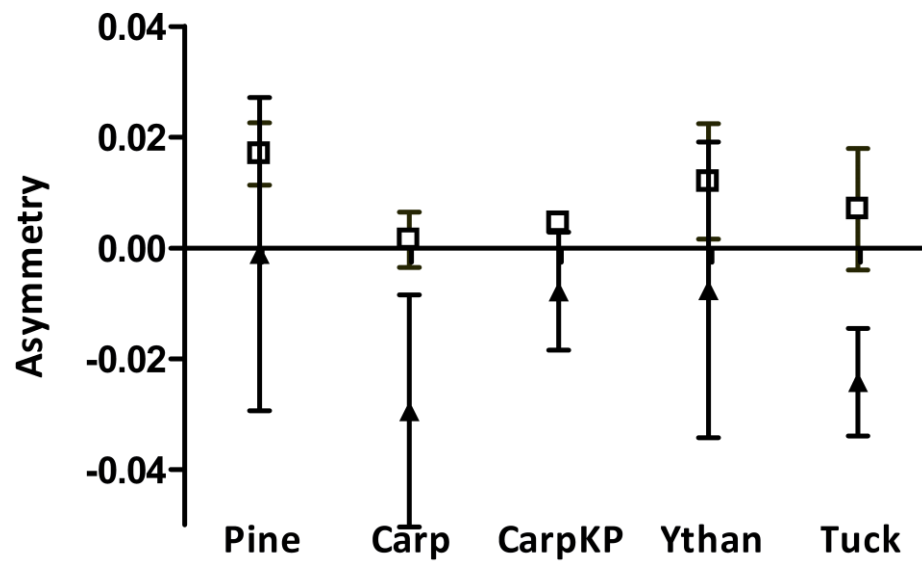


Figure 3.2

Figure 3.3: Observed means (triangles) and expected means (open squares) of the repeated utilization of predator-prey links for parasite transmission in each system. This effectively denotes the frequency with which a predator-prey interaction that is utilized by one or more parasites will be utilized by additional parasites. The difference in the slopes of linear regressions for observed and null values indicates that trophically transmitted parasites repeatedly utilize the same predator-prey interactions. As the richness of parasites increases across systems, the number of predator-prey interactions utilized for transmission increases much slower than would be predicted by random addition. Slope = 1.609 ± 0.2594 and 0.5692 ± 0.02016 respectively, and dotted lines represent 95% C.I. L_p = links utilized for trophic transmission, L_t = total number of links in the system.

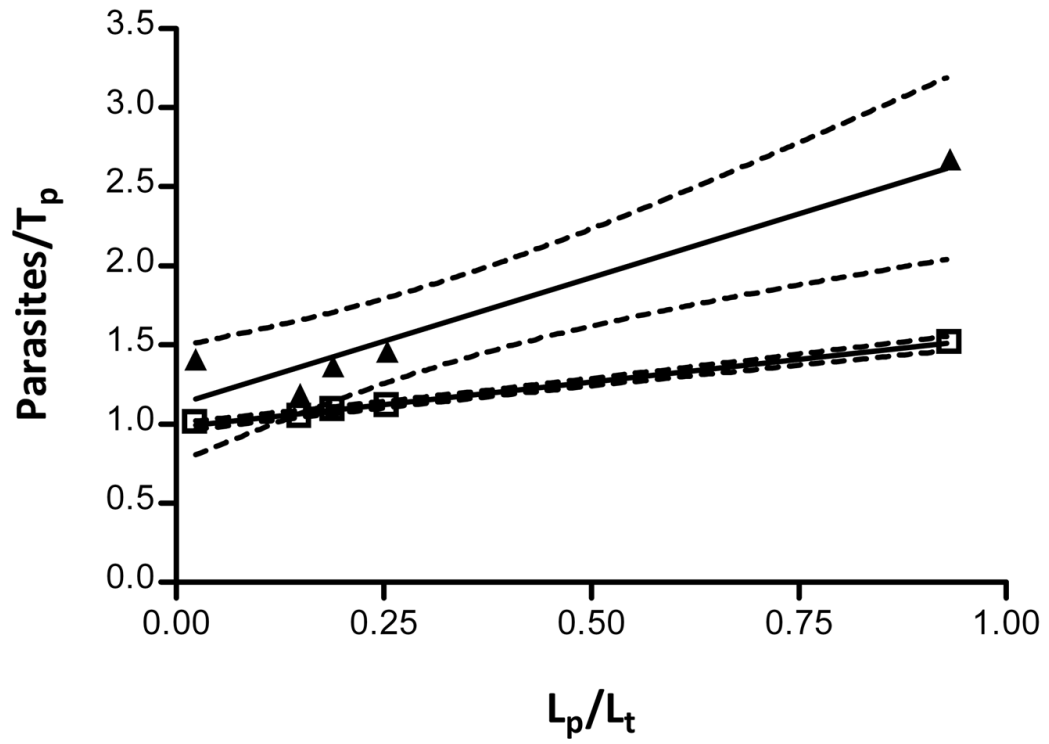


Figure 3.3

Figure 3.4: Relationship between the number of prey species eaten (y-axis) and the number of parasites infecting respective predatory hosts (x-axis). Significant positive slopes indicate that the number of parasites utilizing a predator increases with widening of that predator's diet breadth. Significance of trend for Pinebarrens $p= 0.0327$; Carp $p= 0.0002$; Carpinteria KP $p= 0.0024$; Ythan $p= 0.0432$; Tuckerton $p= 0.1260$.

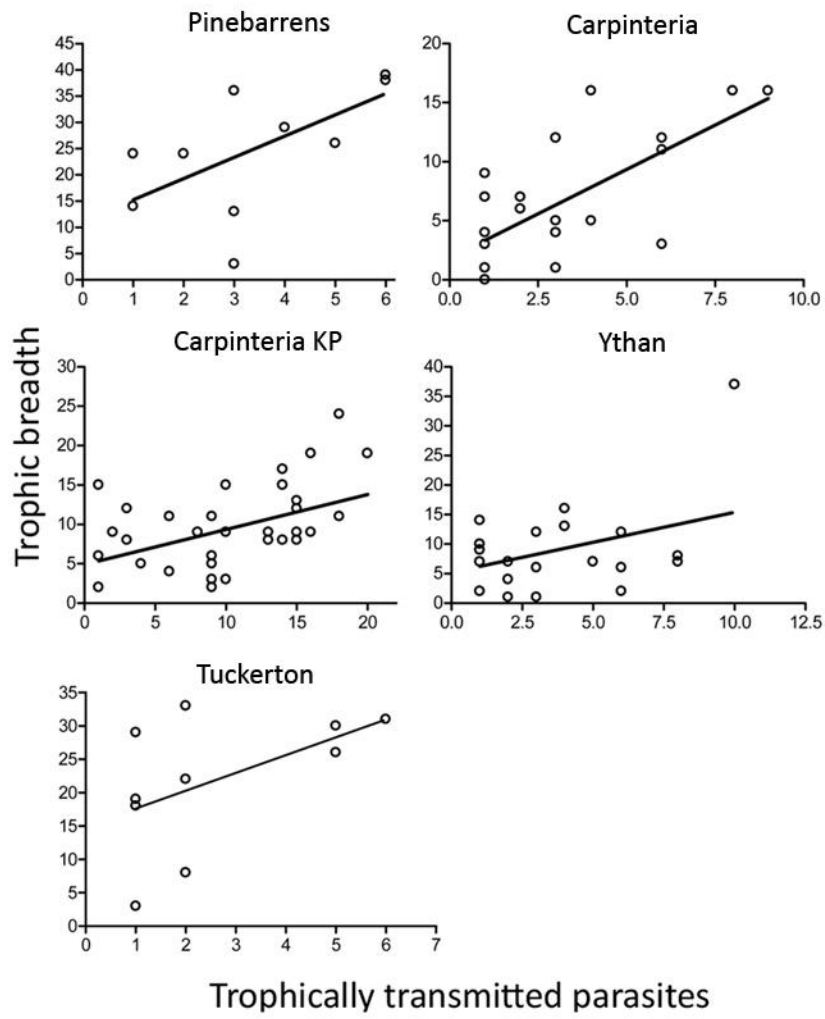


Figure 3.4

Figure 3.5: Relationship between trophic level and mean asymmetry values. As trophic level (x-axis) increases, there is a corresponding precipitous decline in the measures of predator-prey asymmetry values, indicating that top predators have more prey than their prey has predators. This pattern was apparent in all systems, and would suggest that these predators produce more favorable (downwardly symmetric) interactions for trophic transmission.

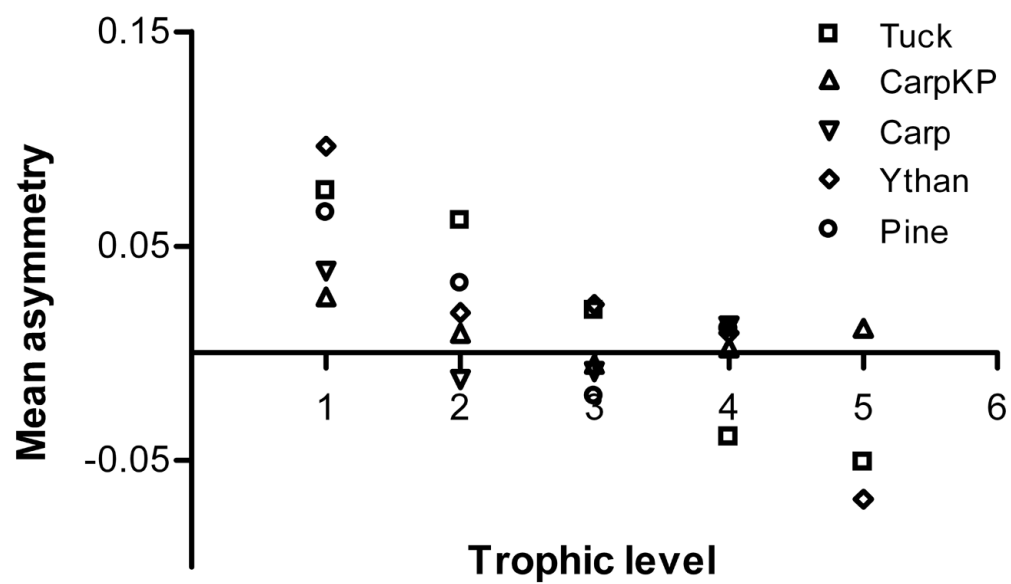


Figure 3.5

Figure 3.6: The first three predictor variables ranked by CART analysis. Asymmetry was the most powerful splitter, accounting for nearly 50% of the decision tree. The first split (asymmetry) successfully calls 68% of the predator-prey interactions that contain parasites. The analysis also indicates that >95% of the predator-prey interactions with asymmetry values above 0.006 are devoid of trophically transmitted parasites. (Amp = amphipod, ann = annelid, bir = bird, biv = bivalve, cla = cladoceran, cni = cnidarians, cop = copepod, dec = decapods, ech = echinoderm, fis = fish, ins = insect, iso = isopod, mam = mammal, nem = nematode, ost = ostracod, pla = plant, sna = snail, tur = turtle). Logworth values represent the logs of adjusted p-values for a chi-squared test of independence. The G2 values are the residual Sum of Squares for a classic OLS regression.

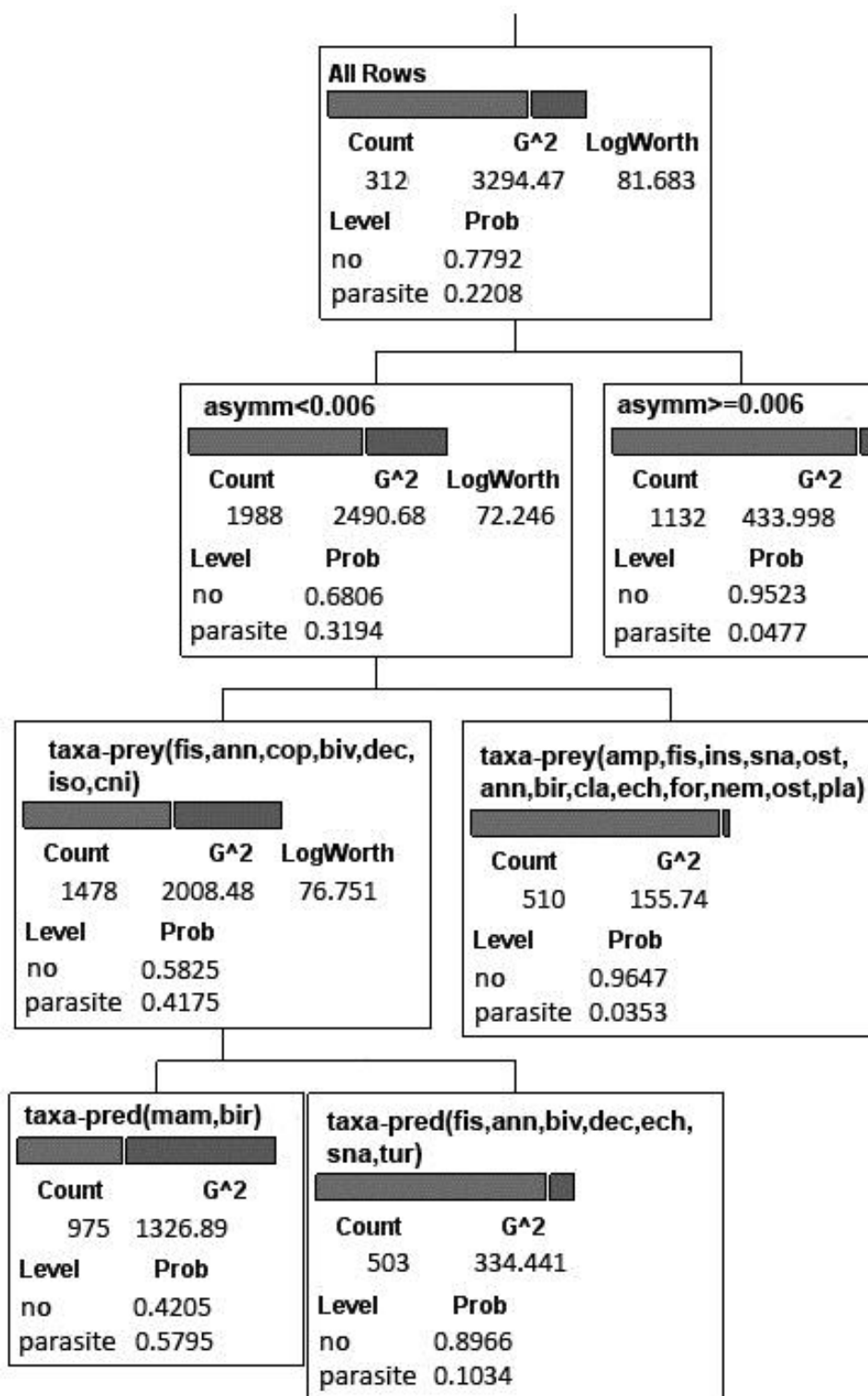


Figure 3.6

CHAPTER 4

Habitat-based constraints on food web structure and parasite life cycles

[in review: Journal of Animal Ecology]

Abstract

While food webs are often discussed in the context of space, few studies explicitly ask whether the spatial distribution of species in a given community affects trophic structure. Here, we examine a high resolution riverine food web that includes data on abundance, biomass and feeding interactions for macroscopic free-living species, as well as microbes, plankton and parasites. To determine whether overlap in species' distributions acts as a constraint on predator-prey interactions, each species' (node) location in the food web was ordinated across three spatially distinct habitat types (riffles, runs and pools) based on species' abundances. In general, species were more "centered" (i.e. occur in multiple habitat types) than would be expected at random (normal distribution), and the distances between species were best described by a Poisson distribution. Distances between interacting species were shorter than would be predicted under a null model derived from the Poisson distribution. The distances between hosts in the life cycles of trophically transmitted parasites were significantly shorter than the overall observed distances, suggesting that interspecific interactions among hosts are significantly constrained by habitat, and that parasites with complex life cycles are sensitive to these constraints. When species abundance was used to position parasite locations in habitat space, parasite-host distances were smaller than would be predicted at random, further suggesting that the life cycles of parasites utilized host species that greatly overlapped in their distribution across habitats.

Introduction

Food web networks have become increasingly popular tools for exploring ecological questions at the community or system level (Ings et al. 2009; Marcarelli et al. 2011). In principle, food webs have great utility, because they can account for all species (every species in the system acts as a predator and/or prey), they capture some aspects of species interactions in the system (trophic links), and they can lend valuable information to assessments of community energetics (Yodzis & Innes 1982). However, in practice, their utility is less clear (Pimm 1988; Paine 1988; Polis 1991; Byers 2009; Sukhdeo 2010). A liability in most current food web models is that they are spatially dimensionless. The underlying matrix by which food webs are constructed and analyzed does not consider spatial information (though the observed patterns could be explained by space *post-hoc*). In their basic form, all food webs are visualized, analyzed and compared via an interaction matrix, which assumes that all predator-prey interactions have an equal probability of occurring, barring the variation produced by differing interaction strengths. However, some interactions (or their absences) may not be the product of abundance or predator preference, but rather a product of the degree of spatial overlap (the incidence of contact) between two species. In principle, some predator-prey interactions may be impossible solely because the two species never come into contact.

Such spatial constraints should be detectable in the topological patterning of food webs, but space cannot be explicitly implicated without additional information. As an example, consider two hypothetical stream communities for which the links between species are identical, but where the spatial distribution of species differs (Fig. 1). By

ordinating the food web along axes of habitat (riffles, pools, runs), we can see that the hypothetical web in 1A is strongly influenced by habitat, and that species seldom interact across habitat space. In web 1B, the topology suggests that habitat has almost no influence on the presence or absence of feeding interactions, and interacting species are just as likely to traverse habitat space as they are to interact with species close to them. If habitat acts to constrain trophic interactions, then the distribution of straight line distances between interacting species in habitat space should be right-skewed (with most edges between nodes being short). However, if species are randomly distributed in space, and trophic links between them are not influenced by habitat, then the observed distribution should conform to a normal distribution (or some other distribution that is not right-skewed; see methods). Thus, adding spatial metrics to the topology of a given food web offers a way to determine the role of space in structuring it.

In addition to the potential for space to constrain trophic interactions among free-living species, these constraints could have profound impacts on the life cycles and transmission patterns of the parasites imbedded within such food webs (Mollison & Levin 1995; Holt & Boulinier 2005). Many parasites have complex life cycles in which several life stages of the parasite require different host species, and these life cycles have evolved under selective pressures to maximize the spatial overlap or incidence of contact between hosts (Parker et al. 2003). Additionally, the proximity of hosts to each other might be particularly important for parasite life stages that actively move through the environment from one host to another, because most free-living parasite larvae are relatively fragile and short lived (Marcogliese 2002). A large subset of parasites with complex life cycles are transmitted by trophic interactions between hosts and these

parasites can be sensitive to the frequency with which feeding interactions occur (Rossiter & Sukhdeo 2012). Thus, the degree of spatial overlap between predator and prey hosts may be a particularly relevant factor in considering patterns of parasitism in ecological communities (Skirnisson et al. 2004; Hechinger & Lafferty 2005; Fredensborg et al. 2006; Médoc & Beisel 2011).

The need for spatial dimensionality in food web analyses is well recognized; a simple Google.com search yields nearly 3 million hits, and the Ecological Society of America recently hosted a symposium on the topic (ESA 2010). While numerous studies contain the terms “spatial” and “food web” in their titles (e.g., Deegin & Garritt 1997; Thomson & Townsend 2005; Amarasekare 2008), space (as a distance measure) is often ignored. Often, space is simply used to imply that two or more sites differ (i.e. sites are either replicates or treatments), but the explicit inclusion of a space variable is absent. Still, some have assessed the degree to which spatial dimensions (namely distance between locations) can explain differences between food webs (e.g. Kitching 1987; Polis et al. 1997; Levesque et al. 2006), but to our knowledge, there are very few studies in which spatial context is given to the patterns observed *within* a given food web (i.e. community; but see Finlay et al. 2002; Soykan & Sabo 2009). In addition, relatively little is known about the ability of species to ‘bridge’ spatially nested modules within food webs. In this discussion, we intentionally exclude other community modeling formats (most notably cellular automata models and spatially explicit geo-statistical models) because they are not able to accommodate the large number of interactions contained in empirical food webs.

The existence of spatial influence on food web structure could potentially explain much of the dynamism in energy flow not explained by abundance or biomass alone, and might provide insights into the types of interactions that can be exploited by parasites. Here we use a riverine community to examine the role of spatial (habitat-based) structure in determining food web topology and biomass distribution using a new metric that offers the opportunity to assess distances in habitat space between predator-prey and host-parasite species.

Methods

We established a long-term sampling location along a nearly pristine reach of the Raritan River (Hunterdon County, New Jersey, USA, Lat 40°38'24" Long 74°54'56"). The Raritan River is a typical lotic freshwater system (Patrick 1994), composed of a mosaic of adjacent aquatic habitats that arise from classic geomorphic features, including pools, runs and riffles. The watershed drains approximately 2,850 square kilometers of central New Jersey, and travels east 50 kilometers before emptying into Raritan Bay. Our collection site was near the western-most reach of the river. Here we collected replicated samples (minimum three replicates) in each of three adjacent habitat types (pools, runs and riffles) seasonally for two years, from June 2009 to June 2011. We quantified (by numerical abundance, biomass and the variation therein) the entire free-living community, ranging in size from bacteria to the largest top predators.

Bacterial samples were taken as subsamples from plankton nets, as well as from benthic coring in each habitat, and counts were performed under fluorescence microscopes using DAPI staining (Porter & Feig 1980). Phytoplankton and zooplankton

were collected using plankton nets and benthic cores, preserved in sugar formalin (4% solution), stained with Rose Bengal, and subsequently counted from gridded slides, under a compound microscope. Biomass was estimated for phyto- and zooplankton by estimating the volumes of particular morphotypes, and calculating the mass of water at that volume. Morphotypes were identified using standard keys (Balcer et al. 1984; Flemer 1970) and contained groupings of similar species under morphological descriptors such as “Nitzschia-like,” “Navicula-like” or broad groups like “circular diatom.” Benthic macrofauna were quantified by replicated Surber sampler collections in each respective habitat type, and identified using Merritt and Cummins (1995) as well as species lists compiled during surveying by the NJDEP (e.g., Miller et al. 2004). Periphyton, filamentous algae and macrophytes were measured by direct density measures in each habitat. Flat cobble or stones from each habitat were sampled and dried, the surface area (in square centimeters) was scraped, and biomass of attached flora was measured. Macroinvertebrates collected in each sample were dried and weighed. For all invertebrates, additional replicate samples were taken specifically for destructive sampling (i.e., parasitological dissection) concurrent with seasonal collections.

Fishes, turtles and other aquatic vertebrates were trapped by seining, minnow traps and crab traps for large fish. Traps were always placed before dusk, and collected by noon the following day. For traps, samples were assumed to measure species abundance across the habitat in which they were placed (i.e., a trap placed in an explicitly defined pool was assumed to sample the fish assemblage for that pool). Densities were then estimated by dividing collection numbers by the size (in square meters) of that habitat. This is much more difficult for run habitats, as they are large and continuous,

and values are almost certainly conservative or underestimates. Seining effort was consistent across habitats, and each sample consisted of 5 consecutive sweeps across a given habitat. These data were supplemented by hook-and-line collections of larger predatory fish that are underrepresented in trap collections (particularly in run habitats). Typically, hook-and-line effort was represented by a one hour period in each habitat at dusk or early morning. Initially, fish were weighed as wet mass and then dehydrated and weighed to establish the relationship between wet and dry mass. Thereafter, only wet mass was recorded and those masses were converted to species-specific dry mass approximations. Typically, fish were caught in numbers that necessitated preservation prior to parasitological dissection. Fish were pithed and frozen for later dissection. This method allows for more reliable sampling of gut contents, but makes it difficult to detect and identify ectoparasites. Thus, representative subsamples of species were kept in aquaria, for freshly euthanized dissection, within three days of collection. Prevalence values for ectoparasites found in these specimens were adjusted according to these smaller sample sizes.

Macroinvertebrates, fish, frogs and turtles were evaluated for parasites by dissection (permit 11-036), and Schell (1970), Hoffman (1999) and Anderson et al. (1974) were used in identifying larval and adult parasites. Fish, turtle and frog blood samples were examined for protozoan parasites by Geimsa staining of blood smears, though protozoan parasites of the blood were not exhaustively sampled. Parasite infracommunities in turtles were also estimated from fecal collection and floatation, to minimize the number of turtles euthanized for dissection. Timed bird counts were conducted during each collection period, but only resident riparian-dwelling birds were

considered for the study. Riparian mammals were quantified by point counts or midden counts in the case of muskrats and raccoons. No trapping was used, and abundance data were necessarily less precise. Bird feces were collected for parasite identification via fecal floatation, but raccoon and muskrat feces were not collected, and no individuals were taken for parasitological dissection. The mass of microscopic parasites (protozoans and some larval forms of helminths) was estimated in the same way that free-living microfauna were calculated (see below). All larger larval and adult parasites were dried and weighed directly.

When the dry-weight biomass could not be directly observed, we approximated per capita masses by calculating the mean volume of organism and converting that volume to a mass value approximated by the most similar conversion value from <http://www.convert-me.com/en/convert/weight2volume> (which has more than 300 mass-volume conversion factors ranging from various forms of vegetation and animal products, to liquids, to minerals). In this study, some parasite types (viruses, bacteria, blood-borne pathogens, and protozoan taxa) were not emphasized, and are consequently underrepresented. Our focus was largely on macroparasite species. Recent findings suggest that the parasite:free living species ratio may be as high as 4:1 (Whitman & Parker 2004), and no study at the community scale has exhaustively sampled the true diversity of parasite fauna. However, the parasite diversity observed in this study is consistent with comparable studies, and is sufficient to detect and extract basic patterns and properties of parasitism within the food web.

Food web construction and metrics

We constructed a binary food web matrix containing all observed species/morphospecies. Feeding interactions were “truthed” for nearly all of the vertebrate species, though the diets of some fish species (derived from gut content analysis) were augmented with diet information from regional literature on each species (aided by Fishbase.org). The presence or absence of feeding interactions between most invertebrate species was gleaned from a wide variety of sources, ranging from general observations (e.g., that filter feeding macroinvertebrates would consume plankton species) to very specific studies (e.g., the variation in diet of Glossosomatid trichoptera of North Eastern United States). As with any food web study, some feeding interactions were assumed based on the size and similarity of known prey items to unverified prey items. Host-parasite interactions were necessarily more precise, because hosts must be collected in order to discover parasite species, and because host identity (or at least taxonomic group) is often diagnostic for many species of parasites.

The entire composite food web contained all of the species observed in the reach of the river being sampled. Trophic height (defined as the mean trophic level of a predator’s prey plus one) was calculated for each species. The biomass of each species in the food web was presented as the logarithm of the average standing crop biomass (as in Cohen et al. 2003). Where species abundance was derived from volumetric measures (e.g., fish, plankton and bacteria), the height dimension was measured for each habitat/collection and then “flattened”, such that the species abundances in the observed volume were presented in square meters. The matrix was read through UCINET (Borgatti et al. 2002) and visualized in NETDRAW (Borgatti 2002), at which point biomass and trophic height were added as attributes and basic food web descriptors were

calculated (nestedness, connectance and linkage density). Because we were interested in detecting food web substructure that might correlate with habitat, we also examined an additional set of grouping metrics using PAJEK (de Nooy et al. 2002), and these included Centrality, Polish Clustering, Blocks and Cutpoints, k-cores, p-cliques, islands, k-neighbours, and an optimized clustering routine. Additionally, three sub-webs were constructed independently, each representing the species that occur in each respective habitat.

In order to examine the role habitat might play in constraining trophic interactions, a metric was needed that considered multiple habitat dimensions, drawn from empirical data and the pre-existing food web topology. For each species, habitat-specific information on abundance, per capita biomass and parasite prevalence and intensity, allowed us to calculate the distribution of species' abundances across respective habitat types. For example, the Virginia river snail (*Goniobasis virginica*) was observed in all three habitat types, but at differing densities and size distributions. Thus, the proportion of total biomass the species represented could be assigned to respective habitats (e.g., 12.13% in pools, 56.27% in riffles and 31.59% in runs). These proportions were used as coordinate points along three habitat axes, each ranging from zero to 100, and were also used in calculating species-species distances (see below). Alternatively, the three values can be combined to produce a “centeredness” value representing the degree to which a species is restricted to specific habitats. To do this, we used the simple equation, $\frac{(p_1 * p_2 * p_3 * \dots * p_i)}{p_{opt}}$, where p_i represents the proportion of a species' biomass assigned to habitat i and p_{opt} represents the optimum biomass distribution value (i.e. the product of all proportions for a species that is evenly distributed across all habitats). The resulting

value falls between zero and one, with a score of one representing a perfectly evenly distributed species. Thus, the distribution of *G. virginica* would yield a value of 0.584. Note that zero values for species proportions in each habitat must be converted to a non-zero value for the calculation. For our purposes, zeros were converted to ones, and this had a negligible impact on the overall distribution of species values.

We predicted that the distribution of realized predator-prey links would be constrained by habitat space, and that the average distance between predator and prey species would be shorter than predicted at random. This would illustrate that predators interact with prey that are more overlapping in habitat space than predicted at random. To assess the relationship between habitat-based species distributions and the presence/absence of trophic interactions, we calculated the straight-line distances between predator-prey pairs in our food web matrix. Here, the difference in proportion for two interacting species in a given habitat (i.e., the percentage of species biomass occurring in that habitat for each species) was used as the height of a right triangle, and the difference in proportion for the same species pair in a second habitat was used as the length of a right triangle. The straight line distance between two species is then represented by the hypotenuse of the triangle for each habitat pair. Thus, for each species pair, three distances were calculated (pool:riffle, pool:run, and riffle:run). This method was also used to evaluate the distances between species that act as hosts in a given parasite's life cycle, as well as for predators and prey that are used in trophic transmission of parasite larval stages. Finally, we ordinated parasite species in habitat space, and assessed the distances between parasites and host species. To do this, we used the prevalence and intensity of each parasite within a given host species, along with the

abundance of that host species in each habitat, summed these values for all host species in the parasite life cycle, and determined the proportion of each parasite's biomass in each habitat. This allowed us to position each parasite's location in habitat space in the same way that free living species were calculated. If a parasite species had only one host, its location could still differ from that of the host species if prevalence and intensity values varied across habitats. Otherwise, parasites are effectively triangulated between host positions in habitat space. This necessarily decreases the mean distance between parasites and hosts, but still permitted us to examine whether a parasite's hosts are nearer to one another than would be predicted at random.

We predicted that species would interact disproportionately with predators or prey nearer to them in habitat space, and that the cumulative distribution of predator-prey link distances would be right-skewed. We initially sought to compare this pattern against a null pattern conforming to a normal distribution, however, this distribution would not be predicted when three dimensions are considered. Specifically, the distance d would be described by the equation

$$d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2 + (z_i - z_j)^2} \geq 0$$

Where x , y and z represent species' positions in each habitat type. When considering a series of randomly generated networks, the distribution of link distances between species was right-skewed. We corrected our null for comparison in two related ways. First, we looked at the link distance distribution of all possible interactions in the web (excluding cannibalism). This produces the true distribution of a random draw of interactions. We then used the connectance value for the original web matrix to inform 10,000 randomly

linked webs that contain the same number of species and links as the original (again excluding cannibalism), using UCINET. We then calculated the straight-line distances between linked species for each randomly generated matrix, allowing us to establish the mean and deviation for each link distance category in the distribution. One concern might be that trophic height would constrain the presence or absence of trophic interactions (i.e., predators cannot have a prey item with a larger trophic height, and thus all such interactions must be eliminated from the pool of possible interactions). However, our model avoids this problem because interactions are undirected (i.e., predator and prey in each pair are not specified, only the presence of a feeding interaction).

The link distance distributions for each set of interactions (randomly assigned, observed predator-prey, observed host-host and observed parasite-host) were fit to optimized curve models, and competing models for each distribution were scored by a rank-test analysis that compares the Kolmogorov-Smirnov and Anderson-Darling statistics for each model (effectively comparing the goodness-of-fit for each model to the observed distribution) in the software package EasyFit 5.5 ©. Because habitat could potentially be a subordinate (minor) driver in food web structure, we performed a Classification and Regression Tree (CART) analysis to determine whether habitat was a significant predictor variable. This method uses a hierarchical decision tree to optimally partition a data set into in-group/out-group membership for a dependent variable using an ordered series of predictor variables (Fichet et al. 2011). Additionally, the CART analysis available in JMP® applies optimal cut-offs within the distribution of a predictor variable. In several different analyses, we used various measures of sub-structure within

our food web network as dependent variables. If structure is correlated with habitat, then species' proportions in each respective habitat should be identified as significant predictors. We used the three habitat-specific values, the composite "centeredness" value, trophic height, degree, and log-biomass of each species as predictor variables, and group or cluster identity as the dependent variable.

Based on our CART analyses, as well as cursory linear models, we suspected that most clustering, partitioning and grouping metrics were strongly affected (drawn to) degree measures (number of links) for species in the network, and that these metrics were not sensitive to habitat variables. To test the role habitat-based species distributions might have in structuring our food web network more directly, we compared the our measures of link distance values within and between called groups (determined using the grouping methods mentioned above). Again, if habitat has an impact on the structure of food web networks, then (1) interacting species within assigned groups should be nearer to each other in habitat space and/or (2) the link distances of trophic interactions between species within groups should be shorter than those across called groups.

Finally, we wanted to test the classic relationships between abundance, trophic height and degree (the number of interactions for each species). Historically, degree increases with trophic height, driven largely by the increasing diet breadth in higher trophic levels (Costa 2009). However, increased resolution at lower trophic levels could change this relationship. Because our food web contained parasites and also offered increased resolution in the bottom three trophic levels, we were able to evaluate these relationships. In addition to simple two-dimensional plots of pair-wise sets of variables, we wanted to assess the relative strength of each variable in predicting degree (which

drives the grouping metrics mentioned above). We constructed a generalized linear model (GLM), using species degree as the response variable and trophic height, $\log(\text{biomass})$ and centeredness values as predictor variables. We assumed a normal distribution and used an identity link function with the overdispersal parameter estimated by a maximum likelihood method.

Results

We identified 121 taxa, 21 of which were parasites. Species richness varied across habitat types, most notably in free living taxa (Table 1), and parasite richness was highest in pools. The distribution of biomass varied greatly between free-living taxa, but predictably across trophic levels, and was best described by an exponential decay curve ($y = 1310.9e^{-1.444x}$, $R^2 = 0.9979$). However, standing stock biomass did not strictly conform to the classical 10% rule of ecological efficiency (Odum 1959). This was particularly pronounced in pool habitats, where the average ratio between a trophic level and the one preceding it was 0.29 (± 4.7). In contrast to this pattern, average ecological efficiency for riffle and run habitats was lower (12.7 and 14.6 respectively), with ratios between lower trophic level carnivores and their predators often well below 5.0. In addition, pool biomass accounted for 55.21% of the total biomass of the system, even though pools made up only 8% of habitat in the system. This suggests that biomass (energy) moves from lower trophic levels in riffles and streams to predators that occur abundantly in pool habitats, and that high turnover rates at lower trophic levels power biomass accumulation in longer lived predators (Benke and Huryn 2010). However it is important to emphasize that standing stock biomass is a poor measure of production in

lower trophic levels. Parasites made up 0.42% of the total animal biomass in the system, and made up a larger proportion of animal biomass in pools than in riffles or runs (0.67%, 0.09% and 0.15% respectively).

Of the 14,520 possible links in our overall food web matrix, 1595 were realized, and predator trophic breadth increased linearly with trophic height (Spearman rank correlation = 0.78, two-tailed $p < 0.001$). However, when parasites were considered along with predators, the relationship became a unimodal curve, peaking at a trophic height of 3.51 and declining at higher trophic levels (Fig. 2). Connectance and linkage density varied across habitat types, with the riffle subweb having substantially lower values than the other habitat subwebs and the overall food web (Table 1). We found no correlation between the average standing stock biomass of a species and its degree (number of interaction links). This was true even when parasites were excluded, and only free-living species were considered. This was confirmed in our GLM analysis, in which trophic height was the only significant predictor of species degree ($\chi^2_1 = 15.57, p < 0.0001$). Parasite nodes occurred in the third trophic level and above, and represented relatively miniscule biomass values relative to other top predators (Fig. 3). When ordinated using habitat as axes, several spatial patterns were apparent (Fig. 4). Taxa represented in the three lower trophic levels tended to be more centered, occurring in all three habitats (t-test, one-sided $p = 0.0412$). Surprisingly, most top predators were more spatially confined to specific habitat types, though very few species were unique to riffle habitats.

Overall, 21% of species fell outside of the 90% confidence interval (i.e. were more centered) than predicted by a normal distribution of centeredness values. Because of this pattern, the pool of possible interactions yielded a right-skewed distribution of link

distances, and was optimally described by a Poisson distribution in our ranks test (Fig. 5). However, the observed distribution of realized link distances was further right-skewed, and was best described by a negative binomial distribution. That is, link distances between predators and prey tended to be shorter than would be predicted by our conservative null (Poisson) model. This was more pronounced among predator-prey interactions that are utilized in parasite trophic transmission. Finally, the distribution of parasite-host distances was extremely biased, with all distances falling into the first two (shortest) distance classes.

No strong relationship was detected between groups or clusters (i.e. substructure) in the overall web and species distributions across habitat space. In our CART analysis trophic height was the strongest predictor of k-core membership, successfully assigning 80.16% of all species to correct k-cores ($G^2 = 319.96$, Logworth = 5.22). The second most powerful predictor was species' distributions in run habitats, with a cut point of 45.28 run value. This split was able to correctly call 64.6% of the remaining species ($G^2 = 116.51$, Logworth = 1.05). However, we observed a strong correlation between trophic height and trophic breadth (Spearman's $\rho = 0.72$, $p < 0.0001$), and the addition of trophic breadth overwhelmed all other predictor variables (with data partitions consisting of repeated splits of the trophic breadth variable). The same pattern was found for all other grouping metrics, suggesting that contemporary network subgroup metrics are strongly influenced by degree (total number of links for a given node). The distribution of link distances between species within groups (k-cores) was best described by a logarithmic curve ($y = -0.07\ln(x) + 0.1983$, $R^2 = 0.9345$), whereas the link distribution of between group interactions fit a polynomial curve ($y = 0.0013x^2 - 0.0309x + 0.2184$, $R^2 =$

0.958). However, the distributions were not significantly different ($F = 1.271, p = 0.296$). Thus, this grouping method was not significantly correlated with the distribution of species-species distances in habitat space.

Discussion

There is an ongoing and concerted effort to incorporate spatial context in ecological networks of community interactions, and numerous studies have compared food webs across a range of spatial scales (see Power & Rainey 2000). In this study, we assess the importance of habitat (a crude surrogate for space) within a food web, using adjacent habitat types within a community. We use species-specific distribution and biomass data to inform food web topology, and attempt to determine the degree to which species location and distribution in habitat space might constrain trophic interactions. We find that producer, herbivore, and first level omnivore species are more centered (shared across habitats) than would be predicted at random, and that higher order predators are more likely to be spatially restricted by habitat. We also find that predators are more likely to feed on prey species that are closer to them in habitat space. Specifically, when we compare the distribution of straight-line distances between predators and prey in habitat space, we find them to be significantly shorter than would be expected, given the distribution of species across habitats. This was more pronounced when we considered predator-prey interactions utilized by trophically transmitted parasites. Further, we found that the distances between parasites and their hosts were extremely short, with all host-parasite links having distances of 20 units or less (roughly meaning that the parasites and hosts have an overlap in habitat of at least 80%). This

suggests that parasite life cycles are strongly constrained by habitat, and is not surprising, given that many studies have found infection status and intensity to be strongly associated with habitat (Rossiter & Sukhdeo 2012) as well as spatial overlap among hosts (Knudsen et al., 2004; Hechinger & Lafferty 2005; Thielges et al. 2008). Further, our findings are consistent with the findings of Taylor (2000) and Finlay et al. (2002), in that riverine predators tended to be restricted to particular habitats and fed on prey sources in close spatial proximity.

The standing stock biomass of pools is higher than that of runs or riffles, and the distribution of biomass across trophic levels is 'top-heavy' (i.e. larger than expected biomass in upper trophic levels). This is partly a product of the disproportionate number of top predators found in pool habitats. However, it also suggests that predators in these environments are sustained not just by preying upon species in pools, but also other habitats. For example, when considering the diets of top predators strongly associated with pool habitats, the average distance from respective prey in habitat space was 48.77, suggesting that more than 50% of the diets of these predators are prey items outside of pools. An alternative interpretation might simply be that the turnover rates of species on lower trophic levels may be higher in pool habitats. However, our food web analysis seems to corroborate our first interpretation, and further suggests that pool predators feed on species in riffle habitats, in addition to prey residing in pools. This might also explain why parasites appear "pulled" towards pool habitats, and suggest pathways by which parasite life cycles are able to traverse these habitats.

Our study also adds additional support to the idea that trophic breadth is strongly correlated with trophic height (Costa 2009), even when resolution is increased to include

those groups that are usually neglected. Surprisingly, the results of our GLM suggest that species degree is largely unrelated to species abundance/biomass or spatial centeredness. This is counterintuitive, and sound arguments can be made for each of these variables being important in predicting degree. Species that are abundant could be supported by numerous prey items, and would be more available as prey than rare species. Likewise, species that have distributions spanning multiple habitats contact a larger number of species, increasing the array of possible interactions. Additionally, there was no strong relationship between the spatial pattern of interactions and the subgroups determined by any of our grouping metrics, which is unexpected, given that species tended to interact with those closest to them in habitat space. We think there are several reasons why our grouping analyses failed to detect this pattern. First, the grouping metrics we utilized were all strongly influenced by degree measures. Our evaluation of the drivers in grouping metrics indicated that trophic height was the strongest predictor of both degree and grouping or category. Because top predators have high degree values, they absorb prey items in these grouping analyses. But, because many of the prey items are shared (a probabilistic result of large diet breadths is large diet overlap), predators also get linked to one another in groups. For example, 82% (31 of 38) of predators with trophic heights larger than 3.0 were grouped into a single k-core, even though they were often restricted in habitat space. For these reasons, we believe that classic grouping algorithms are not sufficient for detecting subweb clustering in the context of space, and further work is needed to iron out this issue.

In this study, we demonstrate the importance of considering ecological dimensions in interpreting species interactions within the context of entire communities

and shed light on hitherto uninvestigated aspects of food webs. While it is intuitive that spatial (habitat) overlap in species' distributions should impact interactions between them, few studies have even broached the subject. We offer a clear and simple way to assess the role of space in structuring the trophic network of a large natural system. Additionally, we find evidence that parasite life cycles are strongly impacted by host-host habitat overlap, a finding occasionally reported in population studies, but never at the scale of entire communities. Additionally, our use of spatial "centeredness" metric for species permits a much more elegant and useful incorporation of parasite species into free-living food webs, positioning individual species based on host spatial distributions and host and habitat-specific prevalence and intensity values. This is a first attempt at this type of analysis, and we hope it will be considered a jumping-off point for additional questions and methodological advances, as further study is needed to verify or refute the patterns observed herein.

Figure 4.1: Two hypothetical food webs in which species are given three dimensional coordinates based on their distribution across habitats. (A) Species are spatially restricted to habitats, and interact with other species in that habitat. (B) The network topology is the same, but species distributions in space are randomly selected, leading to interactions across habitat types. Node size depicts abundance or biomass values.

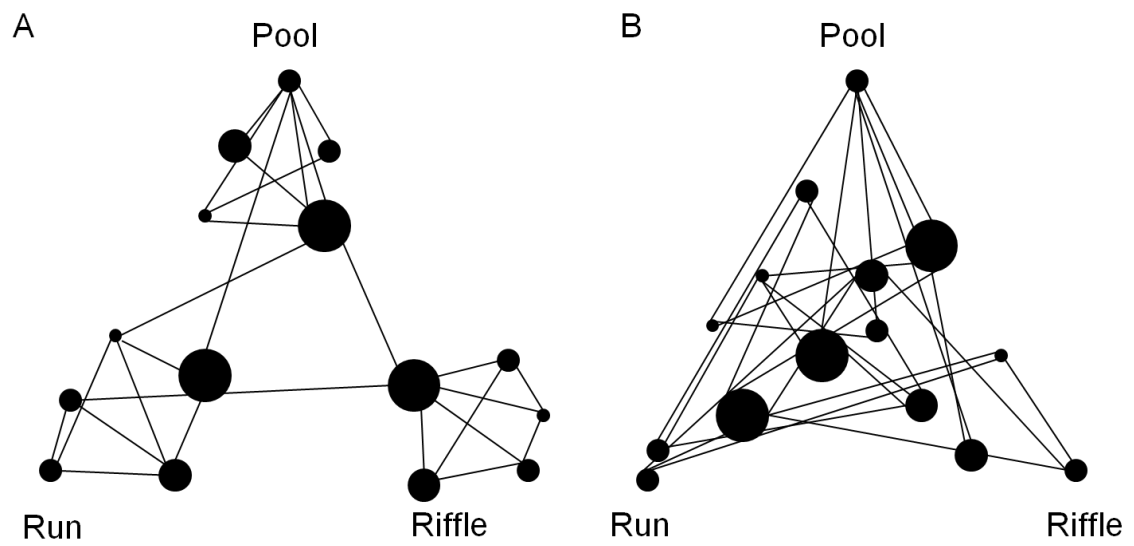


Figure 4.1

Figure 4.2: Predicted distribution of realized predator-prey links compared the null expectation (i.e. that habitat space would not constrain trophic interactions). The predicted distribution would be right-skewed, demonstrating that predators interact with prey that are more overlapping in habitat space than predicted at random.

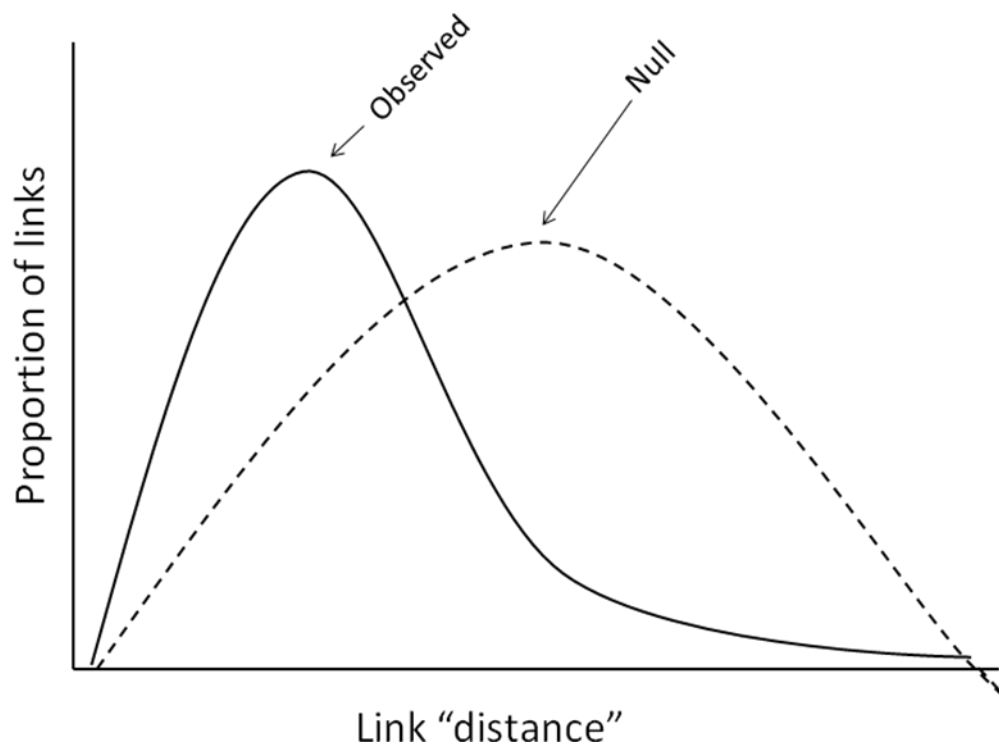


Figure 4.2

Figure 4.3: Relationship between trophic breadth and trophic height for a) free-living species only and b) free-living and parasite species. y-axis is the number of prey items a predator feeds on. x-axis is trophic height. Note that there is a linear positive relationship between trophic height and breadth for free-living species and that parasite taxa tend to have narrow host spectra (i.e. few host species).

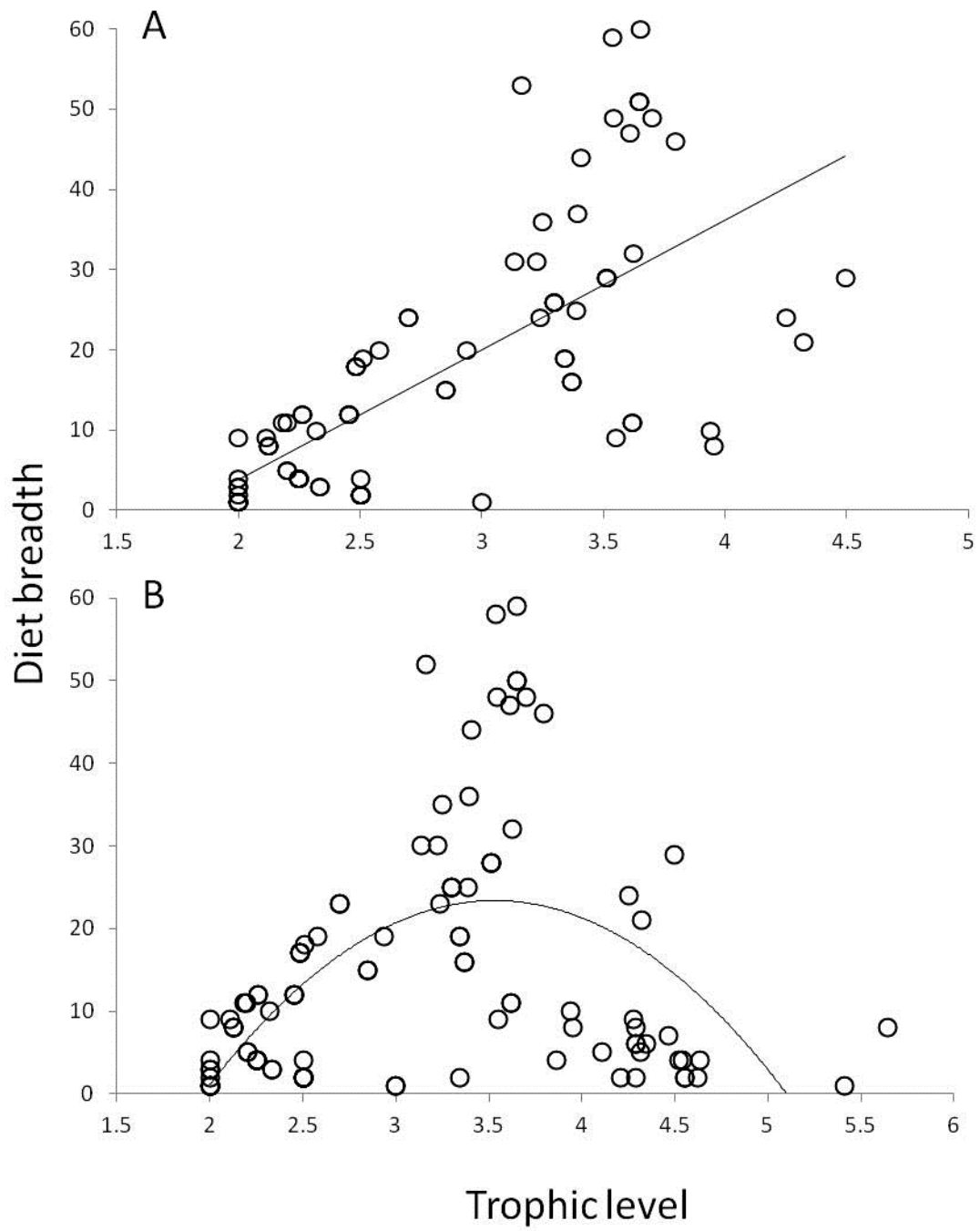


Figure 4.3

Figure 4.4: Ordinated food web network. y -axis is trophic level (rounded to nearest half) and x -axis is $\log(\text{biomass})$ represented as the average standing stock biomass in g/m^2 .

Parasites are depicted in red.

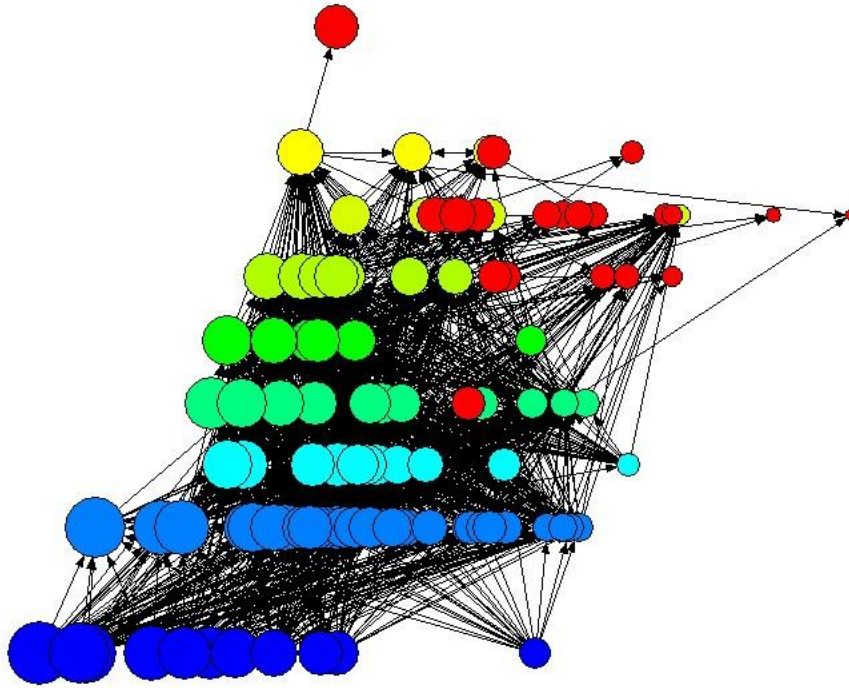


Figure 4.4

Figure 4.5: Trilinear (ternary) plot of complete food web. Each vertice represents habitat type; Riffle habitat = lower right, run habitat = lower left, pool habitat = upper middle. Species that exist in all three habitats are displayed in the center of the web, while those restricted to particular habitats are represented at the respective corners of the web. Color tone represents trophic level (cool = producer and warm colors are ascending trophic levels), and node size represents the $\log(\text{biomass})$ of each species. Note that parasite species (in red) are disproportionately present in pool habitats.

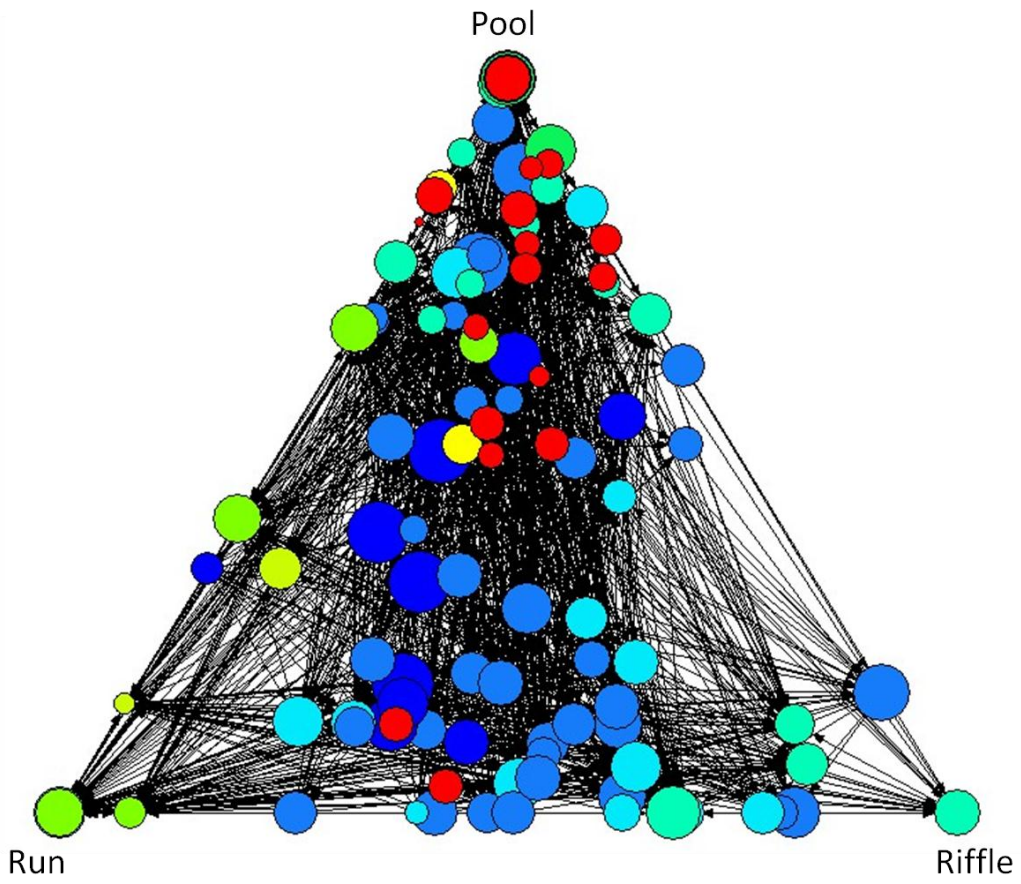


Figure 4.5

Figure 4.6: Link distance distribution for the null model (all possible links), the observed (realized) links, those link utilized in parasite trophic transmission, and parasite-host interactions. y-axis = frequency, x-axis = link distance category. Distance distributions become increasingly right-skewed, indicating that most link distances are very short (i.e. species interact with those spatially proximal to themselves). Poisson fit to null model curve, Kolmogorov-Smirnov (K-S) statistic = 0.16195, Anderson-Darling (A-D) statistic = 390.66. Negative binomial fit to observed predator-prey link distance distribution, K-S = 0.14886, A-D = 123.33. Negative binomial fit to host-host link distance distribution, K-S = 0.14228, A-D = 15.099.

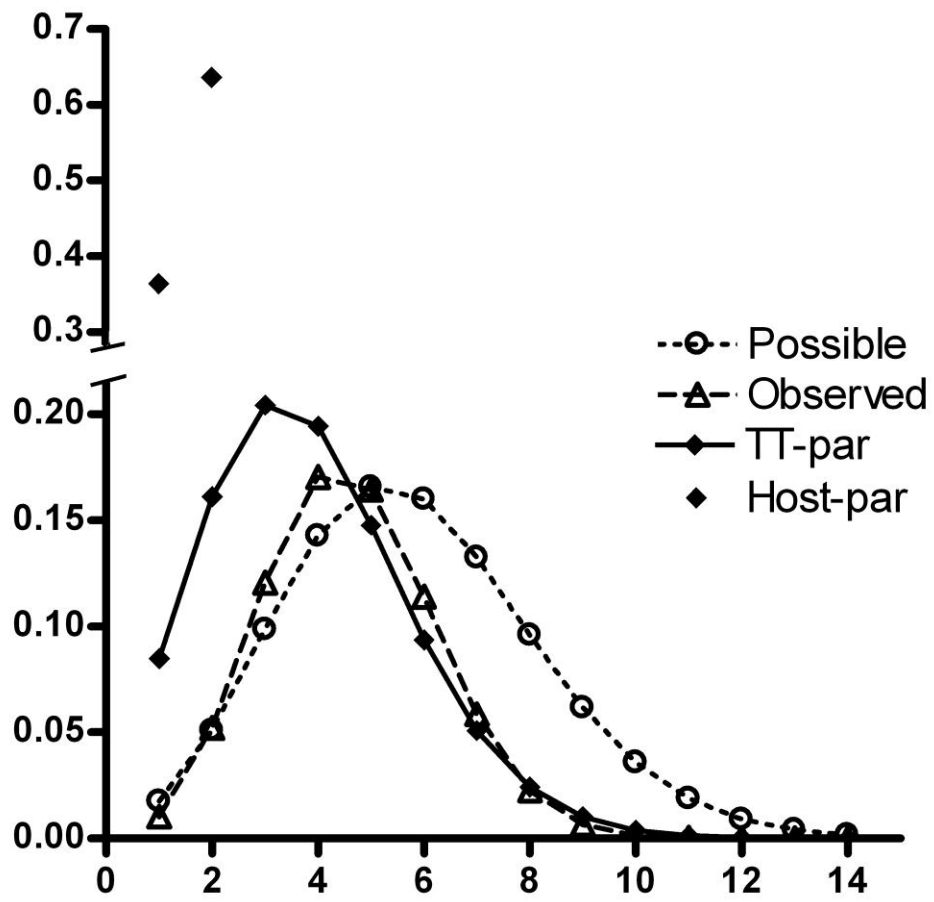


Figure 4.6

Table 4.1: Basic descriptive characteristics of each subweb and the total web. N-free = the number of free-living species. Biomass is represented in g/m^2 .

| | Pool | Riffle | Run | Total |
|---------------|--------|--------|--------|--------|
| N-free | 79 | 77 | 82 | 100 |
| Parasites | 19 | 14 | 15 | 21 |
| Connectance | 0.105 | 0.095 | 0.12 | 0.11 |
| Linkage dens. | 10.36 | 8.79 | 11.25 | 12.97 |
| k-cores | 18 | 16 | 19 | 22 |
| Biomass | 509.53 | 248.63 | 396.06 | 360.91 |

CHAPTER 5

Host-parasite biomass alterations across a disturbance gradient in a riverine system

Abstract

Despite a growing literature investigating parasitism at the community-level, relatively little is known about the relationship between free-living community structure and the subsequent structure of the parasite community embedded within it. In this study, I examine the changes in free-living and parasite communities along a gradient of human impact, using high-resolution food web and biomass data from four communities along a natural riverine system. Species richness (both free-living and parasite) decreases with increasing perturbation (104 to 79 and 24 to 13 respectively), suggesting that the “diversity-begets-diversity” argument holds for this system. However, overall standing stock biomass did not correlate with these changes, and parasite biomass is relatively invariant to changes in parasite species richness. Interestingly, the average change in species’ biomass between sites demonstrated that highly perturbed communities are less efficient in transferring biomass up trophic levels. Parasites utilized hosts that were both abundant and rare, as well those with populations that varied drastically or remained relatively constant. These findings add to the growing (and varied) literature addressing the impacts of environmental perturbation on host-parasite communities, and lead to new questions with regard to what species represent dependable hosts for parasite life cycles.

Introduction

The search for fundamental patterns or rules by which parasites establish and persist in free-living communities is a rapidly expanding area of interest for parasitologists and ecologists alike (reviewed in Guegan et al., 2005; Poulin, 2007). A growing number of studies have reported the distribution of parasites across entire free-living communities, but few have addressed how the structure or dynamics of a free-living community forms or constrains the parasite community embedded within it (Pedersen and Fenton, 2006; but see Anderson and Sukhdeo, 2011). It is assumed that parasite communities are tightly bound to, and therefore reflect, host communities, but the nature of this relationship is almost completely unknown. Perhaps the most obvious community feature to evaluate is the sheer number of free-living and parasite species in a system (Barbehenn, 1969). This is a logical extension of the “diversity-begets diversity” argument, in which an increase in the number of potential hosts is predicted to correlate with (and likely cause) an increase in parasite species richness (Hechinger and Lafferty, 2005). However, to date, evidence has been inconclusive. One of the major reasons that we have yet to identify fundamental relationships between free-living and parasite communities is that most existing studies examine a single community in a single system, and studies are seldom replicated within each system (e.g., Theiltges et al., 2011; Mouritsen et al., 2011; Zander et al., 2011). That is, it would be difficult to discern any richness-based patterns from the comparison of an equatorial rainforest community and a species-depauperate tributary of the Danube River, because the comparison introduces many other possible sources of variation. This makes the search for overarching patterns extremely tenuous, because robust information on the structure, variation and dynamics of each system itself is lacking (though there are several cross-system studies at this time;

e.g., Chen et al., 2008; Hechinger et al., 2011; this chapter). However, many of these variables can be controlled for when two or more similar communities are compared, and it is much easier to directly address the role of species richness in the observed pattern.

One of the first studies to offer replicated community-level data sets for comparison within respective systems was that of Hernandez and colleagues (2007), which evaluated the free-living and parasite communities of four sites within the Pine Barrens blackwater streams of southern New Jersey. They found that, contrary to popular thought, parasite diversity was positively correlated with increased environmental disturbance. However, this was likely due to the fact that blackwater streams are naturally species depauperate, and environmental perturbation makes these streams more hospitable to invasion, leading to increased community diversity. Thus, their findings suggest a positive relationship between host and parasite diversity. Kuris and colleagues (2008) published community level data for three saltmarshes in southern California, offering the first glimpse at the patterns of biomass distribution for free-living and parasite communities. No clear relationship was found between the two, but the authors did observe that parasites can make up a non-negligible proportion of total biomass, sometimes exceeding that of top predators. However, a revised version of these webs was made available (Hechinger et al., 2011), and the most species rich site (Estero de Punta Banda) also contained the most parasite species. However, the contribution of parasites to the total biomass of the system was intermediate, and the pattern was reversed when comparing the two lower-diversity sites. Thus there was no linear relationship between free-living diversity or biomass and that of the parasite community. More recently, Blonar and colleagues (2011) examine the helminth

communities of Mummichog (*Fundulus heteroclitus*) populations across a pollution gradient, and found a positive relationship between faecal coliforms and parasite diversity. Finally, Anderson and Sukhdeo (2011) examined the free-living and parasite fauna of four salt marshes associated with the New Jersey Meadowlands. Each site represented a different stage of salt marsh restoration, ranging in years-since-restoration from 0-30. While the diversity of free-living taxa was positively correlated with the age of restored marshes, the authors found no relationship between host and parasite diversity (effectively the parasite diversity remained constant). This negative result was best explained by the nested nature of food webs, and the idea the parasites are ‘funneled’ toward core-interacting species that exist in all sites.

These findings, taken as a whole, suggest that there may be many factors that play into the establishment of parasites in a given community. While the necessity for obligate hosts in a parasite’s life cycle is obvious, it is curious that the same free-living species tend to act as hosts for many parasites, while others do not (Chen et al., 2008; Rossiter and Sukhdeo, 2011; Benesh et al., 2011). Many of these studies suggest that the dynamics of host-host interactions, the structure of entire free-living interaction networks (namely in the form of food webs) and the spatial context of these interactions might dictate the location, diversity and abundance of parasites embedded within a community. In this study, we explore the relationship between the structure of free-living communities and their respective parasite fauna using high resolution food webs for four sites along a gradient of human impact in a classical riverine system. These food webs include plankton, microbial and parasite species/groups as well as conventional

macroscopic free-living organisms, and are supplemented with abundance and biomass data for each species.

Methods

We established four long-term sampling sites along the Raritan River (New Jersey) extending west to east from a nearly pristine reach of the Raritan River (Hunterdon County, New Jersey, USA, Lat 40°34'45" long 74°52'57") to a highly perturbed site in a reach of the river that is adjacent to intense development and housing (Middlesex County, New Jersey, Lat 40°32'24" long 74°30'41"; Figure 2). The Raritan River is a typical lotic freshwater system (Patrick, 1994), composed of a mosaic of adjacent habitats that arise from classic geomorphic features, including pools, runs and riffles. The watershed drains approximately 1,100 square miles of central New Jersey, and travels east 31 miles before emptying into Raritan Bay. Our first collection site (Stanton Station) was near the western-most portion of the river, and our eastern most site (HW287) lies at the edge of tidal influence, approximately 10 miles upstream of the river's mouth. To quantify human impact along these sites, we utilized long term sampling data from NJDEP's database, using only those sampling stations within 10km of each of our sites. This data base includes multi-year measures of dissolved oxygen (DO), pH, conductance, temperature fish and macroinvertebrate indices of biological integrity (IBI), percent substrate type, and percent open canopy. Twenty-six points were used, and there were at least five sets of sampling data for each site. In order to ordinate our sites along a gradient of perturbation, we used these data in a Canonical Correlation Analysis (CCA), and delimited centers for each site.

We collected replicated samples (minimum three replicates) in each site seasonally for two years, from June 2009 to June 2011. We quantified (by numerical abundance, biomass and the variation therein) the entire free-living community, ranging in size from bacteria to the largest top predators. The details of our collection methods are described in Chapter 4, but in brief, bacterial samples were taken as subsamples from plankton nets, as well as from benthic coring in each habitat, and counts were performed under fluorescence microscopes under oil emersion using DAPI staining (Porter and Feig, 1980). Phytoplankton and zooplankton were collected using plankton nets and benthic cores, preserved in sugar formalin (4% solution), stained with Rose Bengal, and subsequently counted under a compound microscope on gridded slides. Biomass was estimated for phytoplankton and zooplankton by calculating the volume of morphotypes, and calculating the mass of water at that volume. Benthic macrofauna were quantified by replicated Surber sampler collections in each respective habitat type, and identified using Merritt and Cummins (1995) as well as species lists compiled during surveying by the NJDEP (e.g., Miller et al. 2004). Macroinvertebrates were dried and weighed. For all invertebrates, additional replicate samples were taken specifically for destructive sampling (i.e. parasitological dissection) concurrent with seasonal collections. Fishes, turtles and other aquatic vertebrates were collected using various trapping techniques, and the dry-weight of each individual was either directly measure or approximated in a non-invasive way. Most fish were pithed and frozen for later dissection, however representative subsamples of species were kept in aquaria, for live (freshly euthanized) dissection within three days of collection. Timed bird counts were conducted during each collection period and only resident riparian-dwelling birds were considered in the study.

Riparian mammals were quantified by point counts as well as midden counts in the case of muskrats and raccoons. No trapping was used, and abundance data was necessarily less precise. Prevalence values for ectoparasites found in these specimens were adjusted according to these smaller sample sizes.

Macroinvertebrates, fish, frogs and turtles were evaluated for parasites by dissection, and in some cases fish, turtle and frog blood samples were examined for protozoan parasites by Geimsa staining of blood smears, though protozoan parasites of the blood were not exhaustively sampled. Parasite infracommunities in turtles and avifauna were also estimated from fecal collection and floatation. The mass of microscopic parasites (protozoans and some larval forms of helminths) was estimated in the same way that free-living microfauna were calculated (see below). All larger larval and adult parasites were dried and weighed directly. When the dry-weight biomass could not be directly observed, we approximated per capita masses as the mean volume of organism, converted to a mass value approximated by the most similar conversion value from <http://www.convert-me.com/en/convert/weight2volume> (which has more than 300 mass-volume conversion factors ranging from various forms of vegetation and animal products, to liquids, to minerals). In this study, some parasite types (viruses, bacteria, blood-borne pathogens, and protozoan taxa) were not emphasized, and are subsequently underrepresented. Instead, our focus was largely on macroparasite species. Recent findings suggest that the parasite:free living species ratio may be as high as 4:1 (Whitman and Parker, 2004), and no study at the community scale has exhaustively sampled the true diversity of parasite fauna. The parasite diversity observed in this study is consistent

with comparable studies, and is sufficient to detect and extract basic patterns and properties of parasitism within the food web.

Food web construction and metrics

We constructed a binary food web matrix containing all observed species or morphospecies. Feeding interactions were “truthed” for nearly all of the vertebrate species, and the diets of some fish species (derived from gut content analysis) were augmented with diet information from regional literature on each species (aided by Fishbase.org). The presence or absence of feeding interactions between most invertebrate species was gleaned from a wide variety of sources, ranging from general observations (e.g., that filter feeding macroinvertebrates would consume plankton species) to very specific studies (e.g., the variation in diet of *Glossosomatid* trichopterans of North Eastern United States). Host-parasite interactions were necessarily more precise, because hosts must be collected in order to discover parasite species, and because host identity (or at least taxonomic group) is often diagnostic for many species of parasites. The matrix was read through UCINET (Borgatti et al., 2002) and visualized in NETDRAW (Borgatti, 2002), at which point biomass and trophic height were added as attributes and basic food web descriptors were calculated (nestedness, connectance and linkage density). Trophic height (defined as the mean trophic level of a predator’s prey plus one) was calculated for each species. The biomass of each species in the food web was presented as the logarithm of the average standing crop biomass. Where species abundance was derived from volumetric measures (e.g., fish, plankton and bacteria), the height dimension was measured for each collection and then “flattened” such that the

species abundances in the observed volume were presented in square meters. Parasite biomass was calculated using either direct per capita averages or, for microscopic species, based on volume estimates as described above. The per capita average mass for a parasite species in each host was multiplied by the prevalence (percent infection), the intensity (average number of parasites per host individual) and the density of hosts for each site. However, for some free-living species (namely birds and mammals), these values could not be directly measured, so the mass was estimated from those reported in existing literature, and the intensity was assumed to be one (an extremely conservative value).

Community Comparison

The trophic level of each species was approximated by rounding trophic height values to the nearest half, and was combined with biomass data (standing stock averages) to calculate the overall ecological efficiency of each community and to determine the proportion of total biomass represented by parasites. In this case, parasite life stages were incorporated separately, such that biomass for species with complex life cycles would be present at multiple trophic levels. To determine how similar communities were to one another, we calculated a matrix of pair-wise Bray-Curtis dissimilarity values for entire community comparisons, as well as autotroph+zooplankton, macroinvertebrate, vertebrate and parasite subgroups. The Bray-Curtis distance matrix was then visualized using Nonmetric Multidimensional Scaling (NMDS). This method is most appropriate for Bray-Curtis matrices because they do not satisfy triangle inequality, and because NMDS does not assume linearity (Holland, 2008). It has been argued that the stability of

host populations might play an important role in parasite establishment and persistence (Price, 1980), and we observed that host populations differed in abundance and variation across sites. As a crude measure of local stability of host populations, we calculated the quotient for v^2/x , where v is the variance and x is the mean standing stock biomass for a given species, and compared these values to the presence or absence of parasites for those species. Finally, we hypothesized that system perturbation would result in a decrease in the efficiency of biomass transfer up trophic levels (ecological efficiency; Slobodkin, 1962). That is, a pristine system should extend more biomass into upper trophic levels as a proportion of producer biomass. To examine this pattern across sites, we calculated the average difference in species' biomasses in each site-site comparison, again rounding trophic heights to the nearest half (i.e., 1, 2, 2.5, 3, etc). These differences were averaged for each half trophic level, and made proportional to values produced by the most diverse system (in this case, Burnt Mills). This allowed us to visualize and compare the changes in relative biomass for each species (and trophic level) across a perturbation gradient, and evaluate the impact of these changes on parasite biomass.

Results

Biotic and abiotic features varied greatly between the four sites and were strongly correlated, allowing us to clearly separate sites based on predictor variables (Figure 1). In general, indices of biological integrity (fish and invertebrate), habitat quality scores, and water quality metrics declined moving west to east, with Stanton Station and Burnt Mills consistently qualifying as exception warm water habitat (EWH), and North Branch and HW287 consistently scoring poorly, being classified as recreational use waters with

low Biological Condition Gradient (BCG) values (Gerritsen and Leppo, 2005). This also greatly impacted the observed diversity of free-living species from each site respectively. While species diversity varied predictably with habitat quality, Burnt Mills had the highest species richness for both free-living and parasite groups (104 and 24, respectively). Stanton Station, while scoring highest in respective habitat indices, contained 100 and 21 species. North Branch contained 88 free-living and 18 parasite species, and HW287 contained 79 free-living and 13 parasite species. Bray-Curtis dissimilarity values revealed that species presence, absence and abundance varied greatly across sites, with many species being unique to specific sites. However, when considering the dissimilarity values for each subgroup, the variation was predictable and consistent between sites (Figure 3). In general, plankton and vertebrate communities tended to be more similar between sites (mean = 0.3807 ± 0.1220 and 0.4067 ± 0.0812 respectively) while macroinvertebrate and parasite communities were less similar (mean = 0.5331 ± 0.0738 and 0.6298 ± 0.1157 respectively).

While species diversity varied greatly across sites, food web properties did not vary significantly. When parasites are included in the calculation of food web metrics, connectance averaged 0.1087 and was almost invariant across sites (S.D. = 0.0016). However, there was a decline in linkage density with decreasing free-living and parasite species richness (ranging from 13.687 in Burnt Mills to 10.119 in HW287). In terms of the distribution of biomass, total biomass varied unpredictably across sites (with North Branch producing the highest average standing stock biomass at 838.03 g/m^2 and HW782 producing the lowest average at 549.90 g/m^2). The distribution of biomass for each web is displayed in Figure 4. No relationship was detected between our stability measure

(v^2/x) and the presence or absence of parasites, and parasitism was evenly distributed across species that are both highly stable and those that displayed boom and bust populations (data not shown). A weak relationship was observed between free-living biomass and parasitism (particularly in higher trophic levels), but the pattern was not statistically significant (Figure 5). However, a general trend was observed with respect to the differences in biomass at each trophic level across sites (Figure 6). More perturbed sites produced proportionally more biomass at lower trophic levels, but significantly less biomass at higher trophic levels (with trophic level 5 in Stanton Station and North Branch being anomalies produced by particularly robust and persistent turtle populations). However, parasite biomass differences, while statistically significant, were paltry in relation to the observed differences for other trophic guilds, and appear nearly invariant.

Discussion

It has become increasingly clear that the impacts of human (anthropogenic) activity on ecological patterns and processes are quite significant (Paine et al., 1998; Chapin et al., 2006; Morris, 2010). There are now several journals (e.g., Conservation Biology, Ecology and Society, Ecological Restoration) whose scope and mission centers around the exploration of the interactions between human populations and ecological systems. In nearly all cases, the modification of ecological systems by humans is regarded as deleterious to a lesser or larger degree. The overarching metrics by which such impact is measured usually include species richness or diversity, specific services provided by the ecosystem, or the status of particular species of interest, whether as resources or in conservation efforts. Although parasitism at the community level has

been extensively studied in aquatic systems, there remains a paucity of information regarding the impact of human disturbance on parasite communities. Several authors have convincingly argued that parasites should be particularly sensitive to environmental perturbation (e.g., King et al., 2007; Schotthoefer et al., 2011), and this has been the impetus behind developing parasite-based metrics for assessing ecological systems (Marcogliese 2005; Sasal et al., 2007; Palm and S. Rückert, 2009). However, only a few studies have actually quantified this relationship, and we are still far from affirming the predicted patterns. Here we examine changes in diversity and biomass distribution (free-living and parasite) in riverine communities across a gradient of human impact, and find that community diversity can be greatly impacted by environmental perturbation, and that this pattern is reflected in the diversity of parasite fauna in those communities.

While it was predicted that overall free-living biomass would also track with diversity, there was no clear relationship, and one of the most perturbed sites (North Branch) was highly productive. There was a precipitous decline in overall diversity, but the decline was not linear, in that an intermediate site (Burnt Mills) is both the most productive and diverse. Parasite diversity tracks in a nearly linear fashion with changes in the species composition of the free-living communities, lending credence to the “diversity-begets-diversity” hypothesis for parasitism in ecological communities, which argues that increasing diversity in the host community increases diversity in the host community (Hechinger and Lafferty, 2005). This recalls the overall patterns reported in an earlier study by Hernandez and Sukhdeo (2007) but is counter to several existing studies (e.g., Anderson and Sukhdeo, 2011).

While overall standing stock biomass was not related to changes in species diversity, I find that the overall ecological efficiency of communities can be greatly compromised by environmental perturbation, and a smaller fraction of initial producer biomass is extended into higher trophic levels in the most perturbed sites. This suggests that “healthy” systems function better than those that have been altered, and that higher trophic levels are most impacted. However, these findings are tempered by the fact that the total parasite biomass was nearly invariant. This suggests that, while parasite species richness declines with host diversity, the biomass (as expressed by prevalence and intensity) can actually increase for parasites in these systems. It must also be noted that nine parasite species occurred in all sites, and fifteen species are shared in the three less perturbed sites. Thus, these species appear buffered (at least to some threshold) to changes in community structure. Contrary to various modeling studies observing that parasites decrease community stability and are more sensitive to extinction (e.g., Dunne et al., 2002; Lafferty and Kuris, 2009; Rudolf and Lafferty, 2011), our data suggest that some parasites are resistant to extinction because they are harbored within nested subwebs that themselves are stable and persistent. This is a growing point of debate, and evidence has been cast in favor of both views. However, nearly all empirical data from surveys conducted in ecological systems favor the latter (e.g., Anderson and Sukhdeo, 2011; Chen et al., 2011). From an evolutionary standpoint, this is a logical conclusion, because strongly interacting “core” species are thought to be more stable and resilient (Bascompte and Stouffer, 2009; Valladares et al., 2012), representing favorable hosts for parasite establishment and persistence (Price, 1980). This also partly explains why some

free-living species serve as hosts for many parasites, while others do not, even when taxonomic categories are considered (Rossiter and Sukhdeo, 2011).

In conclusion, this study demonstrates a direct link between environmental perturbation and free-living and parasite community structure in a riverine system. By incorporating biomass data into a high resolution food web, we were able to address aspects of community structure and function that would not be possible using binary matrices alone. Specifically, this study shows that biomass distribution across trophic levels changes with perturbation, but that parasite biomass remains relatively constant even when diversity is greatly altered. While continued research in this area is required before and clear community-level rules can be discerned, this study illustrates the utility of replicated studies within systems in allowing us to extract fundamental patterns about the nature of host-parasite communities.

Figure 5.1: Map of Raritan River watershed. Dots indicate sampling locations. Gradient of human impact moves left to right. ST = Stanton Station, BM = Burnt Mills, NB = North Branch, HW = Highway 287.

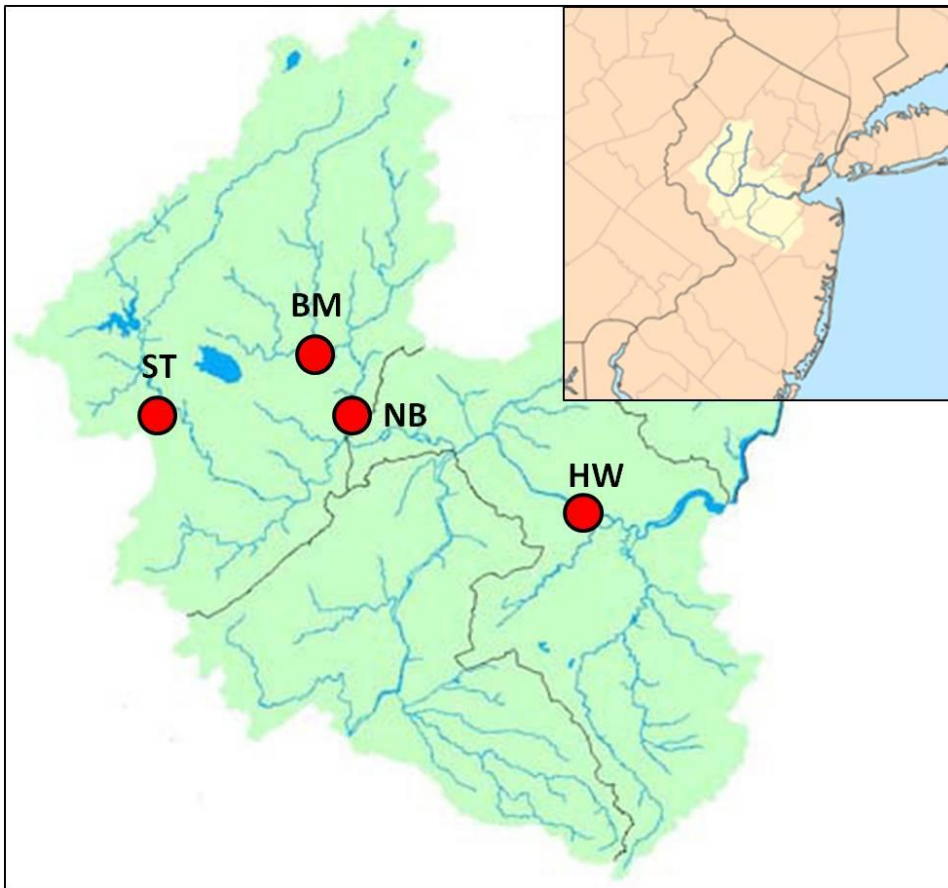


Figure 5.1

Figure 5.2: Cononical Correlation Analysis of multivariate data including abiotic data (dissolved oxygen, pH, conductivity, temperature and habitat), fish and macroinvertebrate indices. Habitat 2 represents a composite variable comprised of % open canopy, riparian corridor values and substrate composition scores. Both axes have been reversed, making the site “centers” correspond to the rough map location of each site.

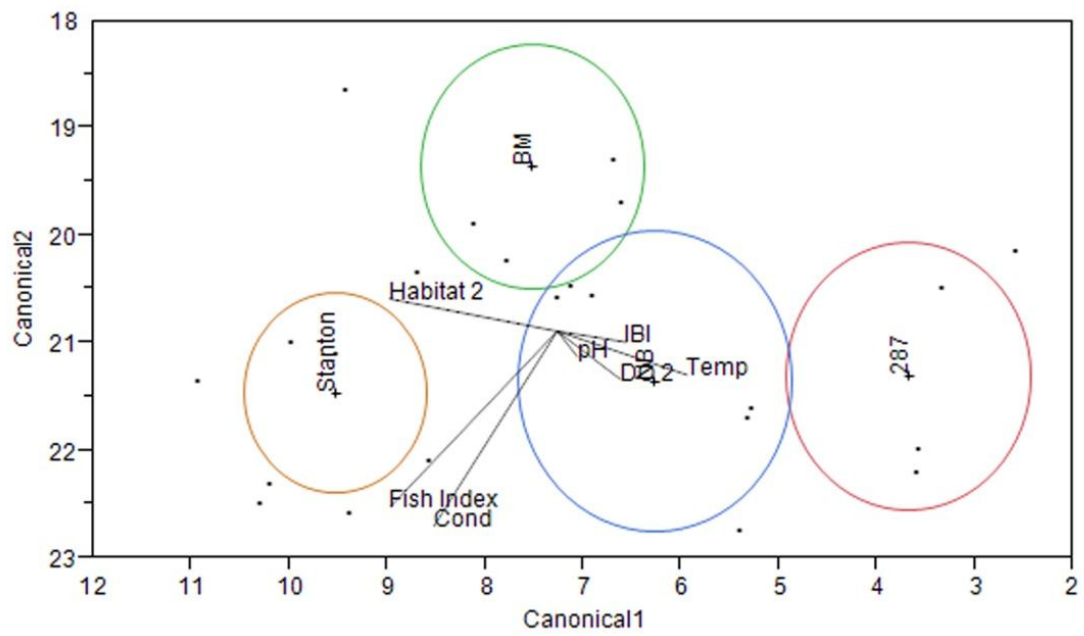


Figure 5.2

Figure 5.3: Visualization of Bray-Curtis scores for each species group (total, plankton-protozoan, macroinvertebrate, vertebrate and parasite) using Nonmetric Multidimensional Scaling (NMDS). In general, total scores are closest to one another (most similar), while parasite communities were most dissimilar (see Results).

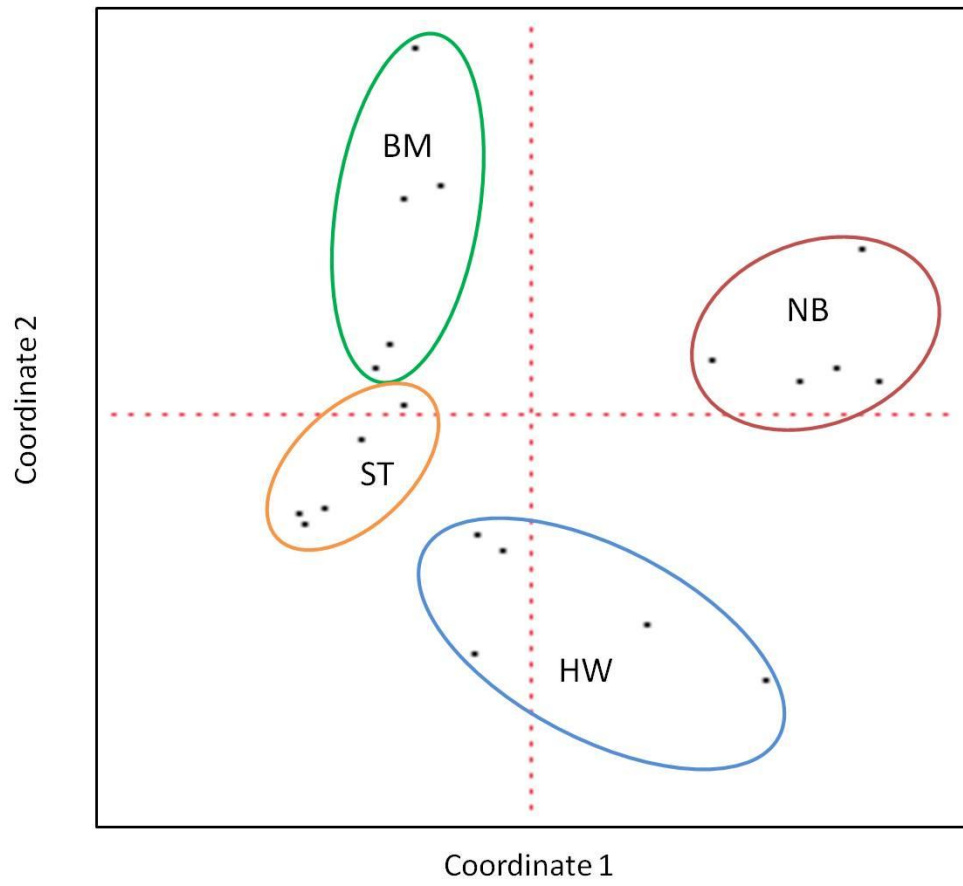


Figure 5.3

Figure 5.4: Food webs for each respective collection site. Node size indicates $\log(\text{g/m}^2)$ of standing stock biomass and red nodes denote parasites. x-axis is biomass and y-axis is trophic height.

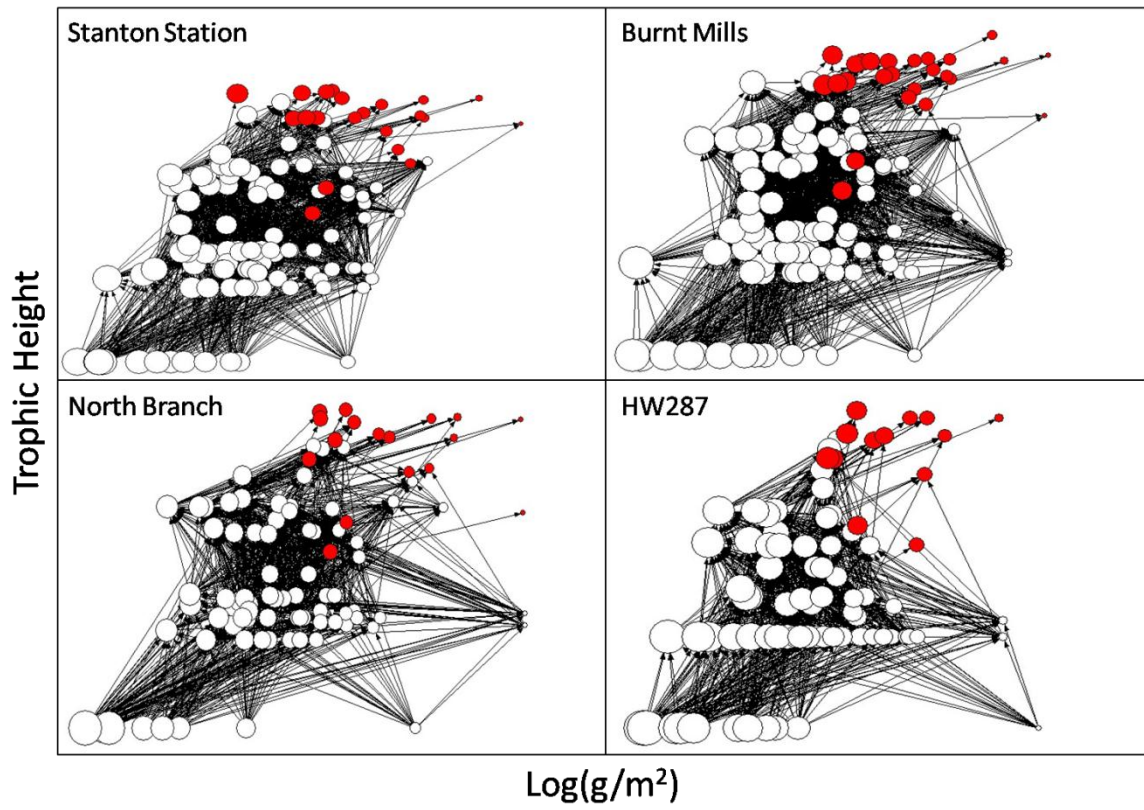


Figure 5.4

Figure 5.5: Relationship between standing stock biomass and parasitism. Red data points indicate free-living species acting as hosts for at least one parasite. Parasites with complex life cycles are represented in each host. No clear relationship was found between standing stock biomass [$\log(\text{g}/\text{m}^2)$] and the presence or absence of parasitism. Note that rare (low biomass) species are greatly reduced in North Branch and HW 287 sites.

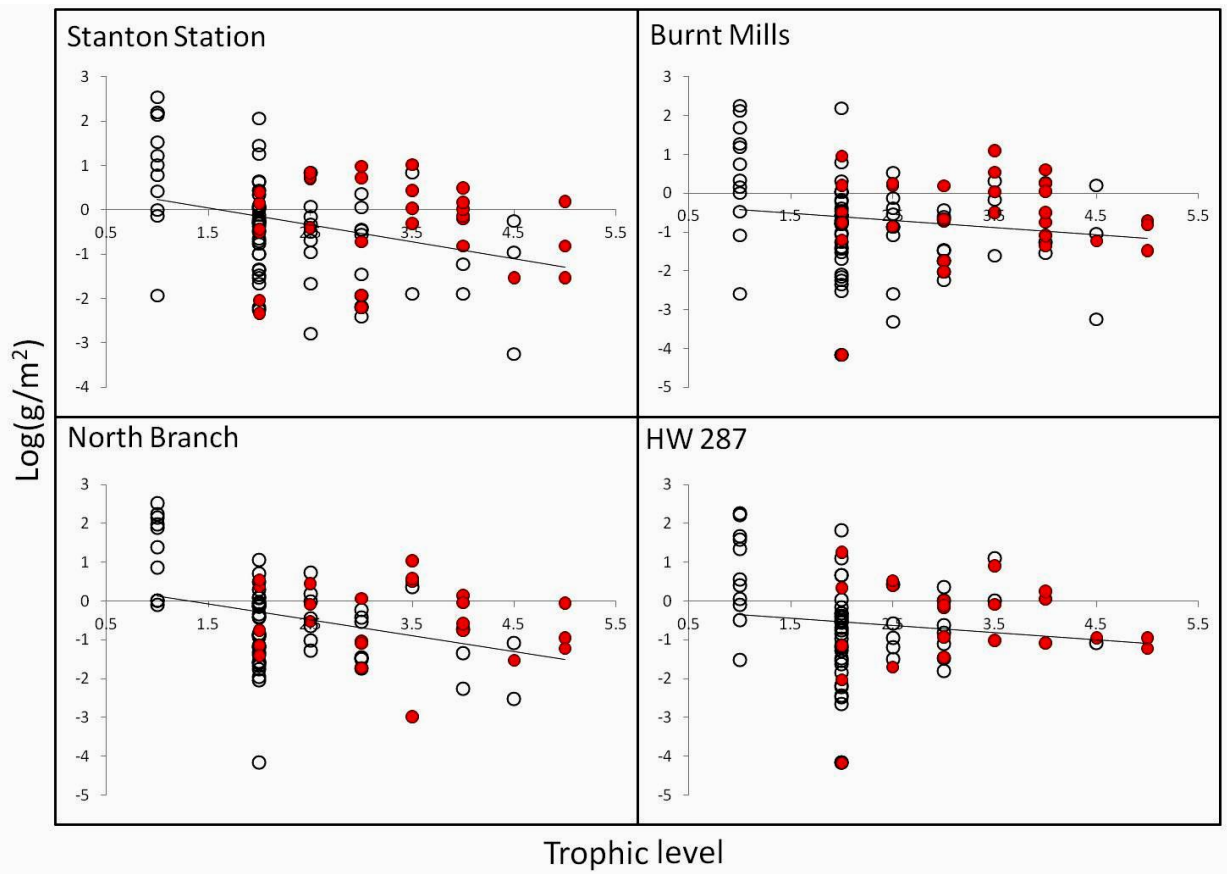


Figure 5.5

Figure 5.6: Average change in species biomass between sites at each trophic level.

Trophic heights were rounded to nearest half, and the 5.5 level denotes parasites.

Differences are proportional such that one unit (1.0) on the y-axis would indicate a 100% increase (negative values) or decrease (positive values) in biomass at that level as compared to the observed biomass of Burnt Mills. Biomass in more perturbed sites tended to have larger biomass values at lower trophic levels and increasingly small relative biomass values at higher trophic levels. However, parasite biomass varied only slightly.

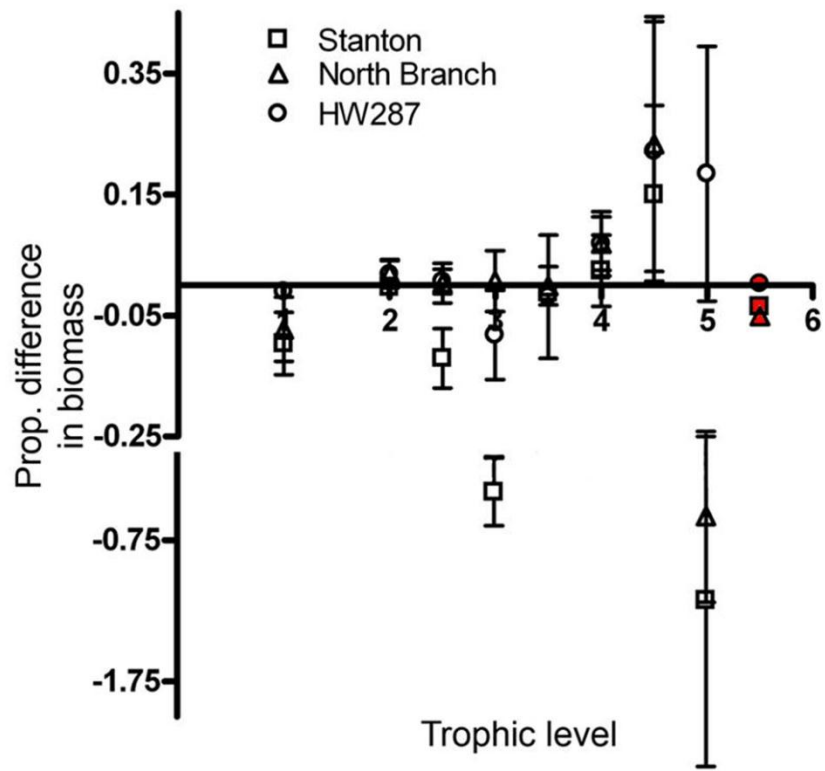


Figure 5.6

CHAPTER 6

General Discussion

Within the growing field of parasite ecology there has been a concerted effort to establish clear relationships between free-living communities and their respective parasite fauna (Dobson and Hudson, 1986; Marcogliese, 2002; Guégan et al., 2005; Poulin, 2010). Even though parasite-host interactions have been exhaustively studied with a high degree of control and precision in classic parasitology, many ecological patterns remain poorly defined, and most lack adequate causal explanations (Poulin, 2007). For good reason, it is assumed that parasite-host interactions are strongly linked co-evolved situations (Price, 1980; Sukhdeo and Sukhdeo, 2004; Combes and Simberloff, 2005). However, the species and community characteristics that allow parasites to establish and persist remain elusive. Oddly, much more is known about the impacts of parasites on free-living communities than the reciprocal (e.g., Huxham et al., 1996; Francisco and Bolker, 2005; Lafferty et al., 2006; Chen et al., 2011). Numerous studies have examined the impacts of parasites on host behavior (Poulin et al., 1994; Libersat et al., 2009), host population dynamics (Dobson and Hudson, 1992), predator-prey feeding interactions (Kuris, 2005), and community food web structure (Byers, 2009; Sukhdeo, 2011), stability (Grami et al., 2011) and network properties (Sukhdeo and Hernandez, 2005). However little is known regarding the constraints that host populations or communities might place on parasite life histories, establishment or persistence. For example, one of the most universal and well established patterns in parasitology is that parasites are highly aggregated within host populations, with a small number of host individuals containing the majority of the

parasite component population (Crofton, 1971; Wilson et al., 1996). Many putative mechanisms have been implicated, but no general explanation has emerged (Poulin, 2007). At the community level, it has been argued that parasite diversity should be tightly bound to diversity of free-living species in a system (Hechinger and Lafferty, 2005). In some cases this relationship has been borne out (Poulin et al., 2011), while other cases are less clear (Anderson and Sukhdeo, 2011). Further, the basic latitudinal patterns of diversity (higher in the tropics) observed in free-living taxa do not seem to apply to parasites (Lindenfors et al., 2007). Finally, there is the question as to why some species (or taxonomic groups) disproportionately harbor parasite species, while others are relatively unparasitized (Benesh et al., 2011).

In this dissertation, I examine the relationship between host and parasite populations and communities at multiple scales and attempt to establish what attributes make some hosts or communities more likely to be invaded by parasites. I first evaluate the spatial patterning of infection of an estuarine snail (*Ilyanassa obsoleta*) by two trematode parasites, using a combination of survey, mark-recapture and manipulation experiments in a salt marsh system (Tuckerton, NJ). I find that parasitism is strongly linked with host quality, and that the underlying driver for both is habitat type. I then examine the larger patterns of parasitism in this salt marsh community (in the context of food web topology) and find that predator-prey asymmetries are strong predictors of the presence or absence of trophically transmitted parasites. I further examine the role of habitat space in constraining both predator-prey interactions and the transmission of parasites in a freshwater riverine system. Finally, I assess the changes in free-living and parasite community structure across a gradient of human impacts.

Spatial patterning of parasitism in host populations and communities

The spatial patterning of parasites in host populations remains a principle area of investigation for parasitologists (e.g., Esch and Fernandez, 1994; Guegan et al., 2005; Poulin 2007, Matthee and Krasnov, 2009), and a long standing goal within parasite ecology has been to elucidate the underlying mechanisms that produce parasite aggregation in host populations (Crofton, 1971; Poulin, 2007). Numerous putative mechanisms have been either suggested or demonstrated, including the linking of infection with population demographics (Grenfell et al., 2002), with differences in the incidence of contact with infective stages and differential host compatibility (Morand et al., 1996). While each of these solutions have been aptly demonstrated, I found another possible explanation that was related to host quality. For parasites that amplify and produce progeny in a host, the quality of that host as a resource can have a direct impact on that production. Thus, if the fitness of a parasite can be linked to host quality, then selective pressures should act to mold parasite life cycles such that they hone in on the highest quality hosts in populations. This would be most evident in a system where host quality varies over space. My work provides evidence for such a system, demonstrating that snail host quality is strongly correlated with spatial patterning in trematode infections, and that habitat type is the underlying driver for both of these variables (Rossiter and Sukhdeo, 2012). These findings are in agreement with several other recent studies which have suggested that the fitness of a parasite can be directly impacted by the quality of its host (Hall, 2009).

In addition to the spatial context of host-parasite population dynamics, there is the larger question of whether or not space plays a role in the evolution and transmission of parasites at the community level. For some time, parasitologists have known that spatial overlap between hosts can be an important predictor in the patterning of infection (Bustnes and Galaktionov, 1999; Skirnisson et al., 2004). Still, because very little work has been done to quantify the spatial distribution of ecological networks (namely food webs), even less is known about the way parasites move through communities over space. My study elucidates the distributions of parasites with respect to their hosts, with emphasis on parasites that utilize trophic interactions in transmission (Rossiter and Sukhdeo, submitted). Using a high resolution riverine food web, I demonstrate that trophic interactions happen over distances that are shorter than would be predicted at random, that host-host distances are significantly shorter than the overall observed distances, and that the life cycles of parasites involve species with high degrees of overlap. This evidence suggests that species-species interactions are significantly constrained by habitat, and that parasites with complex life cycles are particularly sensitive to these constraints.

Parasite position in free-living food webs

An extremely fertile area of research has been the exploration of the evolution of trophic transmission in parasites (e.g., Choisy et al., 2003; Kuris, 2003). However, most studies have had the myopic tendency to focus on only the host-parasite population (or individual) level (but see Marcogliese, 2007). Detailed studies of parasitism across ecological communities have only recently provided data for the exploration of such

large-scale questions. In exploring the pattern of trophic transmission in a salt marsh food web (as well as several other published food webs), I observed a hitherto unknown aspect of trophic transmission (Rossiter and Sukhdeo, 2011). Predator-prey interactions assume a type of asymmetry in which either the predator's diet breadth (the number of species it feeds on) supersedes the prey's vulnerability (the number of predators that feed on it) or vice versa. From the perspective of the parasite, one situation is favorable for trophic transmission (when prey hosts have few predator nonhosts), and other choices should be selected against over time. This is an alternative form of the dilution effect argument (Hechinger and Lafferty, 2005). Additionally, this study found that trophically transmitted parasites gravitate towards particular predator-prey interactions, meaning that the same predator-prey species come to harbor multiple parasites. These findings suggest that food web topology has great bearing on the ecology of trophically transmitted parasites, and that consideration of parasite life cycles in the context of food web organization can provide insights into the forces affecting the evolution of trophic transmission. Such findings have recently been echoed by several authors (Chen et al., 2008; Benesh et al., 2011), and suggest that we have only scraped the surface of the possibilities made available by this type of research.

Species abundance, biomass and food webs

While my work, along with that of others, demonstrates the utility of food web analysis in understanding parasitism, adding proverbial "meat" (abundance and biomass) to existing food webs permits a deeper exploration of the patterns and forces at work in these systems. For example, in the absence of abundance data, I hypothesized that

trophically transmitted parasites would be overrepresented in species that are both abundant and persistent in free-living communities (Rossiter and Sukhdeo, 2011). This argument extended from the prior assertion that parasites evolve tight relationships with hosts that are evolutionarily stable and dependable (Price, 1980). My later work in a riverine food web permitted the examination of this hypothesis, and found that parasites were no more likely to be found in abundant species with stable populations. More importantly, the inclusion of biomass (or abundance) facilitates additional analysis not afforded by the binary matrices of most food webs. Intuitively, it would be important to distinguish between rare and abundant species in trying to understand (or model) trophic flows in a food web. If one prey item is abundant and another rare, it offers additional context to the observed patterns manifested in food webs. Such data are also important if one is interested assessing the function of a community (Andersen et al., 1980) or the way in which parasites are distributed in communities (Arneberg et al., 1998). Again, a parasite infecting a small rare species is notably different than one that parasitizes a large abundant species.

As demonstrated in my research, informing food webs with abundance or biomass data can be particularly useful when doing comparative studies across communities. A classic question within the field of parasite ecology is whether or not parasite diversity tracks with free-living diversity. Superficially, this would seem logical because each new free-living species represents an opportunity for parasitism, and parasites (in general) tend to be host-specific. As of yet, no one has attempted to predict the specific nature of this interaction, and, given that parasites often utilize multiple hosts, it seems likely that the relationship between free-living and parasite diversity would be nonlinear. However,

the easiest null prediction would be a linear relationship between free-living biomass and parasite biomass in a community. Because parasites exist at multiple trophic levels, I initially argued that we should predict a “pyramid within a pyramid” in which the parasite biomass within a community would mirror the patterns observed in the larger free-living community. Thus, changes in the shape of a free-living biomass pyramid (which would depict changes in the ecological efficiency of a system) should result in a direct change in the distribution of parasite biomass within the system. However, in a comparison of four communities across a perturbation gradient, I found small changes in parasite biomass in response to large changes in the biomass distributions of respective free-living communities. Interestingly, this pattern emerged coincident with large changes in parasite diversity across communities. Though less clearly, this pattern was also found when data were combined for three studies in the salt marshes of southern California (Kuris et al., 2008; Hechinger et al., 2011). These findings suggest a complex relationship between parasite and free-living communities, and the need for additional replicated studies within systems.

General conclusion

In my dissertation, I have explored many facets of parasite-host interactions in an attempt to better understand how parasites establish and persist in host communities. To a large degree, my interests gravitated towards the impacts of space on parasite-host interactions; an area in desperate need of attention. Food web analyses have been extremely useful in establishing a basic understanding of the way parasites are imbedded in free-living communities, and these advances have led to deeper questions regarding

why many parasite species come to utilize the same free-living host, and whether or not there are characteristics that make a species more or less invasible by parasites. I have attempted to augment food web matrices with additional information that could impact host-parasite interactions (namely spatial context, abundance and biomass). In assessing food web attributes, I discovered that the way in which predator and prey focal pairs are linked into the large matrix can be used as a powerful predictor of presence or absence of trophically transmitted parasites. In working with a specific snail-trematode system, I established that two trematode species aggregate in spatially explicit host sub-populations in which hosts represent a high quality resource and have a high degree of spatial overlap with downstream hosts. Extending this concept into a community level study in a riverine system, I also concluded that host-host (and subsequently parasite life cycles) interactions happen among species with a high degree of spatial overlap. The idea that some free-living species are simply not possible due to spatial constraints greatly changes the way we have traditionally evaluated parasites in food webs, and opens the door for more rigorous and detailed investigations of the spatial dimensions of host-parasite interactions.

REFERENCES

Chapter 1

- Abrams, P. A. (2001). Describing and quantifying interspecific interactions: a commentary on recent approaches. *Oikos* 94, 209–218.
- Allesina, S., Bodini, A. & Bondavalli, C. (2005). Ecological subsystems via graph theory: the role of strongly connected components. *Oikos* 110(1), 164–176.
- Anderson, R.M. & May, R.M. (1978). Regulation and stability of host-parasite population interactions I. Regulatory processes. *Journal of Animal Ecology* 47, 219–247.
- Arneberg, P., Skorping, A., Grenfell, B. & Read, A. F. (1998). Hosts densities as determinants of abundance in parasite communities. *Proceeding of the Royal Society, London B* 266, 1283–1289.
- Barger, M.A. & Esch G.W. (2002). Host specificity and the distribution-abundance relationship in a community of parasites infecting fishes in streams of North Carolina. *Journal of Parasitology* 88, 446–453.
- Bell, G. & Burt, A. (1991). The comparative biology of parasite species diversity: intestinal helminths of freshwater fishes. *Journal of Animal Ecology* 60, 1046–1063.
- Benesh, D. P., Chubb, J.C. & Parker, G.A. (2011). Exploitation of the same trophic link favors convergence of larval life-history strategies in complex life cycle helminths. *Evolution* 65(8), 2286–2299.
- Berlow, E. L., Neutel, A.M., Cohen, J.E., De Ruiter, Peter, C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Jones, J.I., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M., & Petchey, O. (2004). Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology* 73, 585–598.
- Bersier, L. F., Banasek-Richter, C. & Cattin, M.F. (2002). Quantitative descriptors of food-web matrices. *Ecology* 83, 2394–2407.
- Blaylock, B., Holmes, J.C. & Margolis, L. (1998). The parasites of Pacific halibut (*Hippoglossus stenolepis*) in the eastern North Pacific. *Canadian Journal of Zoology* 76: 536–547.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Bush, A.O., Fernandez, J.C., Esch, G.W. & Seed, J.R. (2001). Parasitism: the diversity and ecology of animal parasites. Cambridge University Press, Cambridge.

- Byers, J. E. (2009). Including parasites in food webs. *Trends in Parasitology* 25(2), 55-57.
- Camacho J., R. G. & Amaral L.A.N. (2002). Robust patterns in food web structure. *Physical Review Letters* 88, 228102.
- Carr D. E., Murphy, J. F. & Eubanks, M. D. (2003). Susceptibility and response of inbred and outbred *Mimulus guttatus* to infection by Cucumber mosaic virus. *Evolutionary Ecology* 17, 85–103.
- Castro, F.D. & B. Bolker. (2005). Mechanisms of disease-induced extinction. *Ecology Letters* 8, 117–126.
- Chase, J.M. (2000). Are there real differences among aquatic and terrestrial food webs? *Trends in Ecology and Evolution* 15, 408–412.
- Chen, X., & Cohen, J.E. (2001). Transient dynamics and food-web complexity in the Lotka-Volterra cascade model. *Proceedings of the Royal Society, London B* 268, 869–877.
- Chen, H., Liu, W.C., Davis, A.J., Jordán, F., Hwang, M.J. & Shao, K.T. 2008. Network position of hosts in food webs and their parasite diversity. *Oikos* 117: 1847–1855.
- Chen, H.W., Shao, K.T., Liu, C.W., Lin, W.H. & Liu, W.C. (2011). The reduction of food web robustness by parasitism: Fact and artefact. *International Journal of Parasitology* (online first).
- Cohen, J.E. (2007). Body sizes in food chains of animal predators and parasites. In: *Body Size: The Structure and Function of Aquatic Ecosystems*, (eds.) A.G. Hildrew, D. G. Raffaelli and R. Edmonds-Brown. Published by Cambridge University Press.
- Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* 62, 67–78.
- Combes, C. (2001). *Parasitism: The Ecology and Evolution of Intimate Interactions*. University of Chicago Press, Chicago, IL.
- Crofton, H.D. (1971). A quantitative approach to parasitism. *Parasitology* 62, 179-193.
- Davies, K.F., Margules, C.R. & Lawrence, J.F. (2004). A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85, 265–271.

- Dietl, G.P. (2003). Interaction strength between a predator and dangerous prey: Sinistrolfulgur predation on Mercenaria. *Journal of Experimental Marine Biology and Ecology*. 289, 287–301.
- Dobson, A.P. & Hudson, P.J. (1986). Parasites, disease and the structure of ecological communities. *Trends in Ecology and Evolution* 1, 11-15.
- Dobson, A.P. and P.J. Hudson. 1992. The population dynamics and control of the parasitic nematode *Trichostrongylus tenax* in red grouse in the North of England. *Applied Population Biology* 67: 149-171.
- Dobson, A., Lafferty, K. & Kuris, A. (2005). Parasites and food webs. In: Pascal, M. and Dunn, J. A. (eds), *Ecological networks: linking structure to dynamics in food webs*. Oxford Univ. Press, pp. 119-135.
- Dorovskikh, G.N. & Stepanov, V.G. (2008). Change in the Structure of Component Parasite Communities with Host Age. *Russian Journal of Ecology* 35(3), 227–232.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2004). Network structure and robustness of marine food webs. *Marine Ecology Progress Series* 273, 291-302.
- Dunne, J.A., Brose, U., Williams, R.J. & Martinez, N.D. (2004). Modeling Food-Web Dynamics: Complexity-Stability Implications. Santa Fe Institute.
- Elton, C.S. (1927). *Animal Ecology*. Sidgwick and Jackson, London.
- Garlaschelli, D., Caldarelli, G. & Pietronero, L. (2003). Universal scaling relations in food webs. *Nature* 423, 165–168.
- Goldwasser, L., & Roughgarden, J.R. (1993). Construction and analysis of a large Caribbean food web. *Ecology* 74, 1216–1233.
- Griffiths, D. (1992). Size, abundance, and energy use in communities. *Journal of Animal Ecology* 61, 307-315.
- Guegan, J.F., Morand, S. & Poulin, R. (2005). Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. In: *Parasitism and Ecosystems*. eds. Thomas, F., Renaud, F. & Guegan, J.F. Oxford: Oxford University Press. pp. 22-42.
- Hall, S.R. (2009). Stoichiometrically-explicit food webs: feedback between stoichiometric constraints and species interactions. *Annual Review of Ecology, Evolution, and Systematics* 40, 503–528.
- Hechinger, R.F. & Lafferty, K.D. (2005). Host diversity begets parasite diversity: bird

- final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society, London B* 272, 1059-1066.
- Hudson, P.J., Dobson, A.P. & Lafferty, K.D. (2006). Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology and Evolution* 21, 381-385.
- Hugot, J.P., Baujard, P. & Morand, S. (2001). Biodiversity in helminths and nematodes as a field of study: an overview. *Nematology* 3, 199-208.
- Huxham, M., Raffaelli, D. & Pike, A. (1995). Parasites and food web patterns. *Journal of Animal Ecology* 64, 168-176.
- Huxham, M., Beaney, S. & Raffaelli, D. (1996). Do parasites reduce the chances of triangulation in a real food web? *Oikos* 76, 284-300.
- Janz, N., Nylin, S. & Wahlberg, N. (2006). Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evolutionary Biology* 6, 4.
- Jonsson T., Karlsson, P. & Jonsson, A. (2006). Food web structure affects the extinction risk of species in ecological communities. *Ecological Modelling* 199, 93-106.
- Jordán, F. & Molnár, I. (1999). Reliable flows and preferred patterns in food webs. *Evolutionary Ecology Research* 1, 591-609.
- Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K., Aguirre-Macedo, L., Boch, C., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F., Mora, A., Pickering, M., Talhouk, N., Torchin, M.E., & Lafferty, K.D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515-518.
- Lafferty, K.D. (2010). Interacting parasites. *Science* 330(6001), 187-188.
- Lafferty, K.D., Dobson, A.P. & Kuris, A.M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences, USA* 103, 11211-11216.
- Lafferty, K.D., Hechinger, R.F., Shaw, J.C., Whitney, K.L. & Kuris, A.M. (2006). Food webs and parasites in a salt marsh ecosystem. In: *Disease ecology: community structure and pathogen dynamics* (eds. Collinge S & Ray C). Oxford University Press Oxford, pp. 119-134.
- Lafferty, K.D. & Kuris, A.M. (2009). Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philosophical Transactions of the Royal Society Biological Sciences* 364, 1659-1663.

- Laska, M. S. & Wootton, J. T. (1998). Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79, 461–476.
- Leibold, M. A. and Wootton, J.T. (2001). Introduction to Animal Ecology. In: Elton, C. *Animal Ecology*. University of Chicago Press, Chicago, 2001.
- Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology* 23, 399–417.
- Lindenfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W. & Gittleman, J.L. (2007). Parasite species richness in carnivores: effects of host body mass, latitude, geographic range and population density. *Global Ecology and Biogeography*. (DOI: 10.1111/j.1466-8238.2006.00301.x).
- Lively, C.M. & Dybdahl, M.F. (2000). Parasite adaptation to locally common host genotypes. *Nature* 405(8), 279-281.
- Marcogliese, D.J. (2002). Food webs and the transmission of parasites to marine fish. *Parasitology* 124, S83–S99.
- Marcogliese D.J. (2007). Evolution of parasitic life in the ocean: paratenic hosts enhance lateral incorporation. *Trends in Parasitology* 23, 519–521.
- Marcogliese, D.J. & Cone, D.K. (1997). Food webs: a plea for parasites. *Trends in Ecology and Evolution* 12, 320–325.
- May, R.M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- Mayer, A. & Pimm, S. L. (1997). Tropical rainforests: diversity begets diversity. *Current Biology* 7, 430–432.
- Memmott, J., Martinez, N.D., & Cohen, J.E. (2000). Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology* 69, 1-15.
- Melian, C. J. & Bascompte, J. (2004). Food web cohesion. *Ecology* 88(2), 352-358.
- Morand, S., Manning, S.D. & Woolhouse, M.E.J. (1996). Parasite-host coevolution and geographic patterns of parasite infectivity and host susceptibility. *Proceedings of the Royal Society of London B* 263, 119–128.
- Morand, S. & Gonzalez, E.A. (1997). Is parasitism a missing ingredient in model ecosystems? *Ecological Modeling* 95, 61-74.

- Morand, S. & Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* 12, 717-727.
- Morand, S. & Krasnov, B.R. (eds). (2010). *The Biogeography of Host-Parasite Interactions*. Oxford University Press, New York.
- Mouillot, D., Krasnov, B.R., & Poulin, R. (2008). High intervality explained by phylogenetic constraints in host-parasite webs. *Ecology* 89, 2043-2051.
- Mouritsen, K.N. & Poulin, R. (2005). Parasites boost biodiversity and changes animal community structure by trait-mediated indirect effects. *Oikos* 108, 344-350.
- Niklas, K.J., Midgley, J.J., & Enquist, B.J. (2003). A general model for mass-growth-density relations across tree-dominated communities. *Evolutionary Ecology* 5, 459-468.
- Odum, E. P. (1959). *Fundamentals of Ecology*. W. B. Saunders Company, Philadelphia. 2nd ed.
- Paine, R.T. (1988). Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69, 1648-1654.
- Pedersen, A.B. & Fenton, A. (2007). Emphasizing the ecology in parasite community ecology. *Trends in Ecology and Evolution* 22, 133-139.
- Petchey, O.L., Eklöf, A., Borvall, C. & Ebenman, B. (2008). Trophically unique species are vulnerable to cascading extinctions. *American Naturalist* 171, 568-579.
- Peters, R. H. (1988). Some general problems for ecology illustrated by food web theory. *Ecology* 69, 1673-1676.
- Pimm, S. L. (2002). *Food Webs*. The University of Chicago Press, Chicago.
- Pimm, S.L. & Kitching, R.L. (1988). Food web patterns: trivial flaws or the basis of an active research program? *Ecology* 69, 1669-1672.
- Pinnegar, J.K., Campbell, N., & Polunin, N.V.C. (2001). Unusual stable isotope fractionation patterns observed for fish host-parasite trophic relationships. *Journal of Fish Biology* 59, 494-503.
- Polis, G.A. (1991). Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138, 123- 155.
- Poulin, R. (1995). Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* 65, 283-302.

- Poulin, R. (1997). Species richness of parasite assemblages: evolution and patterns. *Annual Review of Ecology and Systematics* 28, 341-358.
- Poulin, R. (1999). The functional importance of parasites in animal communities: many roles at many levels? *International Journal of Parasitology* 29, 903-914.
- Poulin R. (2007). Are there general laws in parasite ecology? *Parasitology* 134, 763-776.
- Poulin, R. (2010). Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology* 26, 492-498.
- Poulin, R., & Morand, S. (2000). The diversity of parasites. *Quarterly Review of Biology* 75, 277-293.
- Power, M. & Klein, G.M. (2004). Fish host–cestode parasite stable isotope enrichment patterns in marine, estuarine and freshwater fishes from northern Canada. *Isotopes in Environment and Health Studies* 40, 257–266.
- Price, P.W. (1980). *Evolutionary Biology of Parasites*. Princeton University Press, Princeton.
- Quince, C., Higgs, P.G. & McKane, A.J. (2005). Deleting species from model food webs. *Oikos* 110, 283-296.
- Raffaelli, D.G. (2002). From Elton to Mathematics and Back Again. *Science* 296, 1035-1037.
- Raffel, T.R., Martin, L.B. & Rohr, J.R. (2008). Parasites as predators: unifying natural enemy ecology. *Trends in Ecology and Evolution*. 23, 610-618.
- Reuman, D. C., Mulder, C., Raffaelli, D. & Cohen, J. (2008). Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters* 11, 1216–1228.
- Rohde, K. (1978). Latitudinal differences in the host-specificity of marine Monogenea and Digenea. *Marine Biology* 47, 125-134.
- Rollinson, D. & Anderson, R.M. (1985). *Ecology and genetics of host-parasite interactions (Linnean Society Symposium Series)*. Academic Press. pg 266.
- Rooney, N. McCann, K., Gellner G. & Moore J.C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* 442, 265-269.
- Rossiter, W. & Sukhdeo, M.V.K. (2011). Exploitation of asymmetric predator-prey interactions by trophically transmitted parasites. *Oikos* 120(4), 607-614.

- Rossiter, W. & Sukhdeo, M.V.K. (2012). Host quality and spatial patterning in infections of the eastern mudsnail (*Ilyanassa obsoleta*) by two trematodes (*Himasthla quissetensis* and *Zoogonus rubellus*). *Journal of Parasitology* (in press).
- Ruiter, P.C., Wolters, V. & Moore, J.C. (2005). Dynamic food webs. In: *Dynamic Food Webs- multispecies assemblages, ecosystem development and environmental change* (Eds. P.C. de Ruiter, V. Wolters and J. C. Moore). Academic Press, NY, New York.
- Shaw, D. J., Grenfell, B.T. & Dobson, A.P. (1998). Patterns of macroparasite aggregation in wildlife host populations. *Parasitology* 117, 597-610.
- Shurin, J.B., Gruner, D.S. & Hillebrand, H. (2006). All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society of London B* 273, 1-9.
- Sole, R.V. & Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London*, 268, 2039-2045.
- Srinivasan, U.T., Dunne, J.A., Harte, J. & Martinez, N.D. (2007). Response of complex food webs to realistic extinction sequences. *Ecology* 88, 671–682.
- Stapp, P. & Salkeld, D.J. (2009). Inferring host-parasite feeding relationships using stable isotopes: implications for disease transmission and host specificity. *Ecology* 90, 3268-3273.
- Steele, J.H. (2009). Assessment of some linear food web methods. *Journal of Marine Systems* 76, 186–94.
- Sugden, A.M. (2001). Diversity Begets Diversity. *Science* 292(5516), 399.
- Sukhdeo, M.V.K. (2010). Foodwebs for Parasitologists. A Review. *Journal of Parasitology* 96, 273-284.
- Sukhdeo, M.V.K., & Hernandez, A.D. (2005). Food Web Patterns and the Parasite's Perspective. In: *Parasitism and Ecosystems* (Eds. F. Thomas, J.F. Guegan, and F. Renaud). pp. 54-67. Oxford University Press.
- Thieltges, D.W., de Montaudouin, X., Fredensborg, B.L., Jensen, K.T., Koprivnikar J., & Poulin R. (2008). Production of marine trematode cercariae: a potentially overlooked path of energy flow in benthic systems. *Marine Ecology Progress Series* 372, 147–155.
- Thomas, F., Renaud, F., de Meeus, T. & Poulin, R. (1998). Manipulation of host behaviour by parasites: Ecosystem engineering in the intertidal zone? *Proceedings of the Royal Society of London B* 265, 1091–1096.

Vander Zanden, M. J., & Rasmussen, J.B. (1996). A trophic position model of pelagic food webs: Impact on contaminant bioaccumulation in lake trout. *Ecological Monographs* 66, 451-477.

Va'zquez, D. P., Poulin, R., Krasnov, B.R. & Shenbrot, G.I. (2005). Species abundance patterns and the distribution of specialization in host-parasite interaction networks. *Journal of Animal Ecology* 74, 946-955.

Whiteman, N.K. & Parker, P.G. (2005). Using parasites to infer host population history: A new rationale for parasite conservation. *Animal Conservation* 8, 175-181.

Wilmers, C.C., Sinha, S. & Brede, M. (2002). Examining the effects of species richness on community stability: an assembly model approach. *Oikos* 99, 363–367.

Wilson, W. G., Lundberg, P., Vazquez, D. P., Shurin, J. B., Smith, M. D., Langford, W., Gross, K. L. & Mittelbach, G. G. (2003). Biodiversity and species interactions: extending Lotka-Volterra theory to predict community properties. *Ecology Letters* 6, 944-952.

Winiwarter, P. & Cempel, C. *Evolutionary Hierarchies of Energy processing in Nature*, to be published in R. Trappl (ed.) Proceedings of EMCSR'96 conference, Vienna, April 1996.

Wood, C.L., Byers, J.E., Cottingham, K.L., Altman, I., Donahue, M.J. & Blakeslee, A.M.H. (2007). Parasites alter community structure. *Proceedings of the National Academy of Science USA* 104, 9335–9339.

Wootton, J. T., & Emmerson, M.C. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution and Systematics* 36, 419–444.

Verhoef, H. A. & Morin, P. J. (eds) (2010). *Community Ecology: Processes, Models and Applications*. Oxford University Press.

Yodzis, P. (1984). The structure of assembled communities II. *Journal of Theoretical Biology* 107, 115–126.

Chapter 2

Alizon, S., & Baalen, M.V. (2005). Emergence of a convex trade-off between transmission and virulence. *American Naturalist* 165, E155-167.

Bertness, M.D., & Grosholz, E. (1985). Population dynamics of the ribbed mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. *Oecologia* 67, 192–204.

- Bize, P., Jeanneret, C., Klopfenstein, A. & Roulin, R. (2008). What makes a host profitable? Parasites balance host nutritive resources against immunity. *American Naturalist* 171, 107–118.
- Blanar, C.A., Munkittrick, K.R., Houlahan, J., MacLatchy, D.L. & Marcogliese, D.J. (2009). Pollution and parasitism in aquatic animals: A meta-analysis of effect size. *Aquatic Toxicology* 93, 18–28.
- Brenchley, G.A. (1982). Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. *Marine Ecology Progress Series* 9, 255–262.
- Burke, J.S., Miller, J.S. & Hoss, D.E. (1991). Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Proceedings of the First International Symposium on Flatfish Ecology, Texel, 1990, Part 1. *Netherlands Journal of Sea Research* 27, 393–405.
- Bustnes, J., & Galaktionov, K. (1999). Anthropogenic influences on the infestation of intertidal gastropods by seabird trematode larvae on the southern Barents Sea coast. *Marine Biology* 133, 449–453.
- Byers, J.E., Blakeslee, A., Linder, E., Cooper, A. & Maguire, T. (2008). Controls of spatial variation in the prevalence of trematode parasites infecting a marine snail. *Ecology* 89, 439–451.
- Cattadori, I.M, Albert, R. & Boag, B. (2007). Variation in host susceptibility and infectiousness generated by co-infection: The *Myxoma-Trichostrongylus retortaeformis* case in wild rabbits. *Journal of the Royal Society Interface* 4, 831–840.
- Cheng, T.C., Shuster, C.N. & Anderson, A.H. (1966). A comparative study of the susceptibility and response of eight species of marine pelecypods to the trematode *Himasthla quissetensis*. *Transactions of the American Microscopical Society* 85, 284–295.
- Cranford, P.J. (1986). Behaviour and ecological importance of a mud snail (*Ilyanassa obsoleta*) population in a temperate macrotidal estuary. *Canadian Journal of Zoology* 66, 459–466.
- Crofton, H. D. (1971). A quantitative approach to parasitism. *Parasitology* 62, 179–193.

- Curtis, L.A. (1993). Parasite transmission in the intertidal zone: Vertical migrations, infective stages and snail trails. *Journal of Experimental Marine Biology and Ecology* 173, 197-209.
- Curtis, L.A. (1995). Growth, trematode parasitism, and longevity of a long-lived marine gastropod (*Ilyanassa obsoleta*). *Journal of the Marine Biological Association of the United Kingdom* 75, 913–925.
- Curtis, L.A. (2002). Ecology of larval trematodes in three marine gastropods. *Parasitology* 124, S43-56
- Curtis, L.A. (2005). Movements of *Ilyanassa obsoleta* (Gastropoda) on an intertidal sandflat. *Marine Biology* 148, 307–317.
- Curtis, L.A. (2007). Larval trematode infections and spatial distributions of snails. *Invertebrate Biology* 126, 235–246.
- Curtis, L.A. (2009). The gastropod *Ilyanassa obsoleta* as a resource: utilization by larval trematodes in a low-prevalence system. *Journal of Parasitology* 95, 799-807.
- Curtis, L.A., & Hurd, L.E. (1979). On the broad nutritional requirements of the mud snail, *Ilyanassa (Nassarius) obsoleta* (Say), and its polytrophic role in the food web. *Journal of Experimental Marine Biology and Ecology* 41, 289-297.
- Curtis, L.A., & Hurd, L.E. (1983). Age, sex, and parasites: Spatial heterogeneity in a sandflat population of *Ilyanassa obsoleta*. *Ecology* 64, 819–828.
- Curtis, L.A., Kinley, J.A. & Tanner, N.L. (2000). Longevity of oversized individuals: Growth, parasitism, and history in an estuarine snail population. *Journal of the Marine Biological Association of the United Kingdom* 80, 811–820.
- Day, T. (2002). On the evolution of virulence and the relationship between various measures of mortality. *Proceedings of the Royal Society of London Series B* 269, 1317–1323.
- Díaz-Ferguson, E., Robinson, J.D., Silliman, B. & Wares, J.P. (2010). Comparative phylogeography of North American Atlantic salt marsh communities. *Estuaries and Coasts* 33, 828-839.
- Dickens, T.D. (1998). Categorical data analysis. *Annual Review of Psychology* 48, 537–58.
- Durieux, E.D.H., Bégout, M., Pinet, P. & Sasal, P. (2010). Digenean metacercariae parasites as natural tags of habitat use by 0-group common sole *Solea solea* in nearshore

coastal areas: A case study in the embayed system of the Pertuis Charentais (Bay of Biscay, France). *Journal of Sea Research* 64, 107-117.

Erwin, R.M., Galli, J. & Burger, J. (1981). Colony site dynamics and habitat use in Atlantic coast seabirds. *The Auk* 98, 550-561.

Esch, G.W., & Fernandez, J.C. (1994). Snail-trematode interactions and parasite community dynamics in aquatic systems: A review. *American Midland Naturalist* 131, 209-237.

Fingerut, J.T., Zimmer, C.A. & Zimmer, R.K. (2003). Larval swimming overpowers turbulent mixing and facilitates transmission of a marine parasite. *Ecology* 84, 2502-2515.

Fredensborg, B.L., Mouritsen, K.N. & Poulin, R. (2006). Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail – from small to large scale. *Marine Biology* 149, 275-283.

Galli, P., Crosa, G., Mariniello, L., Ortis, M. & D'Amelio, S. (2001). Water quality as a determinant of the composition of fish parasite communities. *Hydrobiologia* 452, 173-179.

Galvani, A.P. (2003). Immunity, antigenic heterogeneity, and aggregation of helminth parasites. *Journal of Parasitology* 89, 232-241.

Gervasi, S.S. & Foufopoulos, J. (2008). Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. *Functional Ecology* 22, 100-108.

Giannotti, A.L., & McGlathery, K.L. (2001). Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta*. *Journal of Phycology* 37, 1-7.

Gooch, J.L., Smith, B.S. & Knupp, D. (1972). Regional survey of gene frequencies in the mud snail *Nassarius obsoletus*. *Biological Bulletin* 142, 36-48.

Gower, C. M., & Webster, J.P. (2004). Fitness of indirectly transmitted pathogens: Restraint and constraint. *Evolution* 58, 1178-1184.

Guegan, J.G., Morand, S. & Poulin, R. (2005). Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. *In Parasitism and ecosystems*, F. Thomas, F. Renaud, and J.F. Guégan (eds.). Oxford University Press, Oxford, U.K., p 22-42.

Holt, R.D., Jones, C.G., Randolph, S.E. & Rohani, P. (2008). Is infectious disease just another type of predator-prey interaction? *In Infectious disease ecology: The effects of*

ecosystems on disease and of disease on ecosystems, R.S. Ostfeld, F. Kessing, and V.T. Eviner (eds.). Princeton University Press, Princeton, New Jersey, p. 223–241.

Hall, S. R., Becker, C.R., Simonis, J.L., Duffy, M.A., Tessier, A.J. & Cáceres, C.E. (2009). Friendly competition: Evidence for a dilution effect among competitors in a planktonic host parasite system. *Ecology* 90, 791–801.

Hall, S.R., Knight, C.M., Becker, C.R., Duffy, M.A., Tessier, A.J. & Cáceres, C.E. (2009). Quality matters: food quality and the course of epidemics in a planktonic host-parasite system. *Ecology Letters* 12, 118–128.

Harvey J.A. & Gols, G.J.Z. (1998). The effect of host quality on progeny and sex allocation in the pupal ectoparasitoid, *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae). *Bulletin of Entomological Research* 88, 299-304.

Hechinger, R.F., & Lafferty, K.D. (2005). Host diversity begets parasite diversity: Bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London, Series B* 272, 1059–1066.

Hurd, L.E. (1985). On the importance of carrion to reproduction in an omnivorous estuarine neogastropod, *Ilyanassa obsoleta* (Say). *Oecologia* 65, 513-515.

Johnson, P.T., & Thielges, D.W. (2010). Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *The Journal of Experimental Biology* 213, 961-70.

Karvonen, A., Hudson, P.J., Seppälä, O. & Valtonen, E.T. (2004). Transmission dynamics of a trematode parasite: Exposure, acquired resistance and parasite aggregation. *Parasitology Research* 92, 183–188.

Kelaher, B.P., Levinton, J.S. & Hoch, J.M. (2003). Foraging by the mud snail, *Ilyanassa obsoleta* (Say), modulates spatial variation in benthic community structure. *Journal of Experimental Marine Biology and Ecology* 292, 139– 157.

Knudsen, R., Curtis, M.A. & Kristoffersen, R. (2004). Aggregation of helminthes: The role of feeding behavior of fish hosts. *Journal of Parasitology* 90, 1-7.

Koprivnikar J., Forbes, M.R. & Baker, R.L. (2007). Contaminant effects on host parasite interactions: Atrazine, frogs, and trematodes. *Environmental and Toxicological Chemistry* 26, 2166–2170.

Krause, R.J., Grant, J.W.A., McLaughlin, J.D. & Marcogliese, D.J. (2010). Do infections with parasites and exposure to pollution affect susceptibility to predation in Johnny Darters (*Etheostoma nigrum*)? *Canadian Journal of Zoology* 88, 1218-1225.

- Krist, A.C., Lively, C.M., Levri, E.P. & Jokela, J. (2000). Spatial variation in susceptibility to infection in a snail-trematode interaction. *Parasitology* 121, 395–401.
- Lathrop, R.G., Cole, M. B. & Showalter, R.D. (2000). Quantifying the habitat structure and spatial pattern of New Jersey (USA) salt marshes under different management regimes. *Wetlands Ecology and Management* 8, 163-172.
- Lafferty, K.D., Sammond, D.T. & Kuris, A.M. (1994). Analysis of larval trematode communities. *Ecology* 75(8), 2275-2285.
- Lefèvre T., & Thomas, F. (2008). Behind the scene, something else is pulling the strings: Emphasizing parasitic manipulation in vector-borne diseases. *Infection, Genetics and Evolution* 8, 504–519.
- Levinton, J.S., Martinez, D.R., McCartney, M.M. & Judge, M.L. (1995). The effect of water flow on movement, burrowing, and distributions of the gastropod *Ilyanassa obsoleta* in a tidal creek. *Marine Biology* 122, 417–424.
- Levri, E. P. & Fisher, L.M. (2000). The effect of a trematode parasite (*Microphallus* sp.) on the response of the freshwater snail *Potamopyrgus antipodarum* to light and gravity. *Behaviour* 137, 1141-1151.
- Lion, S., Baalen, M.V. & Wilson, W.G. (2006). The evolution of parasite manipulation of host dispersal. *Proceedings of the Royal Society of London Series B* 273, 1063–1071.
- Marcogliese, D.J., & Pietroock, M. (2011). Combined effects of parasites and contaminants on animal health: Parasites do matter. *Trends in Parasitology* 27, 123-130.
- Massad, E. (1987). Transmission rates and the evolution of pathogenicity. *Evolution* 41, 1127-1130.
- Matthee, S., & Krasnov, B.R. (2009). Searching for mechanisms of generality in the patterns of parasite abundance and distribution: Ectoparasites of a South African rodent, *Rhabdomys pumilio*. *International Journal for Parasitology* 39, 781–788.
- McDermid, G., Franklin, S.E. & LeDrew, E.F. (2005). Remote sensing for large-area habitat mapping. *Progress in Physical Geography* 29, 449-474.
- McDermott, J. J. (1951). Larval trematode infection in *Nassa obsoleta* from New Jersey waters. Master's Thesis. Rutgers University, New Brunswick, New Jersey, 72 p.
- Ostfeld, R.S., & Keesing, F. (2000). The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Canadian Journal of Zoology* 78, 2061-2078.

- Paramor, O.A.L. & Hughes, R.G. (2007). Restriction of lateral development of *Spartina anglica* marsh by the infaunal polychaete *Nereis diversicolor*. *Estuarine and Coastal Shelf Science* 71, 202-209.
- Poulin, R. (2006). Variation in infection parameters among populations within parasite species: intrinsic properties versus local factors. *International Journal for Parasitology* 36, 877-885.
- Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology* 134, 763-776.
- Rigaud, T., Perrot-Minnot, M.J. & Brown, M.J.F. (2010). Parasite and host assemblages: Embracing the reality will improve our knowledge of parasite transmission and virulence. *Proceedings of the Royal Society of London Series B* 277, 3693–3702.
- Schell, S.C. (1970). *How to know the trematodes*. W. C. Brown Co., Dubuque, Iowa, 355 p.
- Scheltema, R.S. (1964). Feeding habits and growth in the mud snail, *Nassarius obsoletus*. *Chesapeake Science* 5, 161-166.
- Schoebel, C.N., Wolinska, J. & Spaak, P. (2010). Higher parasite resistance in *Daphnia* populations with recent epidemics. *Journal of Evolutionary Biology* 23, 2370-2376.
- Seppälä, O., Liljeroos, K., Karvonen, A. & Jokela, J. (2008). Host condition as a constraint for parasite reproduction. *Oikos* 117, 749-753.
- Shenker, J.M. & Dean, J.M. (1979). The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. *Estuaries* 2, 154-163.
- Sheridan, L. A., Poulin, R., Ward, D.F. & Zuk, M. (2000). Sex differences in parasitic infections among arthropod hosts: Is there a male bias? *Oikos* 88, 327-334.
- Sherwood, R.M., & Petraitis, P.S. (1998). Mortality differences of two intertidal mussels, *Mytilus edulis* L. and *Geukensia demissa* (Dillwyn), in a New Jersey salt marsh. *Journal of Experimental Marine Biology and Ecology* 231, 255-265.
- Skirnisson K., Galaktionov, K.V. & Kozminsky, E.V. (2004). Factors influencing the distribution of digenean (Trematoda, Digenea) infections in a mudsnail (*Hydrobia ventrosa*) population inhabiting saltmarsh ponds in Iceland. *Journal of Parasitology* 90, 50-59.
- Smith, N.F. (2001). Spatial heterogeneity in recruitment of larval trematodes to snail intermediate hosts. *Oecologia* 127, 115-122.

Stone, L., & Roberts, A. (1990). The checkerboard score and species distributions. *Oecologia* 85, 74-79.

Stunkard, H. W. (1938a). The morphology and life cycle of the trematode *Himasthla quissetensis* (Miller and Northup, 1926). *Biological Bulletin* 75, 146–164.

Stunkard, H. W. (1938b). *Distomium lasium* Leidy, 1891 (Syn. *Cercariaeum lintoni* Miller and Northup, 1926), the larval stage of *Zoogonus rubellus* (Olson, 1898) (Syn. *Z. mirus* Looss, 1901). *Biological Bulletin* 75, 308–334.

Thieltges, D.W., Jensen, K.T. & Poulin, R. (2008). The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology* 135, 407–426.

Tschirren, B., Bischoff, L., Saladin, V. & Richner, H. (2007). Host condition and host immunity affect parasite fitness in a bird–ectoparasite system. *Functional Ecology* 21, 372–378.

Vinson, S.B. (1976). Host selection by insect parasitoids. *Annual Review of Entomology* 21, 109-133.

Ward, H. (2007). Prevention strategies for sexually transmitted infections: importance of sexual network structure and epidemic phase. *Sexually Transmitted Infections* 83 (Suppl. 1), i43-49.

Wilson, K., Bjornstad, O.N., Dobson, A.P., Merler, S., Pogladyen, G, Randolph, S.E., Read, A.F. & Skorping, A. (2002). Heterogeneities in macroparasite infections: patterns and processes. In *The ecology of wildlife diseases*, P.J. Hudson, A. Rizzoli, B.T. Grenfell, H. Heesterbeek, and A.P. Dobson (eds.). Oxford University Press, Oxford, U.K., p. 6-44.

Wullschleger, E., & Jokela, J. (1999). Does habitat-specific variation in trematode infection risks influence distributions of two closely related freshwater snails? *Oecologia* 121, 32–38.

Yan, G., & Norman, S. (1995). Infection of *Tribolium* beetles with a tapeworm: variation in susceptibility within and between beetle species and among genetic strains. *Journal of Parasitology* 81, 37–42.

Zimmermann, M.R., Luth, K.E. & Esch, G.W. (2011). The unusual life cycle of *Daubaylia potomaca*, a nematode parasite of *Helisoma anceps*. *Journal of Parasitology* 97, 430-434.

Chapter 3

- Allesina, S. & Pascual, M. (2008). Network structure, predator-prey motifs, and stability in large food webs. *Theoretical Ecology* 1(1), 55-64.
- Barber, I., Hoare, D. & Krause, J. (2000). Effects of parasites on fish behaviour: a review and evolutionary perspective. *Reviews in Fish Biology and Fisheries* 10, 131-165.
- Brown, J.H. & Gillooly, J.F. (2003). Ecological food webs: High-quality data facilitate theoretical unification. *Proceedings of the National Academy of Science U. S. A.* 100(4), 1467-1468.
- Byers, J. E. (2008). Including parasites in food webs. *Trends in Parasitology* 25(2), 55-57.
- Chen, H., Liu, W.C., Davis, A.J., Jordán, F., Hwang, M.J. & Shao, K.T. (2008). Network position of hosts in food webs and their parasite diversity. *Oikos* 117, 1847-1855.
- Choisy, M., Brown, S.P., Lafferty, K.D. & Thomas, F. (2003). Evolution of trophic transmission in parasites: Why add intermediate hosts? *American Naturalist* 162, 172-181.
- Combes, C. (2001). *Parasitism: The Ecology and Evolution of Intimate Interactions*. University of Chicago Press, Chicago, IL.
- Dambacher, J.M. Li, H.W. & Rossigno, P.A. (2002). Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology* 83(5), 1372-1385.
- De'Ath, G. & Fabricius, K.E. (2000). Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178-3192.
- Dobson, A., Lafferty, K.D. & Kuris, A.M. (2006). Parasites and Food Webs. In: *Ecological Networks: Linking Structure to Dynamics in Food Webs*. eds. Pascual, M. & Dunne, J.A. New York: Oxford University Press. pp. 119-137.
- Fell, P.E. (1982). Distribution and abundance of macroinvertebrates on certain Connecticut tidal marshes, with emphasis on dominant molluscs. *Estuaries* 5, 234-239.
- Gandon, S. (2004). Evolution of multihost parasites. *Evolution* 58(3), 455-469.
- Gregory, R.D., Keymer, A.E. & Harvey, P.H. (1991). Life history, ecology and parasite community structure in Soviet birds. *Biological Journal of the Linnean Society* 43(4), 249 - 262.
- Hairston, N.G., Jr. & Hairston, N.G. (1993). Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* 142, 379-411.

- Hernandez, A.D. & Sukhdeo, M.V. K. (2008). Parasites alter the topology of a stream food web across seasons. *Oecologia* 156, 613–624.
- Huxham, M., Raffaelli, D. & Pike, A. (1995). Parasites and food web patterns. *Journal of Animal Ecology* 64, 168-176.
- Inouye, R. S. (1980). Stabilization of a predator-prey equilibrium by the addition of a second "Keystone" victim. *American Naturalist* 115(2), 300-305.
- James-Pirri, M.J., Raposa, K.B. & Katena, J.G. (2001). Diet composition of Mummichogs, *Fundulus heteroclitus*, from restoring and unrestricted regions of a New England (U.S.A.) salt marsh. *Estuarine, Coastal and Shelf Science* 53, 205-213.
- Keesing, F., Holt, R.D. & Ostfeld, R.S. (2006). Effects of species diversity on disease risk. *Ecology Letters* 9, 485–498.
- Kneib, R.T. (1986). The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *Integrative and Comparative Biology* 26, 259–269.
- Kreeger, D.A., Langdon, C.J. & Newell, R.I.E. (1988). Utilization of refractory cellulosic carbon derived from *Spartina alterniflora* by the ribbed mussel *Geukensia demissa*. *Marine Ecology Progress Series* 42, 171-179.
- Kuris, A. M. (2003). Evolutionary ecology of trophically transmitted parasites. *Journal of Parasitology* 89(S), S96-S100.
- Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F., Mora, A., Pickering, M., Talhouk, N., Torchin, M.E., & Lafferty, K.D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515-518.
- Lafferty, K.D. (1999). The evolution of trophic transmission. *Parasitology Today* 15(3), 111-115.
- Lafferty, K.D., Hechinger, R.F., Shaw, J.C., Whitney, K.L. & Kuris, A.M. (2006). Food webs and parasites in a salt marsh ecosystem. In: *Disease ecology: community structure and pathogen dynamics* (eds. Collinge S & Ray C). Oxford University Press Oxford, pp. 119-134.
- Lafferty, K.D., Dobson, A.P. & Kuris, A.M. (2006). Parasites dominate food web links. *Proceedings of the National Academy of Sciences, USA* 103, 11211-11216.
- Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., DeLeo, G., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.J., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R., Thieltges,

- D.W. (2008). Parasites in food webs: the ultimate missing links. *Ecology Letters* 11, 533-546.
- Lafferty, K.D. & Kuris, A. M. (2009). Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philosophical Transactions of the Royal Society of London B* 364(1524), 1659–1663.
- Lapchin, L. & Guillemaud, T. (2005). Asymmetry in host and parasitoid diffuse coevolution: when the red queen has to keep a finger in more than one pie. *Frontiers in Zoology* 2(1), 4.
- Layman, C.A., Quattrochi, J.P., Peyer, C.M., Allgeier, J.E. & Suding, K. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* 10, 937-944.
- Lettni, S. & Sukhdeo, M.V.K. (2010). The energetic cost of parasitism in isopods. *Ecoscience* 17(1), 1-8.
- Marcogliese, D. J. (2002). Food webs and the transmission of parasites to marine fish. - *Parasitology* 124, S83–S99.
- Marcogliese, D.J. (2007). Evolution of parasitic life in the ocean: paratenic hosts enhance lateral incorporation. *Trends in Parasitology* 23(11), 519-521.
- Martinez, N.D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61, 367-392.
- Montoya, J.M., Woodward, G., Emmerson, M.C. & Sole, R.V. (2009). Press perturbations and indirect effects in real food webs. *Ecology* 90(9), 2426-2433.
- Nachman G. (1988). Regional persistence of locally unstable predator/prey populations. *Experimental and Applied Acarology* 5, 293–318.
- O’Gorman, E.J. & Emmerson, M.C. (2009). Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Science U.S.A.* 106(32), 13393–13398.
- Paine, R.T. (1988). Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69, 1648-1654.
- Parker, G. A., Chubb, J.C., Ball, M.A. & Roberts, G.N. (2003). Evolution of complex life cycles in helminth parasites. *Nature* 425, 480–484.
- Post, D.M., Connors, M.E. & Goldberg, D.S. (2000). Prey preferences by a top predator and the stability of linked food chains. *Ecology* 81(1), 8–14.

- Poulin, R. (1992). Determinants of host-specificity in parasites of freshwater fishes. *International Journal of Parasitology* 22, 753–758.
- Price, P. W. (1980). *Evolutionary Biology of Parasites*. Princeton University Press, Princeton, NJ.
- Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London Series B* 267, 1947-1962.
- Raffaelli, D. (2007). Food webs, body size and the curse of the Latin binomial. In: Rooney, N., McCann, K.S., Noakes, D.L.G. (eds), *From energetic to ecosystems: The dynamics and structure of ecological systems*. Springer, The Netherlands, pp. 53-64.
- Ronn, C., Bonsdorff, E. & Nelson, W.G. (1988). Predation as a mechanism of interference within infauna in shallow brackish water soft bottom; experiments with an infaunal predator, *Nereis diversicolor* O.F. Muller. *Journal of Experimental Marine Biology and Ecology* 116, 143-15.
- Sukhdeo, M.V.K. and Hernandez, A.D. (2005). Food web patterns and the parasite's perspective. In: F. Thomas, J.F. Guegan, and F. Renaud (eds), *Parasitism and Ecosystems*. Oxford University Press. pp. 54-67.
- Sukhdeo, M.V.K. (2010). Foodwebs for parasitologists: A Review. *Journal of Parasitology* 96(2), 273-284.
- Thompson, J.N. (1982). *Interaction and Coevolution*. John Wiley & Sons Inc., New York, NY.
- Thompson R.M, Mouritsen, K.N. and Poulin, R. (2005). Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *Journal of Animal Ecology* 74, 77–85.
- Vázquez, D.P. & Aizen, M.A. (2004). Asymmetric specialization: a pervasive feature of plant–pollinator interactions. *Ecology* 85(5), 1251-1257.
- Vázquez, D.P. Poulin, R., Krasnov, B.R. & Shenbrot, G.I. (2005). Species abundance patterns and the distribution of specialization in host–parasite interaction networks. *Journal of Animal Ecology* 74, 946-955.
- Vázquez, D.P., Melián, C.J., Willams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116, 1120-1127.

Waters, T.F. & Hokenstrom, J.C. (1980). Annual production and drift of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota. *Limnology and Oceanography* 25, 700-710.

Chapter 4

Amarasekare, P. (2008). Spatial dynamics of food webs. *Annual Review of Ecology, Evolution, and Systematics* 39, 479 – 500.

Anderson, R.C., Chaubaud, A.G. & Willmott, S., eds. 1974. *CIH Keys to the Nematode Parasites of Vertebrates*. Slough, UK: Commonw. Agric. Bur.

Blanar, C.A., Marcogliese, D.J. & Couillard, C.M. (2011). Natural and anthropogenic factors shape metazoan parasite community structure in mummichog (*Fundulus heteroclitus*) from two estuaries in New Brunswick, Canada. *Folia Parasitologica* 58, 240-248.

Balcer, M. D., Korda, N.L. & Dodson, S.I. (1984). *Zooplankton of the Great Lakes: A Guide to the Identification and Ecology of the Common Crustacean Species*. University of Wisconsin Press. Madison, Wisconsin.

Benke, A. C. & Huryn, A. D. (2010). Benthic invertebrate production: facilitating answers to ecological riddles in freshwater ecosystems. *Journal of the North American Benthological Society* 29, 264-285.

Borgatti, S.P., (2002). *NetDraw Software for Network Visualization*. Analytic Technologies: Lexington, KY.

Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002). *Ucinet for Windows: Software for Social Network Analysis*. Analytic Technologies:Harvard, MA

Byers, J. E. (2009). Including parasites in food webs. *Trends in Parasitology* 25(2), 55-57.

Critchlow, R. E. & Stearns, S.C. (1982). The structure of food webs. *American Naturalist* 120, 478-499.

Costa, G.C. (2009). Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* 90(7), 2014–2019.

Deegan, L.A. & Gerritt, R.H. (1997). Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series* 147, 31-47.

- Fichet, B.; Piccolo, D.; Verde, R.; Vichi, M. (Eds.) 2011. *Classification and Multivariate Analysis for Complex Data Structures (Studies in Classification, Data Analysis, and Knowledge Organization)*. Springer publ. NY, NY (USA). 492 p.
- Finlay, J.C., Khandwala, S. & Power, M.E. (2002). Spatial scales of carbon flow in a river food web. *Ecology* 83(7), 1845–1859.
- Flemer, D. (1970). Primary production in Chesapeake Bay. *Chesapeake Science* 11, 117-129.
- Fredensborg, B.L., Mouritsen, K.N. & Poulin, R. (2006). Relating bird host distribution and spatial heterogeneity in trematode. *Marine Biology* 149, 275–283.
- Hechinger, R.F. & Lafferty, K.D. (2005). Host diversity begets parasite diversity: Bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London, Series B* 272, 1059–1066.
- Hoffman, G. L. (1999). *Parasites of North American freshwater fishes (2nd edition)*. Comstock Publishing Associates, Ithaca and London.
- Holt, R.D. & Boulinier, T. (2005). Ecosystems and parasitism: the spatial dimension. In F. Thomas, F. Renaud and I.F. Guegan, eds. *Parasitism and Ecosystems*. Oxford University Press. Pages 68-84.
- Ings, T.C., Montoya, J.M., Bascompte, J., Bluthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., et al. (2009). *Ecological networks—Beyond food webs*. *Journal of Animal Ecology* 78, 253–269.
- Kitching, R. L. (1987). Spatial and temporal variation in food webs in water-filled tree-holes. *Oikos* 48, 280-288.
- Knudsen, R., Curtis, M.A. & Kristoffersen, R. (2004). Aggregation of helminthes: The role of feeding behavior of fish hosts. *Journal of Parasitology* 90, 1-7.
- Levesque, C., Juniper, S.K. & Lime' n, H. (2006) Spatial organization of food webs along habitat gradients at deep-sea hydrothermal vents on Axial Volcano, Northeast Pacific. *Deep Sea Research I* 53, 726–739.
- Marcarelli, A.M., Colden, V. B., Mineau, M.M. & Hall, R.O. (2011). Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92,1215–1225.

- Marcogliese, D.J. (2002). Food webs and the transmission of parasites to marine fish. *Parasitology* 124, 83-99.
- Médoc, V. & Beisel, J.N. (2011). When trophically-transmitted parasites combine predation enhancement with predation suppression to optimize their transmission. *Oikos* 120, 1452-1458.
- Merritt, R. W. & Cummins, K.W. (1996). *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Co., Dubuque, Iowa.
- Mollison, D. & Levin, S. A. (1995). Spatial dynamics of parasitism. In Ecology of infectious diseases in natural populations. In (ed. B. T. Grenfell & A. P. Dobson), *Ecology of Infectious Diseases in Natural Populations*. Cambridge University Press. pp. 394-398.
- Miller, T., Sell, J., Korndoerfer, A., McGeorge, L. & Baldwin-Brown, A. (2004). *Ambient biomonitoring network: Raritan water region*. <http://www.state.nj.us/dep/wms/bfbm/download/rarRnd3.pdf>
- de Nooy W., Mrvar A., Batagelj V. (2002) *Exploratory Social Network Analysis With Pajek. Structural Analysis in the Social Sciences (27)*. Cambridge University Press, UK.
- Odum, E. P. (1959). *Fundamentals of Ecology (Second ed.)*. Philadelphia and London: W. B. Saunders Co. p. 546.
- Paine, R.T. (1988). Food webs: road maps of interactions or grist for theoretical development? *Ecology* 69, 1648-1654.
- Parker, G. A., Chubb, J. C., Ball, M.A. & Roberts, G.N. (2003). Evolution of complex life cycles in helminth parasites. *Nature* 425, 480–484.
- Patrick, R.(1994). *Rivers of the United States: volume I estuaries*. John Wiley, New York, N.Y.
- Pimm, S.L. & Kitching, R.L. (1988). Food Web Patterns: Trivial Flaws or the Basis of an Active Research Program? *Ecology* 69(6), 1669-1672.
- Polis, G.A. (1991). Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138, 123- 155,
- Polis, G. A., Anderson, W.B. & Holt, R.D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28, 289–316.

- Porter, K.G., & Feig, Y.S. (1980). The Use of DAPI for Identifying and Counting Aquatic Microflora. *Limnology and Oceanography* 25(5), 943-948
- Power, M.E. & Rainey, W.E. (2000). Food webs and resource sheds: Towards spatially delimiting trophic interactions. pp. 291-314 In M.J. Hutchings, E.A. John and A.J.A. Stewart (eds.) *Ecological Consequences of Habitat Heterogeneity*. Blackwell Scientific, Oxford, UK.
- Rossiter, W. & Sukhdeo, M.V.K. (2011). Exploitation of asymmetric predator-prey interactions by trophically transmitted parasites. *Oikos* 120(4), 607–614.
- Rossiter, W. & Sukhdeo, M.V.K. (2012). Host quality and spatial patterning in infections of the Eastern mudsnail (*Ilyanassa obsolete*) by two trematodes (*Himasthla quissetensis* and *Zoogonus rubellus*). *Journal of Parasitology* (in press).
- Schell, S. C. (1970). *How to Know the Trematodes*. William C. Brown. Company Publishers, Dubuque, Iowa, 355 p.
- Skirnisson K., Galaktionov, K.V. & Kozminsky, E.V. (2004). Factors influencing the distribution of digenean (Trematoda, Digenea) infections in a mudsnail (*Hydrobia ventrosa*) population inhabiting saltmarsh ponds in Iceland. *Journal of Parasitology* 90, 50-59.
- Soykan, C.U. & Sabo, J.L. (2009). Spatio-temporal food-web dynamics along a desert riparian-upland transition. *Ecography* 32(2), 354-368.
- Sukhdeo, M.V.K. (2010). Foodwebs for Parasitologists. A Review. *Journal of Parasitology* 96, 273-284.
- Thieltges, D.W., Jensen, K.T. & Poulin, R. (2008). The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology* 135, 407–426.
- Thompson, R.M. & Townsend, C.R. (2005). Food-web topology varies with spatial scale in a patchy environment. *Ecology* 86, 1916–1925.
- Whiteman, N.K. & Parker, P.G. (2005). Using parasites to infer host population history: a new rationale for parasite conservation. *Animal Conservation* 8(2), 175–181.
- Yodzis, P. & Innes, S. (1992). Body size and consumer resource dynamics. *American Naturalist* 139, 1151-1175.

Chapter 5

- Anderson, T.K. & Sukhdeo, M.V.K. (2011). Host centrality in food web networks determines parasite diversity. *PLoS ONE* 6(10): e26798.

- Barbehenn, K.R. (1969). Host-parasite relationships and species diversity in mammals: a hypothesis. *Biotropica* 1, 9-25.
- Bascompte, J. & Stouffer, D.B. (2008). The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society of London, Series B* 364, 1781-1787
- Benesh, D. P., Chubb, J. C. & Parker, G.A. (2011). Exploitation of the same trophic link favors convergence of larval life-history strategies in complex life cycle helminthes. *Evolution* 65, 2286–2299.
- Blanar, C.A., Marcogliese, D.J. & Couillard, C.M. (2011). Natural and anthropogenic factors shape metazoan parasite community structure in mummichog (*Fundulus heteroclitus*) from two estuaries in New Brunswick, Canada. *Folia Parasitol (Praha)* 58(3), 240-248.
- Borgatti, S.P., (2002). *NetDraw Software for Network Visualization*. Analytic Technologies: Lexington, KY.
- Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002). *Ucinet for Windows: Software for Social Network Analysis*. Analytic Technologies:Harvard, MA
- Chapin, F.S., Robards, M.D., Henrey, P.H., Johnstone, J.F., Trainor, S.F., Kofinas, G.P., Ruess, R.W., Fresco, N., Natcher, D.C. & Naylor, R.L. (2006). Directional Changes in Ecological Communities and Social-Ecological Systems: A Framework for Prediction Based on Alaskan Examples. *American Naturalist* 168, S36-S49.
- Chen, H., Liu, W.C., Davis, A.J., Jordán, F., Hwang, M.J. & Shao, K.T. (2008). Network position of hosts in food webs and their parasite diversity. *Oikos* 117, 1847–1855.
- Chen, H.W., Shao, K.T., Liu, C.W., Lin, W.H. & Liu, W.C. (2011). The reduction of food web robustness by parasitism: fact and artefact. *International Journal of Parasitology* 41(6), 627-34.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5, 558–567.
- Gerritsen, J. & Leppo, E.W. (2005). *Biological condition gradient for tiered aquatic life use in New Jersey*. Tetra Tech, Inc. Owings Mills, MD.
- Guégan, J.F., Morand, S. & Poulin, R. (2005). Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. In: *Parasitism and ecosystems* (ed. by F. Thomas, F. Renaud and J.-F. Guégan), pp. 22–42. Oxford University Press, Oxford.
- Hechinger R.F. & Lafferty, K.D. (2005). Host diversity begets parasite diversity: bird final

hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London, Series B* 272, 1059-1066.

Hechinger, R.F., Lafferty, K.D., McLaughlin, J.P., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Sandhu, P.K., Shaw, J.C., Torchin, M.E., Whitney, K.L. & Kuris, A.M. (2011). Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. *Ecology* 92, 791.

Hernandez, A.D., Bunnell, J.F. & Sukhdeo, M.V.K. (2007). Composition and diversity patterns in metazoan parasite communities and anthropogenic disturbance in stream ecosystems. *Parasitology* 134, 91-102.

Holland, S.M. (2008). Non-metric multidimensional scaling (MDS). R user manual.

Karr, J.R. & Dudley, D.R. (1981). Ecological perspective on water quality goals. *Environmental Management* 5, 55–68.

King, K.C., McLaughlin, Daniel, J., Gendron, A.D., Pauli, B.D., Giroux, I., Rondeau, B., Boily, M., Juneau, P. & Marcogliese, D.J. (2007). Impacts of agriculture on the parasite communities of northern leopard frogs (*Rana pipiens*) in southern Quebec, Canada. *Parasitology* 134(14), 2063-2080.

Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K., Aguirre-Macedo, L., Boch, C., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F., Mora, A., Pickering, M., Talhouk, N., Torchin, M.E., & Lafferty, K.D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515-518.

Lafferty, K.D. & Kuris, A.M. (2009). Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. *Philosophical Transactions of the Royal Society of London, Series B* 364(1524), 1659–1663.

Marcogliese, D.J. (2005). Parasites of the superorganism: are they indicators of ecosystem health? *International Journal of Parasitology* 35, 705–716.

Merritt, R. W. & Cummins, K.W. (1996). *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt Co., Dubuque, Iowa.

Miller, T., Sell, J., Korndoerfer, A., McGeorge, L. & Baldwin-Brown, A. (2004). *Ambient biomonitoring network: Raritan water region*.
<http://www.state.nj.us/dep/wms/bfbm/download/rarRnd3.pdf>

Morris, R.J. (2010). Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society of London, Series B* 365(1558), 3709-3718.

- Mouritsen, K.N., Poulin, R., McLaughlin, J.P. & Thieltges, D.W. (2011). Food web including metazoan parasites for an intertidal ecosystem in New Zealand. *Ecology* 92, 2006.
- Paine, R.T., Tegner, M.J. and Johnson, E.A. (1998). Compounded Perturbations Yield Ecological Surprises. *Ecosystems* 1, 535–545.
- Palm, H.W. & Rückert, S. (2009). A new approach to visualize ecosystem health by using parasites. *Parasitology Research* 105(2), 539-553.
- Patrick, R. (1994). *Rivers of the United States: volume I estuaries*. John Wiley, New York, N.Y.
- Pedersen, A.B. & Fenton, A. (2007). Emphasizing the ecology in parasite community ecology. *Trends in Ecology and Evolution* 22, 133-139.
- Porter, K.G., & Feig, Y.S. (1980). The Use of DAPI for Identifying and Counting Aquatic Microflora. *Limnology and Oceanography* 25(5), 943-948.
- Poulin R. (2007). Are there general laws in parasite ecology? *Parasitology* 134, 763-776.
- Poulin, R. & Morand, S. (2000). The diversity of parasites. *Quarterly Review of Biology* 75(3), 277-93.
- Price, P.W. (1980). *Evolutionary Biology of Parasites*. Princeton University Press: Princeton, NJ.
- Rossiter, W. & Sukhdeo, M.V.K. (2011). Exploitation of asymmetric predator-prey interactions by trophically transmitted parasites. *Oikos* 120(4), 607–614.
- Rudolf, H.W. & Lafferty, K.D. (2011). Stage structure alters how complexity affects stability of ecological networks. *Ecology Letters* 14, 75–79.
- Sasal, P., Mouillot, D., Fichez, R., Chifflet, S. & Kulbicki, M. (2007). The use of fish parasites as biological indicators of anthropogenic influences in coral-reef lagoons: a case study of Apogonidae parasites in New-Caledonia. *Marine Pollution Bulletin* 54(11), 1697-706.
- Schotthoefer, A.M., Rohr, J.R., Cole, R.A., Koehler, A.V., Johnson, C.M., Johnson, L.B. & Beasley, V.R. (2011). Effects of wetland vs. landscape variables on parasite communities of *Rana pipiens*: links to anthropogenic factors. *Ecological Applications* 21(4), 1257-1271.
- Slobodkin, L.B. (1962). Energy in animal ecology. *Advances in Ecology* 4, 69-101.
- Thieltges, D.W., Reise, K., Mouritsen, K.N., McLaughlin, J.P., & Poulin, R. (2011). Food web including metazoan parasites for a tidal basin in Germany and Denmark. *Ecology* 92, 2005

Valladares, G., Cagnolo, L. & Salvo, A. (2012). Forest fragmentation leads to food web contraction. *Oikos* 121, 299–305.

Whiteman, N.K. & Parker, P.G. (2005). Using parasites to infer host population history: A new rationale for parasite conservation. *Animal Conservation* 8, 175–181.

Zander, C.D., Josten, N., Detloff, K.C., Poulin, R., McLaughlin, J.P., & Thieltges, D.W. (2011). Food web including metazoan parasites for a brackish shallow water ecosystem in Germany and Denmark. *Ecology* 92, 2007.

Chapter 6

Andersen, D.C., MacMahon, J.A., & Wolfe, M.L. (1980). Herbivorous Mammals along a Montane Sere: Community Structure and Energetics. *Journal of Mammalogy* 61(3):, 500–519.

Anderson, T.K. & Sukhdeo, M.V.K. (2011). Host centrality in food web networks determines parasite diversity. *PLoS ONE* 6(10): e26798.

Arneberg, P., Skorping, A., Grenfell, B. & Read, A. F. (1998). Hosts densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London, Series B* 266, 1283–1289.

Benesh, D. P., Chubb, J.C. & Parker, G.A. (2011). Exploitation of the same trophic link favors convergence of larval life-history strategies in complex life cycle helminths. *Evolution* 65(8), 2286–2299.

Bustnes, J., & Galaktionov, K. (1999). Anthropogenic influences on the infestation of intertidal gastropods by seabird trematode larvae on the southern Barents Sea coast. *Marine Biology* 133, 449–453.

Chen, H., Liu, W.C., Davis, A.J., Jordán, F., Hwang, M.J. & Shao, K.T. (2008). Network position of hosts in food webs and their parasite diversity. *Oikos* 117, 1847–1855.

Choisy, M., Brown, S.P., Lafferty, K.D. & Thomas, F. (2003). Evolution of trophic transmission in parasites: Why add intermediate hosts? *American Naturalist* 162, 172–181.

Combes, C. & Simberloff, D. (2005). *The Art of Being a Parasite*. University Of Chicago Press. 280 pgs.

Crofton, H.D. (1971). A quantitative approach to parasitism. *Parasitology* 62, 179–193.

- Dobson, A.P. & Hudson, P.J. (1986). Parasites, disease and the structure of ecological communities. *Trends in Ecology and Evolution* 1, 11-15.
- Dobson, A.P. & Hudson, P.J. (1992). The population dynamics and control of the parasitic nematode *Trichostrongylus tenax* in red grouse in the North of England. *Applied Population Biology* 67, 149-171.
- Esch, G.W. & Fernandez, J.C. (1994). Snail-trematode interactions and parasite community dynamics in aquatic systems: A review. *American Midland Naturalist* 131, 209–237.
- Francisco, D.C. & Benjamin, B. (2005). Mechanisms of disease-induced extinction. *Ecology Letters* 8, 117–126.
- Grami, B., Rasconi, S., Niquil, N., Jobard, M., Saint-Béat, B., et al. (2011). Functional Effects of Parasites on Food Web Properties during the Spring Diatom Bloom in Lake Pavin: A Linear Inverse Modeling Analysis. *PLoS ONE* 6(8), e23273. doi:10.1371/journal.pone.0023273.
- Grenfell, B.T., Amos, W., Arneberg, P., Bjørnstad, O.N., Greenman, J.V., Harwood, J., Lanfranchi, P., McLean, A., Norman, R.A., Read, A.F. & Skorpung, A. (2002). Visions for future research in wildlife epidemiology. In: *The Ecology of Wildlife Diseases*. (ed. by P. J. Hudson, A. Rizzoli, B.T. Grenfell, H. Heesterbeek and A. P. Dobson). pp 151-164.
- Guégan, J.F., Morand, S. & Poulin, R. (2005). Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. In: *Parasitism and ecosystems* (ed. by F. Thomas, F. Renaud and J.-F. Guégan), pp. 22–42. Oxford University Press, Oxford.
- Hall, S.R., Knight, C.M., Becker, C.R., Duffy, M.A., Tessier, A.J. & Cáceres, C.E. (2009). Quality matters: food quality and the course of epidemics in a planktonic host-parasite system. *Ecology Letters* 12, 118–128.
- Hechinger R.F. & Lafferty, K.D. (2005). Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London, Series B* 272, 1059-1066.
- Hechinger, R.F., Lafferty, K.D., McLaughlin, J.P., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Sandhu, P.K., Shaw, J.C., Torchin, M.E., Whitney, K.L. & Kuris, A.M. (2011). Food webs including parasites, biomass, body sizes, and life stages for three California/Baja California estuaries. *Ecology* 92, 791.
- Huxham, M., Beaney, S. & Raffaelli, D. (1996). Do parasites reduce the chances of triangulation in a real food web? *Oikos* 76, 284–300.

- Kuris, A.M. (2005). Trophic transmission of parasites and host behavior modification. *Behavioural Processes* 68, 215–217.
- Kuris, A. M. (2003). Evolutionary ecology of trophically transmitted parasites. *Journal of Parasitology* 89(S), S96-S100.
- Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K., Aguirre-Macedo, L., Boch, C., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L. Mancini, F., Mora, A., Pickering, M., Talhouk, N., Torchin, M.E., & Lafferty, K.D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515-518.
- Lafferty K.D., Hechinger R.F., Shaw, J.C., Whitney, K.L. & Kuris, A.M. (2006). Food webs and parasites in a salt marsh ecosystem. In: *Disease ecology: community structure and pathogen dynamics* (eds. Collinge S & Ray C). Oxford University Press Oxford, pp. 119-134.
- Libersat, F., Delago, A., & Gal, R. (2009). Manipulation of Host Behavior by Parasitic Insects and Insect Parasites. *Annual Review of Entomology* 54, 189–207.
- Marcogliese D.J. (2007). Evolution of parasitic life in the ocean: paratenic hosts enhance lateral incorporation. *Trends in Parasitology* 23, 519–521.
- Matthee, S., & Krasnov, B.R. (2009). Searching for mechanisms of generality in the patterns of parasite abundance and distribution: Ectoparasites of a South African rodent, *Rhabdomys pumilio*. *International Journal for Parasitology* 39, 781–788.
- Morand, S., Manning, S.D. & Woolhouse, M.E.J. (1996). Parasite-Host Coevolution and Geographic Patterns of Parasite Infectivity and Host Susceptibility. *Proceedings of the Royal Society of London, Series B* 263(1366), 119-128.
- Marcogliese, D.J. (2002). Food webs and the transmission of parasites to marine fish. *Parasitology* 124, S83–S99.
- Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology* 134, 763-776.
- Poulin, R. (2010). Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology* 26, 492-498.
- Poulin, R., Brodeur, J. & Moore, J. (1994). Parasite Manipulation of Host Behaviour: Should Hosts Always Lose? *Oikos* 70(3), 479-484.

Poulin, R., Guilhaumon, F., Randhawa, H., Luque, J. L. & Mouillot, D. (2011). Identifying hotspots of parasite diversity from species-area relationships: Host phylogeny versus host ecology. *Oikos* 120(5), 740-747.

Price, P.W. (1980). *Evolutionary Biology of Parasites*. Princeton University Press: Princeton, NJ.

Rossiter, W. & Sukhdeo, M.V.K. (2011). Exploitation of asymmetric predator-prey interactions by trophically transmitted parasites. *Oikos* 120(4), 607-614.

Rossiter, W. & Sukhdeo, M.V.K. (2012). Host quality and spatial patterning in infections of the eastern mudsnail (*Ilyanassa obsoleta*) by two trematodes (*Himasthla quissetensis* and *Zoogonus rubellus*). *Journal of Parasitology* (in press).

Skirnisson K., Galaktionov, K.V. & Kozminsky, E.V. (2004). Factors influencing the distribution of digenean (Trematoda, Digenea) infections in a mudsnail (*Hydrobia ventrosa*) population inhabiting saltmarsh ponds in Iceland. *Journal of Parasitology* 90, 50-59

Sukhdeo, M.V.K. & Sukhdeo, S.C. (2004). Trematode behaviours and the perceptual world of parasites. *Canadian Journal of Zoology* 82, 292-315.

Sukhdeo, M.V.K. & Hernandez, A.D. (2005). Food Web Patterns and the Parasite's Perspective. In: *Parasitism and Ecosystems* (Eds. F. Thomas, J.F. Guegan, and F. Renaud). pp. 54-67. Oxford University Press.

Wilson, K., Grenfell, B.T. & Shaw, D.J. (1996). Analysis of Aggregated Parasite Distributions: A Comparison of Methods. *Functional Ecology* 10(5), 592-601.