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FOOD WEB NETWORKS AND PARASITE DIVERSITY

by

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ABSTRACT OF THE DISSERTATION

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The structure of free-living trophic interactions, detailed as food webs, describes potential parasite transmission routes and is likely to provide considerable insight into parasite community dynamics. Despite this framework, a lack of empirical data has largely restricted food web analyses to addressing fundamental questions asking how parasites ‘fit’ into food webs and food web theory. The purpose of this dissertation was to determine how the complex dynamics in the host food web affects the establishment and persistence of parasites. This study focused on helminth parasites with obligate bird, fish and macroinvertebrate hosts that are intimately tied to trophic interactions in food webs from salt marshes throughout the New York-New Jersey Harbor estuary complex. This study was done in four salt marshes, one unrestored and three that were restored at 0, 10 and 20 years previously, and which reflected a gradient in host diversity. There was no relationship between the diversity of the free-living community and the diversity of the parasite community. However, there was a strong correlation between the trophic structure of the host community and complex life cycle parasite presence. The topology of each salt marsh food web was highly nested with clusters of generalists forming

distinct core/periphery structure. Two thirds of all parasite stages were constrained to these core species and their physical location in the food web. Community matrices constructed with randomly determined interaction coefficients to assess community stability confirmed a correlation between system stability and parasite species richness in our sentinel fish species. These data suggest that core free-living species within the food web represent stable trophic relationships that allow for the persistence of complex parasite life cycles. Further, these data suggest a prominent role for clusters of free-living trophic interactions in the establishment of trophically transmitted parasites and the potential for the evolution of complex life cycles.

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‘A man alone is easy prey’ – Clint Eastwood in the film “Pale Rider”

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CHAPTER 1

Introduction

The structure of free-living trophic interactions, detailed as food webs, describes potential parasite transmission routes and is likely to provide considerable insight into parasite community dynamics. Despite this framework, a lack of empirical data has largely restricted food web analyses to addressing fundamental questions asking how parasites ‘fit’ into food webs (Sukhdeo & Hernandez 2005) and food web theory (Lafferty *et al.* 2008). Consequently, there are no studies that use food web structure as a predictive tool to describe parasite community dynamics. Host-parasite models are generally restricted to homogenous one-host, one-parasite systems (Grenfell & Dobson 1995; Pedersen & Fenton 2007), with the caveat that the dynamics should be nested in a larger heterogeneous community (Dobson 2004; Lafferty *et al.* 2008). The purpose of this study is to determine how the complex dynamics in the host food web affects the establishment and persistence of parasites.

Parasites represent more than 50% of trophic interactions in food webs (Price 1980) and are tightly entwined in the host system. The evidence suggests that parasite-host interactions may strongly influence ecological dynamics (Combes 2001), and that host trophic connections are ‘highways’ that dictate trophically transmitted parasite dynamics (Hudson *et al.* 2006). Consequently, I adopt the view that the simple inclusion of parasites in host food webs is not sufficient (see Marcogliese & Cone 1997), and that it is more important and necessary to understand how structures within the host food web can inform the dynamics of parasite communities. In essence, we need to address how

the entire network of trophic interactions affects the establishment and persistence of parasites and how it affects patterns of parasite diversity within different ecosystems.

Numerous empirical food webs have been described since the idea of a food web was first proposed by Elton (1927), and they have led to the development of a large body of theory (reviewed in Dunne & Pascual 2006). Of note is the use of food webs as predictors of the dynamics of host populations and the diversity of host communities (Lindeman 1942; Odum 1953; Hairston & Hairston 1993; Winemiller & Polis 1996; Belgrano *et al.* 2005; de Ruiter *et al.* 2005; Thomas *et al.* 2005; Pascual & Dunne 2006). Though simple, the simple depiction of energy flow through ecosystems using trophic links has revealed much about fundamental principles in ecology (May 1983; Cohen 1989; Pascual & Dunne 2006), primarily through the emergence of unifying patterns in empirical and theoretical studies (see reviews Pascual & Dunne 2006). These patterns are broadly grouped as: how consumer-resource interactions cascade across trophic levels; how web structure alters the outcome of competition and predation; and the complex interactions between diversity and stability (Winemiller & Polis 1996). Though these patterns are the subject of much debate as to their universality (de Ruiter *et al.* 2005; Pascual & Dunne 2006), the power of food web analysis has allowed for simple biological explanations that are derived from fundamental aspects of the natural history of organisms, such as: biological constraints on population dynamics; physical limitations of energy flow; and the inherent nature of animal diversity (Pimm 1982). Thus, it appears that simple processes operating on the level of individual species result in regularity and predictably structured communities (May 1973; Pimm 1982; Pascual & Dunne 2006).

It is the observed structure of biological systems, a consequence of a long evolutionary and co-evolutionary period, which is crucial in the discussion of parasite community dynamics (May 1973; Pianka 2000; Combes 2001). It is likely that over time the component parts of communities have ended up in configurations that endow systems with long-term stability, that provide systems with predictable dynamics, and that are shaped by a limited number of biological processes (May 1973; Pimm 1982; Bar-Yam 1997). For a parasite, the structured and predictable nature of host communities has provided a fertile resource (Poulin 1998; Combes 2001). The selective pressure to ensure transmission has resulted in parasite life strategies that are integrally coupled with host species and which are dependent upon the long-term stability of food web systems (Rohde 1993; Poulin 1998; Combes 2001). Indeed, the interaction between the parasite and its host is so critical that the death or absence of that host will result in the death of the parasite. The host, thus, is not only exploited as an energy source but as an essential habitat (Esch *et al.* 1990; Roberts & Janovy 1997). As a result, the dynamics of the host population will necessarily reflect in the dynamics of the parasite population (Lafferty *et al.* 2008). Accordingly, the study of food webs and patterns of host interactions within them should strongly correlate with patterns of parasite species diversity and community structure.

The main objective of my dissertation is to understand how parasites fit into the structure of ecological networks. I will argue that patterns exist within free-living communities that reflect potential evolutionary stable associations that facilitate parasite establishment and predict parasite community diversity patterns. I will present empirical data detailing parasite diversity patterns within four food webs, describe how parasite

communities form within naïve fish host populations, and develop a conceptual model to predict parasite community using free living host position within the observable food web.

The historical paradigm in parasite ecology

Parasitologists have long accepted that the presence of a parasite species reflects the presence of a functioning host community (Combes 2001), but these data have not addressed how a parasite establishes and persists in the host community. There is some evidence that suggests that the abundance and diversity of definitive and intermediate hosts may determine the parasite community (Hoff 1941; Smith 2001; Huspeni & Lafferty 2004), but the structure of the host food web and its link to parasite community assembly is not considered. Those studies that do elucidate how parasite persistence depends on host community structure tend to be mathematical and have become more complex with the recognition that the entirety of the community may alter parasite persistence and establishment (e.g. Dobson 1990; Hochberg & Holt 1990; Yan 1996; Greenman & Hudson 1997, 1999, 2000). However, these models have failed to provide general insight because of specificity to the system studied, the absence of correlates in biological systems (see review in Keesing *et al.* 2006), and have become so analytically challenging that the results are often not biologically realistic (Begon & Bowers 1995; Hudson & Greenman 1998; Grenfell *et al.* 2002; Keesing *et al.* 2006). Although these works do include more species than the typical one parasite-two host approach common in empirical systems (see Bowers & Begon 1991; Gilbert *et al.* 2001; LoGuidice *et al.* 2003) it has been suggested that new statistical and analytical approaches to solving them

are necessary before progress can be made in interpreting and applying these models to biology (Hudson & Greenman 1998; Grenfell *et al.* 2002; Keesing *et al.* 2006). Despite the difficulty in describing biological systems mathematically, the parameters and component processes that operate and are successful in describing single-host parasite dynamics also arise in multi-host models (Keesing *et al.* 2006). Additionally, these studies have provided a testable conceptual framework that describes parameters thought to be important in parasite establishment and persistence in host populations.

Two central concepts have come to form the main paradigm of parasite population ecology because they tap into two universal evolutionary themes; namely, the basic reproductive rate of an individual, R_0 , and the threshold host population size necessary to sustain a viable population, N_T (Anderson 1982). In seminal work, Anderson (1982) and Anderson & May (1979, 1981) tied the intrinsic rate of population growth, R_0 , to host dynamics using a simple model combining the density of susceptible and infected hosts with transmission rate. In doing so they revealed how the persistence of a parasite population is highly dependent on the density of hosts. Consequently, a natural extension of the susceptible-infected equation was the identification of a deterministic criterion for the long term persistence of a parasite within a host population, where the total host population size must be larger than the rate of recovery and death associated with infected individuals (Anderson & May 1991). With these parameters it has been possible to generalize criteria for parasite population success to one biological process: the instantaneous growth rate of parasite infection as a function of host density and susceptible individuals (Holt & Pickering 1985; Begon *et al.* 1992; Holt *et al.* 2003).

Theoretical studies have extended the work of Anderson (1982) and Anderson & May (1991) in an attempt to delineate under what general conditions host community diversity should alter parasite dynamics (Holt *et al.* 2003; Dobson 2004; Rudolf & Antonovics 2005). Two features appear to alter parasite establishment and are described as density- or frequency-dependent transmission: where the parasite population is a function of the absolute density of the host population or the proportion of infected hosts within the population (Keesing *et al.* 2006). Density-dependent models of transmission are typically used to describe parasites that are spread through environmental propagules or random contact (e.g. Gao & Hethcote 1992). Frequency-dependent models are normally used to describe the transmission of sexually transmitted diseases and epidemiology in human systems (see Getz & Pickering 1983; Thrall *et al.* 1993). Vector-borne diseases conform broadly to the structure of frequency-dependent models of transmission and theoretical work has demonstrated how contact between vector and host is a function of search rate and infected host density (Antonovics *et al.* 1995; Rudolf & Antonovics 2005). It has been argued by Dobson (2004) and Rudolf & Antonovics (2005) that if parasite transmission is density-dependent, a more diverse community will result in lower parasite transmission only if the increased diversity reduces the density of the focal host species. Conversely, in parasites that follow the frequency-dependent mode of transmission, an increase in host community diversity will always result in reduced transmission and establishment success (Dobson 2004; Rudolf & Antonovics 2005).

A secondary consequence of increasing host diversity for metazoan parasites is the potential for transmission success to change depending upon whether the parasite

species uses a single- or multi-host life cycle. The assumption that transmission is higher for single-host parasites than for species that rely on multiple hosts is common in almost all models of disease transmission (Holt & Pickering 1985; Begon *et al.* 1992; Dobson 2004; Rudolf & Antonovics 2005; Keesing *et al.* 2006). Begon *et al.* (1999) and Woolhouse *et al.* (2001) argue that this assumption is appropriate and a requirement for hosts to coexist in mathematical models. These models also suggest that the validation of this assumption is necessary for increasing host diversity to decrease the transmission success of parasites. There are few examples where multi-host pathogen transmission is higher than single host transmission; importantly, these examples are restricted to a virus (Rhodes *et al.* 1998) and a bacteria (Caley & Hone 2004). Evidence suggests that all other metazoan parasites and vector-borne diseases fit the assumption that transmission is higher for single-host parasites (see reviews in Kuris & Lafferty 2000; Keesing *et al.* 2006).

Using a simple graphical isocline framework, Holt *et al.* (2003) further explored the consequences of single- and multi-host pathogen transmission and described a series of critical thresholds for parasites to establish in host communities. In a single-host parasite, the density of that host provides a single threshold to establishment whereas parasites that use multiple hosts have various combined host densities that enable establishment. If the assumption that single-host transmission is higher than multi-host transmission, an increase in diversity increases the probability of parasite establishment more than when there is lower diversity in the system. Further, Holt *et al.* (2003) demonstrated that increasing the diversity of the system resulted in higher critical host population thresholds i.e. as the density of a non-target host increases there must be a

concomitant increase in the target host density for the parasite to establish – the non-target host dilutes the pool of target hosts (for empirical examples see Norman *et al.* 1999; Ostfeld & Keesing 2000; Schimdt & Ostfeld 2001). In general, additional species within a system are likely to inhibit parasite establishment because of higher critical thresholds in host density, this may be offset by the higher probability of encountering a target host in more diverse systems, a phenomenon similar to the sampling effect (see Loreau *et al.* 2001).

In spite of the considerable discussion and development of theoretical frameworks describing the influence of host diversity on parasite population dynamics, there has been little progress in developing a similar empirical host-parasite community framework (Holt *et al.* 2003; Huspeni & Lafferty 2004). This stems principally from difficulty estimating core parameters such as R_0 for all parasite species and critical host thresholds for all hosts in the system, a necessity given that multiple host-parasite systems are the norm (Becker & Yip 1989; Anderson & May 1991). Consequently, literature over the last ten years has detailed how a litany of factors, some biotic and others abiotic, may impact upon the parasite community with few unifying patterns discovered (see Poulin 1998; Poulin *et al.* 2000 for a review). Biotic factors have been demonstrated to drive the dynamics of parasite communities in sea birds (Bush & Holmes 1986; Combes 2001), and in salmonid and coral reef fishes (Holmes 1990; Kennedy & Bush 1994). In contrast, there are examples where abiotic factors such as ‘harsh’ environmental conditions (Galaktionov 1993; Marcogliese & Cone 1996; Biserkov & Kostadinova 1998) and anthropogenic perturbations (MacKenzie *et al.* 1995; Marcogliese & Cone 1996) determine the dynamics of parasite community. In all cases, successful description of

parasite community dynamics within the host environment has relied on local processes with relatively small spatial scales. In tackling parasite community dynamics on a local scale, parasitologists have gained considerable insight into what host factors (i.e. host age, density) may impact upon parasite community dynamics but have lost the universal appeal of the early population biology studies of Anderson & May (1991).

Modern parasite community ecology

Mainstream community ecology has explicitly considered community assembly within a framework consisting of regional and local processes (Ricklefs & Schluter 1993; Brown 1995; Rosenzweig 1995; Lawton 1999; Gaston & Blackburn 2000). While the dominant forces structuring communities varies by system, by including regional processes alongside local, ecologists have developed a solid theoretical framework and considerable empirical evidence explaining patterns and processes in many free-living communities (Pianka 1974; Chesson & Case 1986; Hubbell 2001; Rohde 2005). Further, the approach for integrating regional and local processes is frequently in the form of food webs (see Cohen 1978; Pimm 1982; Belgrano *et al.* 2005; de Ruiter *et al.* 2005; Pascual & Dunne 2006). This contrasts with the traditional parasitological approach that has focused on local characteristics to explain the structure and dynamics of parasite communities and which largely has not used the powerful tools of network analysis to integrate local with regional processes. It has been argued that it is this ‘disconnect’ between local and regional processes that has stymied parasitologists.

Regional and local approaches are complementary and are likely to provide important insight into parasite community assembly and diversity patterns. The potential

benefit of studying parasite community dynamics using multiple scales stems from advances made in the field of complex system analysis (Bar-Yam 1997, 2004; Thomas *et al.* 2005; Pascual & Dunne 2006). This approach suggests that molecules, cells, cells with organelles, multicellular organisms, herds, or other organismal groupings and the relationship between these individual parts, may effectively describe system level behaviors (Bar-Yam 1997, 2004; de Ruiter *et al.* 2005; Pascual & Dunne 2006). This approach seems particularly useful in parasite study. Recent work has demonstrated the interaction between global environmental change and local parasite dynamics (see Harvell *et al.* 1999) and how local transmission dynamics may scale to affect global disease dynamics (see Hahn *et al.* 2000; Daszak & Cunningham 2002). It seems then plausible to suggest that regional processes coupled with detailed population and community studies, and the relationship between the two scales, will provide more insight into parasite community dynamics than either approach alone.

Food web ecologists have been using a ‘complex system’ approach since the work of Charles Elton in the 1920s. The description of trophic interactions between consumers and resources has, in effect, unified local and regional dynamics. Local interactions between species – trophic links – are in part determined by regional dynamics for two reasons: resource competition and energy. The topology of ‘webs’ and the interactions within them influence the dynamics and persistence of populations through resource availability and mortality caused by predation (de Ruiter *et al.* 2005). Moreover, trophic interactions represent transfer rates of energy and matter, a fundamental concept in ecosystem and community processes. Food webs therefore, provide a way to analyze the relationship between populations, communities, and ecosystems and core ecological

concepts such as stability, diversity, and community assembly (de Ruiter *et al.* 2005; Sukhdeo & Hernandez 2005; Pascual & Dunne 2006; Hernandez & Sukhdeo 2008; Lafferty *et al.* 2008).

The utility of food web analysis to reveal underlying concepts in parasite ecology has largely been ignored: less than 20 webs in the literature contain parasites, and usually that data includes only a small subset of the total parasite community (Marcogliese & Cone 1997; Sukhdeo & Hernandez 2005; Lafferty *et al.* 2008). The paucity of data belies the potential role parasites may play in food web structure with anecdotal evidence suggesting far reaching ecosystem effects, for example, pathogen driven die-offs of sea urchins in the Caribbean (Lessios *et al.* 1984; Lessios 1988). Further, cascading predation effects through food webs that change the density of host species have been observed to influence the frequency of bacterial epidemics (Lafferty 2004), the epidemics in turn have altered the end community stable state (Berhens & Lafferty 2004). Consequently, identifying patterns in the ecology and mathematics of host food webs and linking regularities in the networks to parasite population and community dynamics is central to understanding how parasites establish and persist in host communities.

Food webs and parasitism

The understanding that parasitology and ecology are not exclusive disciplines is not new; parasitology began incorporating ecological theory in and around the 1950s (see Park 1948; Holmes 1961; Schad 1963). Since this time, parasite ecology has flourished with studies addressing parasite community assembly (Guegan *et al.* 2005), the role of parasites in population regulation (Cattadori *et al.* 2004; Moller 2005), and the

evolutionary and ecological implications of parasite mediated trophic interactions (Esch 1977; Anderson & May 1979; May & Anderson 1979; Esch *et al.* 1990; Minchella & Scott 1991; Hudson *et al.* 1998; Lafferty *et al.* 2000; Torchin *et al.* 2003; Thomas *et al.* 2005). Although these data suggest a strong influence of parasitism on community structure, the specific role of parasitism in community dynamics remains a hotly debated topic (see Thomas *et al.* 2005; Poulin 2007). Confounding attempts to develop a generalized host-parasite ecological framework (Poulin 2007) is the inability of theoretical parameters such as R_0 to be accurately quantified in empirical systems. Further, the role of the free-living community on parasite dynamics, and how parasites can be integrated with food web theory remains difficult because few studies address the question with the correct rigor and multi-scale approach (Mouritsen & Poulin 2002; Thompson *et al.* 2005; Sukhdeo & Hernandez 2005; Hernandez & Sukhdeo 2008; Kuris *et al.* 2008; Lafferty *et al.* 2008).

The lack of taxonomic resolution and inclusion of parasites in food web descriptions and theory is a major criticism leveled at food web ecology (Huxham *et al.* 1995; Marcogliese & Cone 1997; Lafferty *et al.* 2006). Frequently, published webs include relatively few of the species present in the system; further, they rarely describe all the potential interactions. The most common consumer strategy, parasitism, is generally left out of food web analyses (Lafferty & Kuris 2002). Given the difficulty quantifying parasite-host interactions using standard ecological techniques this is not surprising, yet parasitism appears to be a fundamental feature of all natural systems. Price (1980) estimates that parasitism is a strategy used by over 50% of all species at some point in their life history. Esch & Fernandez (1993) make the claim that the number of non-

parasitic species that are parasitized approaches 100%, similarly Rohde (1993) suggests that all marine species are infected with parasites. Despite the obvious ubiquitous nature of parasitism, there remain few food webs in the literature (Polis 1991; Goldwasser & Roughgarden 1993; Huxham *et al.* 1995; Sukhdeo & Hernandez 2005; Lafferty *et al.* 2006; Hernandez & Sukhdeo 2008) that contain metazoan parasites, and those that are included represent a small fraction of possible species and potential trophic links likely to be present. In some cases, there is acknowledgement of the omission of parasites from community webs (Huxham *et al.* 1995; Marcogliese & Cone 1997) but the size and feeding strategies used by parasites make it very difficult to retrofit them into the 50 years of food web theory.

It is possible to construct food webs anew including parasites (e.g. Lafferty *et al.* 2006; Hernandez & Sukhdeo 2008) or add parasite information to existing food webs using parasite-host records (i.e. Yamaguti 1958). Systematic inclusion and consideration of all parasites for all free-living species in food webs would be ideal but it is clearly intractable to include all species in a system. Further, not all food web datasets are appropriate for expansion to include parasites because of the high degree of taxonomic aggregation i.e. functional groups, while others are dominated by species with few historical parasite-host records. Consequently, including parasites in food webs and understanding how they impact upon food web dynamics and topology results in exhaustive multi-year empirical studies (Hernandez & Sukhdeo 2008; Kuris *et al.* 2008). Including parasites then seems to run counter to the initial goal of food web analyses; the description of complex multi-scale processes in simple webs that provide insight into

patterns and processes. A more fruitful question may then be what can host food webs tell us about parasites?

Patterns in host food webs and parasite communities

For several decades a dominant ecological paradigm was that complex communities are more stable than simple ones (MacArthur 1955; Elton 1958; Hutchinson 1959; Hasting 1988; Williams & Martinez 2000). MacArthur (1955) postulated that a large number of ‘paths’ through each species is necessary to ameliorate the effects of dominant or overpopulated species. He concluded that “stability increases as the number of links increases”, tying together the concept of community stability with two core food web properties, trophic linkage and number of species. May (1972, 1973) challenged this general paradigm using dynamic models of abstract communities, finding that communities tended towards unstable behavior as system complexity increased. He made the observation that stability in food webs is conditional on the interaction between species diversity (S), connectance between species (C), and interaction strength (i) and that systems would be stable if $i(SC)^{1/2} < 1$. Several papers since May (1972, 1973) have pointed out the limitations in his analyses of abstract communities (for example, Lawlor 1978; Cohen & Newman 1985; Taylor 1988), stemming largely from evidence suggesting that species interactions in biological systems are not random. Regardless, May’s work provided a framework to empirically address two universal network parameters: the interplay between diversity and connectance and the ratio of species to links within the food web (linkage density).

Connectance is a frequently used value describing community complexity and a key parameter in describing general patterns in food webs: measured as the proportion of potential links among species that are realized, it is predicted to decrease hyperbolically as species richness increases to maintain system stability (Warren 1989; Dunne 2006). Given the ease of empirical verification and simple way of expressing it mathematically, $C = L/S^2$ (Martinez 1991), connectance has often been used in food web models to test theoretical predictions (Gardner & Ashby 1970; Pimm 1984; Solow *et al.* 1999; Williams & Martinez 2000). Original analyses provoked criticism as a measure because they included only a fraction of species present in natural systems (Paine 1988; Polis 1991; Hall & Raffaelli 1993). Subsequent analyses of food webs had higher taxonomic resolution and detailed how an increase in species, including parasite links, resulted in a decrease in connectance (Huxham *et al.* 1995; Memmott *et al.* 2000; Thompson *et al.* 2005). However, re-analysis of these data along with other parasite-host webs suggests that previous measures underestimated the percentage of possible links that were realized (Lafferty *et al.* 2006). Lafferty *et al.* (2006) used techniques common in plant-pollinator web analysis (see Oleson & Jordano 2002; Bascompte *et al.* 2003; Jordano *et al.* 2006) and omitted illogical parasite-parasite and predator-parasite links from analysis and found an increase in connectance. These data do not fit the expected inverse relationship between connectance and species diversity (Dunne 2006). However, a food web with parasites is not ‘unstable’ and inclusion of realized parasite links and the concomitant increase in connectance with increasing species diversity must be offset by decreases in interaction strength or increased web cohesiveness i.e. nestedness (Bascompte *et al.* 2002; Dunne 2006; Lafferty *et al.* 2006).

Parasites with complex life cycles may help explain the apparent paradox of a diverse, highly connected communities retaining stability. A major impact of including parasites in food web analyses is the extension of trophic chains (Williams & Martinez 2004), which should decrease system stability. However, complex life cycle parasites, though extending the length of trophic chains, introduce relatively weak interactions into 'long loops' that may offset the effect of increasing connectance (Neutel *et al.* 2002).

Many parasitic helminthes with complex life cycles have strong impacts on some species in their life cycle (i.e. Lafferty & Morris 1996) but have weak or non-detectable impacts on others (reviews in Lewis *et al.* 2002). Further, when parasitic helminths infect intermediate hosts in their life cycle, they parasitize a small fraction of the total population of that host and a smaller fraction of that goes on to infect the next host in the life cycle (Roberts & Janovy 1997; Poulin & Morand 2000). A consequence of this is that the interaction link between a parasite and host has been suggested to be a relatively weak interaction (Dobson *et al.* 2006). Additionally, direct life cycle parasites may be a strong stabilizing force because their dynamics are typically frequency dependent and the commonest host species suffers the greatest pathology (Dobson 2004; Lafferty *et al.* 2008). Consequently, though the net effect of including parasites in food webs is an increase in species diversity and an increase in connectance seemingly resulting in lower system stability, any effects may be offset by relatively weak links with a significant number of free-living species on multiple trophic levels (Neutel *et al.* 2002; Dobson *et al.* 2006).

Considerable effort has gone into explaining food web regularities beyond diversity and the distribution and density of feeding links between species (see reviews in

Belgrano *et al.* 2005; Pascual & Dunne 2006). Cohen (1977) observed a constant ratio of prey items to predators of approximately $\frac{3}{4}$ across all webs of varying species diversity. Further, Cohen (1977) found that most webs tended to be interval: that is, all species in a food web may be placed in a fixed order on a line so that each predator's set of prey items forms a contiguous section on that line. This property implies that a species trophic niche space may be represented by a single dimension: though the mechanism and reason for this pattern remains unknown (Williams & Martinez 2000) it presents an example of a pattern consistent across all reported food webs. Examples of other scale invariant properties that have come to be considered theoretically valid for all food webs (Martinez & Lawton 1995) and those that alter common ecological themes (i.e. competition, predation) have been documented (Lawton & Warren 1988). The first attempts at explaining these patterns was made by in a series of papers (Cohen & Newman 1985; Cohen *et al.* 1985; Cohen *et al.* 1986; Cohen 1990; Cohen & Palka 1990; Cohen *et al.* 1990) that drew heavily on random graph theory pioneered by Erdos & Renyi (1960) and approached food web structure using a static model that featured trophic cascades and dynamics determined by body size.

The cascade model (see Cohen *et al.* 1990 and references therein) uses two parameters, species richness S and link density L/S , to describe food web structure. The model creates web matrices through the random distribution of species and feeding links subject to only two constraints: species are placed in a one-dimensional hierarchy; species may only feed on species lower in the hierarchy than themselves. Given the random binary link approach used by the cascade model, explanations for the behavior of food webs could be developed using a small number of hypotheses (Erdos & Renyi 1960;

Cohen *et al.* 1990). Of further utility are inherent mathematical properties that prohibit complex biological interactions such as cannibalism. Cohen and Newman (1985) were the first to explore whether this model reproduced patterns of food web structure finding that it was effective at reproducing qualitative species and link scaling laws in all but the smallest of webs. However, while the cascade model produced values similar to those observed in empirical data, it was ineffective at explaining variation in the data (Cohen & Newman 1985). Further work by Cohen *et al.* (1985), Cohen *et al.* (1986) and Cohen & Palka (1990) found similar results: species proportions, link distributions, food chain length and frequency of interval webs were adequately described but variance in the data was more poorly described. Solow (1996) extended these analyses: data was highly over-dispersed in relation to model predictions and consequently led to the rejection of the model at all significance levels.

In the tradition of the stochastic cascade model, Williams & Martinez (2000) proposed a new food web structure model called the niche model. This model addressed three of the key assumptions of the cascade model: link-species scaling; exclusion of looping (cannibalism); and the lack of trophic overlap. The distribution of feeding links in the niche model allows for three possible results: feeding on higher species in higher trophic levels and cannibalism; species with similar niche values use similar consumers creating high trophic overlap; created food webs are interval due to contiguous feeding by consumers on resources within a single range. The third outcome represents a limitation of the model in that the some empirical food webs are not interval in nature (Cohen & Palka 1990). Williams & Martinez (2000) have argued that because intervality is a delicate mathematical property, if webs are analyzed quantitatively for the degree

rather than presence/absence of intervality it is quite high in empirical webs. Regardless, along with the use of C as a parameter the model addressed the three major criticisms of original cascade model. Further, arrangement of consumers and resource species along an interval may provide realistic biological information about species size, metabolic rate and trophic position (Stouffer *et al.* 2005). The critical output of the niche model has been that food web structure is not random and that simple link distribution rules result in complex web structure that ape patterns observed in empirical data. Secondly, two recent variants – the nested-hierarchy model (Cattin *et al.* 2004) and the generalized analytical model (Camacho *et al.* 2002; Stouffer *et al.* 2005) – document two conditions for these models to fit empirical data: species niche values must form an ordered set, a condition met by the cascade model; each species has a determined probability of preying on a species with lower niche values, a condition based largely on a species diet range. To date, no models have explicitly considered parasites, due perhaps to the violation of core assumptions when parasites are included.

A central aspect of all models and empirically constructed food webs is how general or specific a species is in its feeding habits and how vulnerable it is to predation by other species (Schoener 1989): these biological concepts are described as link distribution. In analyses, these interactions are visualized as frequency histograms of the number of trophic links each species has and describe how many resources a consumer has (generality), how many consumers eat a resource (vulnerability) and total number of links a species has to other species. Frequency distributions, beyond the overall description – Poisson, constant, power-law, exponential – may be divided further to discuss the place of species in the network by two values, clustering coefficient and

characteristic path length. These values describe firstly, the average fraction of pairs of nodes that are connected to the same node that are also connected to each other and secondly, the average shortest distance between pairs of nodes. These quantifiable network traits have been included in food web analyses to ask whether the distribution and topology of a feeding network is similar to other social and abiotic (i.e. internet and road) networks. Searching for 'small world' network structure (Watts & Strogatz 1998) within feeding link distribution has enabled ecologists the ability to address whether or not feeding links are structured like a random graphs (Erdős & Rényi 1960), highly ordered and regularly connected like a lattice (Albert & Barabasi 2002), or another form unique to feeding networks.

Beginning in 2002, a series of studies addressed the question of whether food webs are similar to the structure of small world networks with a high degree of clustering and short paths between nodes (see reviews in Cartozo *et al.* 2006; Dunne 2006). Montoya & Sole (2002) used three empirical food webs and found that web topology was very similar to those of small world, scale-free networks. Contradicting these results was the meta-analysis conducted on seven food webs by Camacho *et al.* (2002) who found that the degree of clustering in empirical food webs was no higher than would be expected from random expectations, and significantly lower than clustering in small world networks. Camacho *et al.* (2002) further concluded that the empirical food webs they analyzed did not display scale-free structure with regards the distribution of feeding links. Instead of a scale-free distribution, across six of the seven food webs, the feeding link degree distribution displayed exponential decay in its tail i.e. the probability of finding a highly linked species in the food web decreased exponentially. In an attempt to

bridge the conflict, Dunne *et al.* (2002) expanded analysis to 16 food webs, including those used by Montoya & Sole (2002) and Camacho *et al.* (2002a), and concluded that most food webs displayed low clustering coefficients and link distributions that deviated from those of scale-free networks. The exception is the result that food webs have relatively short path lengths similar to random expectations and consistent with small world network topology (Montoya & Sole 2002; Camacho *et al.* 2002; Dunne *et al.* 2002; Williams *et al.* 2002). The implication of these studies is that food webs deviate from ‘small world’ network structure (Watts & Strogatz 1998) and are not randomly connected ‘graphs’ or regular lattices in which every species has the same number and pattern of links. Instead, the majority of food webs seem to have a unique topology, one that has relatively low diversity, high connectance, a degree distribution that is exponential in form and a short path length between species i.e. within a food web there are a few highly connected species that give the appearance of compartments in webs.

Early food web research presented conflicting accounts of the presence (Paine 1966; May 1972; Yodzis 1982; Raffaelli & Hall 1992) or absence (Pimm & Lawton 1980) of compartments in food web topology. The conflict likely caused by analytical difficulties, high connectance, a trait of most food webs, may obscure the presence of compartments. However, recent studies have suggested a variety of ways of identifying compartments derived from methods used in social network analyses. Particularly relevant for food web structure and parasites, is the presence of nested structure within webs (Bascompte *et al.* 2003). The degree to which a food web is nested has rapidly become a universal tool in describing topology (e.g. Jordano 1987; Memmott and Waser 2002; Jordano *et al.* 2003; Bascompte *et al.* 2003). Originally used in the study of island

biogeography to describe how a regional pool of species is distributed among islands (Atmar & Paterson 1993), nestedness has come to be useful in providing a quantitative measure of how species within a food web are feeding. Should the value of nestedness be high, it may be interpreted as suggesting a non-random structure in which generalist species tend to interact amongst themselves (Melian & Bascompte 2002), and where specialist species interact with the generalist species creating asymmetrical interaction webs i.e. a generalist-generalist web attached to a series of smaller specialist ‘subwebs’ (Melian & Bascompte 2004; Vazquez & Aizen 2004). In almost all webs ($n = 66$), particularly mutualistic networks, Bascompte *et al.* (2003) found a degree of nestedness higher than one would expect by random. Thus, though not strict compartmentalization as per the description of Pimm & Lawton (1980), food webs have largely been found to have distinct asymmetry resulting from the presence of a small set of generalist ‘core’ species that are responsible for the bulk of interactions.

A promising direction for detecting compartments within food webs has been to borrow techniques from the field of social network analysis, in particular the common concept of core-periphery structure (Borgatti & Everett 1999). The concept is prevalent in diverse fields of inquiry such as world systems (Snyder & Kick 1979; Nemeth & Smith 1985), economics (Krugman 1996), organization studies (Faulkner 1987) and proximity among Japanese monkeys (Corradino 1990). A variety of algorithms have been proposed (Krause *et al.* 2003; Melian & Bascompte 2004) which approach the analysis differently but seek to identify the same thing, subwebs with concentrated interactions. Subwebs are defined as a subset of species that are connected to at least one predator and/or prey species within that subset: a species membership in a subweb is an

iterative process and determined to be where the species has the highest number of links to other species. Krause *et al.* (2003) found distinct core-periphery structure in three of five food webs examined, similarly, Melian & Bascompte (2004) found cores of tightly interacting species surrounded by species with few connections in five food webs. If the core-periphery topology of food webs is universal it is likely to have far reaching effects for the study of disease transmission and the establishment and persistence of multi-host parasites (Pastor-Satorras *et al.* 2001).

Parasite establishment in food webs: directions of my dissertation

Despite increasing attention, parasite community assembly mechanisms remain undocumented (Rohde *et al.* 1994; Lafferty *et al.* 2008). The principles of colonization-extinction and subsequent equilibrium in community assembly (MacArthur & Wilson 1967) have been applied to many ecosystem types (Simberloff & Wilson 1969; see review in Morin 1999), but the establishment of parasites in host systems has not been explored beyond epidemiological settings. Intuitively, the absence of necessary host resources will be reflected in the absence of parasite species. Consequently, the presence of a diverse host community will create the opportunity for parasites and pathogens to complete their life cycle (Hudson *et al.* 2006). The supposition, therefore, is that parasite species richness will have a parallel successional dynamic that free-living organism's demonstrate.

Ecological succession is a ubiquitous process of temporal species change in the composition of populations following a perturbation (natural or anthropogenic) to the initial observed communities (see Keever 1950; Bard 1952). The majority of concepts

and systems considered in the development of 'succession theory' have focused on terrestrial plant communities (see Keever 1950; Bard 1952; Tilman 1985; Pickett & McDonnell 1989). Succession, however, can occur in any situation where a disturbance creates opportunities for the establishment of, and transition to, other species. Sousa (1979) demonstrated in the intertidal zone, a succession of algal species following disturbance; he concluded that succession was accelerated when disturbances or herbivores removed early-successional species allowing other species to establish. There have been few attempts to correlate successional changes in vegetation with temporal changes in animal species composition. Johnson & Odum (1956) demonstrated important changes in bird species composition and correlated them with changes in plant community structure and Whittaker (1952) was able to show a similar correlation with arthropods and the plant community. There are, however, no examples of parasite species change along a successional gradient.

A severe perturbation, where all hosts are eliminated from the environment and the subsequent colonization of the area by free-living hosts provides an excellent opportunity to study parasite establishment and community diversity patterns. It is plausible to suggest that parasite colonization following disturbance will reflect the colonization of the habitat by suitable host species; not only definitive species but also all species involved in the parasite life cycle. A corollary concept is that the species richness of hosts, a function of individual abundance and species heterogeneity, and a high diversity of hosts should contribute to a high diversity of parasites. Further, a necessary part of host-parasite ecology is the study of all links, and the distribution of these links, in the network of host-host and host-parasite interactions. Given the wealth of food web

theory (see reviews in de Ruiter *et al.* 2005; Pascual & Dunne 2006) describing community regularities and the tight evolutionary link between host and parasite, there are likely predictable structures within the host food web that facilitate establishment and persistence of parasites.

My dissertation is a preliminary step towards achieving an understanding of how parasites establish and persist within host food webs. I will report results from four independent observational studies conducted over 2 years in a New Jersey salt marsh. These results will address specifically: 1) the relationship between communities of birds, fishes and invertebrate fauna and the community of helminth parasites in the marsh killifish, *Fundulus heteroclitus* (Chapter 2 and 3); 2) the establishment and diversity patterns of helminth parasites in naive marsh killifish (Chapter 3 and 4); 3) topological phenomena within four salt marsh food webs that facilitate the establishment of trophically transmitted helminth parasites (Chapter 2). These data will describe structural and biological parameters of estuarine food webs that will likely enable the prediction of metazoan parasite establishment and persistence.

CHAPTER 2

Core/periphery structure in food web networks constrains parasite diversity.

Abstract

Food web topology was investigated in four restored salt marshes that reflect a gradient in host diversity and time post restoration. Key food web metrics such as species diversity, linkage density, connectance, nestedness, and the presence or absence of network modules were compared. It was predicted that parasite diversity would correlate positively with host diversity, and that trophically transmitted parasites would be restricted to highly connected subsets or modules of the host network. The topology of each salt marsh food web was highly nested with clusters of generalists forming distinct core/periphery structure. The predominant core module was significantly similar between marshes. There was a strong correlation between the diversity of trophically transmitted parasites and the structure of the predominant core group of species in each web. Two thirds of all parasite stages were constrained by the core species in the food web. These data suggest that core free-living species within the food web represent stable trophic relationships that allow for the persistence of complex parasite life cycles. This study suggests a prominent role for clusters of free-living trophic interactions in the establishment of trophically transmitted parasites and the potential for the evolution of complex life cycles.

Key-words: Ecological networks; Modules; Parasitism; Trophic transmission

Introduction

Food webs are abstractions of nature that describe community topology via networks of trophic interactions (e.g. Cohen *et al.* 1990; Pimm *et al.* 1991; Huxham *et al.* 1995; Williams & Martinez 2000; Montoya & Sole 2003; Thompson *et al.* 2005). The information provided by existing topological (who eats whom) webs has provided a fertile resource for the generation of theory on the determinants of community structure and the stability of ecosystems (MacArthur 1955; May 1972, 1973; Cohen 1978; Cohen & Newman 1985; Williams & Martinez 2000). For example, the topology of a food web may help in understanding the flow of energy through systems and whether population dynamics are more or less stable in highly diverse communities relative to low diversity communities (May 1972; Warren 1994; Dunne, Williams & Martinez 2002; Neutel *et al.* 2007). Further, several topology-based metrics have become key parameters in the theoretical search for general patterns in food webs (Warren 1994) and as determinants of food web stability (Dunne 2006).

Parasites have largely been understudied in these systems and there have been few attempts to use the topology of the free-living host community to describe parasite or disease dynamics (Lafferty *et al.* 2008). However, highly resolved topological food webs that include parasites (Thompson & Townsend 2003; Lafferty *et al.* 2006; Hernandez & Sukhdeo 2008) show features of real structure that may be important in the persistence of complex parasite life cycles (Parker *et al.* 2003). First, free-living hosts serve as both habitat and dispersal agents, and if transmission of a parasite is a function of the density of the final host, an abundance of hosts will result in an abundance of parasites (Holt *et al.* 2003; Keesing *et al.* 2006). Second, because many parasites tend towards high host

specificity (Combes 2001; Poulin 2007), increasing the diversity of host communities results in a concomitant increase in the diversity of parasites (Poulin & Mouillot 2004; Hechinger & Lafferty 2005). Third, trophically transmitted parasites are dependent upon the feeding habits of predators and prey for transmission (Marcogliese 2003).

Consequently, patterns of parasite diversity are contingent upon, and susceptible to, the structure and distribution of feeding interactions and the abundance of host in the free-living community (Marcogliese & Cone 1997). In essence, the structure of the host food web is likely to have exerted a strong selective pressure on the evolution of parasite transmission strategies and subsequent patterns of parasite diversity observed in extant systems (Marcogliese & Cone 1997; Poulin & Morand 2000; Hernandez & Sukhdeo 2008).

Clusters of species that have a critical place in the topology of the host network (core species) are likely to provide insight into the diversity of parasites in ecosystems for two reasons. First, those host species that fall into the core cluster of an ecological network are likely to experience fewer fluctuations in abundance relative to those that fall in the periphery of a network (Allesina *et al.* 2006) providing a reliable resource for parasites. Second, clusters of tightly interacting species that drive nestedness and modularity in food webs yield stable predator-prey trophic links (Wasserman & Faust 1994; Jordano *et al.* 2006) and exploiting these stable links may ensure successful completion of the parasite life cycle. The potential for the structure of free-living communities to change local parasite dynamics is supported by studies that demonstrate the effects of climate-mediated physiological stress on host resistance to pathogens and the relationship between host range shifts and the emergence of new or known pathogens

in local populations (Harvell *et al.* 1999). Additionally, system dynamics driven by predator-prey interactions have been shown to cause bacterial epidemics in an aquatic system (Lafferty 2004; Berhens & Lafferty 2004). Consequently, identifying patterns in the topology of ecological networks and linking regularities in the networks to parasite community dynamics is central to understanding how parasites establish and persist in host communities.

There is a broad correlation between host community diversity and parasite community diversity that has provided the impetus for studies on the effect of network structure on the dynamics of parasite communities. Though these studies have typically recovered positive linear relationships between the two (Smith 2001; Hechinger & Lafferty 2005; Fredensborg *et al.* 2006; Hechinger *et al.* 2007), it is not clear how or if the structure of the host food web affects the diversity of parasites. Despite the intuitive proposition that the network of trophic interactions provides a roadmap of potential transmission routes for trophically transmitted parasites (Marcogliese & Cone 1997), there is as yet no hard evidence that parasites are restricted by the topology of the host network (Price 1980; Poulin & Morand 2000; Sukhdeo & Hernandez, 2005; Dobson *et al.* 2008). Thus, this study uses network structure to investigate the relationship between host food webs and parasite communities to identify mechanisms driving patterns of parasite diversity. We use methods modified from social network theory (Wasserman & Faust 1994; Borgatti & Everett 1999) to identify cohesive subgroups within networks of trophic interactions. These cohesive subgroup modules represent species with relatively direct and frequent interactions.

An ideal situation in which to test the effect of network topology on the emergent patterns of system parasite species richness would be within a series of islands of varying ages as in MacArthur & Wilson's (1967) classic island biogeography study. MacArthur & Wilson (1967) posited that the number of species within a discrete and isolated system was a consequence of the species previously located there and the processes of immigration, extinction and speciation. A consequence of this is that as a community assembles, the network and trophic structure of the food web should also change revealing patterns of community complexity (i.e. Piechnik *et al.* 2008). In this study, we use a system of differently aged estuarine salt marshes, each with a distinct host diversity and community composition as a surrogate for individual islands with a range of host diversity and community complexity. We investigate the structures necessary for complex parasite life cycles to persist and potential mechanisms driving parasite species richness. We report that the diversity of the parasite community is not strictly correlated with the diversity of the host community (birds, fishes and benthic invertebrates). Second, we report that the structure of the host network limits the establishment and diversity of trophically transmitted parasite species. To our knowledge, our study is the first to use the host network structure as a predictor of parasite community structure.

Methods

Defining the study system

Sampling occurred within four salt marshes in the New Jersey Hackensack Meadowlands (USA): over 90% of estuarine marshes in the Meadowlands are heavily impacted due to decades of anthropogenic disturbances (Sipple 1972; Tiner, Swords &

McClain 2002). Recent large-scale restoration projects with the goal of recreating ‘pristine’ New-England type salt marshes (Adam 1993) have created spatially delineated habitats reflecting a gradient in time since restoration: Oritani marsh (unrestored); Mill Creek marsh (20 years since restoration); Harrier Meadow (10 years); Secaucus High School marsh (0 years).

Mill Creek marsh (20 year) is a 57 hectare tidal marsh bordered by highways and residential land (40°47'45" N, 74°02'30" W). The marsh restoration has resulted in low marsh habitats (*Spartina* sp. and *Distichlis* sp. dominated) that are flushed daily by the tides, tidal impoundments, and lowland scrub-shrub habitats along the marsh/upland ecotone. Harrier Meadow marsh (10 year) is a 32 hectare tidal marsh surrounded by tidal mudflats and urban development (40°47'12" N, 74°07'3" W). The marsh has low marsh habitats similar in vegetation to Mill Creek, shallow open water impoundments that are hydrologically connected to the surrounding mudflats, areas of higher elevation dominated by *Phragmites australis*, *Lythrum salicaria*, and lowland scrub-shrub habitats. Secaucus High School marsh (0 year) is a 43 hectare tidal marsh bordered by a river and residential development (40°48'17" N, 74°02'52" W). The site is currently dominated by the common reed (*P. australis*) and contains narrow sinuous channels, several mosquito ditches, and tide gates. Tidal flow is restricted and large sections of the marsh receive rare inundation at high tide. Oritani marsh (unrestored) is a 224 hectare tidal marsh that has no record of human alteration or use (40°47'57" N, 74°05'07" W). The marsh is undeveloped and includes more than 150 hectares of upland area, and a smaller area of high and low marsh with small tidal channels. The upland areas are dominated by a dense monoculture of common reed (*P. australis*). The high marsh areas are dominated

by saltmarsh hay (*Spartina patens*), while the low marsh areas are predominately smooth cordgrass (*S. alterniflora*), marsh fleabane (*Pluchea pupurascens*) and dwarf spikerush (*Eleocharis pavula*).

Although the ‘real’ food web is likely to span the entire New York-New Jersey estuary complex, we construct four food webs that are constrained by physical boundaries (roads, urban development) that surround each marsh site. In addition, we limit the food webs to those species found in tidally influenced sediment and the vegetated habitat within the marsh (*sensu* Lafferty *et al.* 2006b). By constraining each food web spatially, we omit terrestrial birds, mammals and invertebrates that are transient in the marsh habitat. Further, we do not consider the edge of each marsh, and the species located within this habitat, as part of our community as these species are likely indicative of the mud flats in the estuary complex or the urban development that surrounds each site.

Our preferred taxonomic unit for constructing each food web was species, although we were limited by our source data. As a consequence, some members of our food web were lumped into large categories (e.g. Nematoda, copepods, ostracods). Where possible we empirically validated literature records for birds (point count surveys), benthos (Hester-Dendy sampling plates and benthic cores sieved through 5 mm mesh) and fishes (active seine netting, gill netting in marsh channels, minnow traps and trap nets). However, the majority of species we document in our food webs were based upon host community data collected from the literature for birds (Seigel, Hatfield & Hartman 2005; Seigel 2006; pers. comm.), fishes (Bragin *et al.* 2005; pers. comm.) and benthos (Yugas 2001; Yugas, Hartman & Weis 2005; pers. comm.). We included species

from these records if they comprised more than 0.5% of the individuals sampled, but relaxed this criteria for top predators given their relative importance in the structure of food webs and role as potential definitive hosts for parasites (*sensu* Lafferty *et al.* 2006b). For basal species we lumped: terrestrial and aquatic detritus; micro and macroalgae; and the producer component of the food chain together. Though this represents a gross simplification of a high level of diversity (e.g. Breitbart *et al.* 2004), it has been used in other parasite food web studies as a method of minimizing complexity that may not be relevant in parasite transmission (Lafferty *et al.* 2006b). These criteria were used consistently for each food web: the species that fulfil these rules are listed in Tables 1 (invertebrates), 2 (fishes) and 3 (birds).

To determine variation in the compositional structure of the host community between sites, we used non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index. Bray-Curtis coefficients were based on host species abundances; to control for the influence of abundant species relative to rare species, all species abundances were square root transformed. Ordination was implemented using the software PC-ORD version 5 (McCune and Mefford 2002) with 500 iterations and 250 runs of both real and randomized data. NMDS checks for the structure of the matrix in a two-dimensional ordination space producing a measure of goodness-of-fit: the adequacy of NMDS is contingent upon stress values <0.3 .

Food web metrics and analyses

Topological food webs consist of a predator(i)-prey(j) matrix with n species, and may be constructed following the methods in Cohen *et al.* (1990, 1993). Given our

interest in the structure of the free-living host network, we did not construct parasite subwebs *sensu* Lafferty *et al.* (2006a). Consequently, our matrices and analyses were limited to traditional predator-prey interactions. Binary entries in these matrices indicate whether a predator eats a prey species. Trophic links were determined for all taxa using primary publications and monographs (Diaber 1982 and references therein; Poole & Gill 2003; Froese & Pauly 2009 and references therein). In cases where the diet description was overly vague (e.g. benthic invertebrates) we used our discretion, based upon body-size relationships, in assigning trophic links. Predators typically consume prey items smaller than themselves (Elton 1927; Memmott, Martinez & Cohen 2000), and we used adult body sizes of predators to identify likely prey items. We further extended links between predators and prey by inferring links using our empirical parasite records. Parasites are a useful indicator of host diet (see Knudsen, Klemetsen & Staldvik 1996): the presence of a parasite species within a host provides a robust indicator of host diet (see Marcogliese 2003). Thus, a host species that serves as an intermediate host for a parasite species found in a specific predator will be a prey item for that predator (Huxham *et al.* 1995; Marcogliese 2003). Food web diagrams for each site were drawn using UCINET 6 (Borgatti, Everett & Freeman 2002) and Netdraw: Network Visualization Software (Borgatti 2002).

Food web metrics were calculated for each predator-prey matrix and include the number of species (S), the number of observed links (L_o), the number of potential links (calculated as the number of cells in the matrix, S^2), linkage density (d), directed connectance (C) (Martinez 1991), nestedness (N ; Atmar & Paterson 1993), and core/periphery structure (Borgatti & Everett 1999). Connectance ($C = L_o/S^2$) is the

number of realized links (L_o) divided by the number of possible links (S^2). Measured in this way, C is the average fraction of species in a community consumed by the average species i.e. when $C = 0$ no species consume each other and when $C = 1$ all species consume all other species and themselves. Nestedness describes the extent to which a group of specialist consumers feed upon a subset of the prey eaten by generalists. To estimate nestedness we calculated matrix temperature using the software ANINHADO (Guimaraes & Guimaraes 2006) which compares the extent to which a matrix is significantly nested relative to a series of null model generated matrices. The null model used to assess significance was implemented as Ce in ANINHADO (Guimaraes & Guimaraes 2006) and created random matrices using a function such that the probability of cell a_{ij} being filled was $(a_i/C + a_j/R)/2$ (where a_i , number of links in row i ; a_j , number of links in column j ; C , number of columns; R , number of rows). To allow for across network comparisons we calculated relative nestedness (Bascompte *et al.* 2003). We also calculated the cumulative degree distribution, the fraction of trophic species $P(k)$ that have k or more trophic links. We examined the distributions by fitting three different models: (a) exponential, $P(k) \sim \exp(-\gamma k)$; (b) power-law, $P(k) \sim k^{-\gamma}$; and (c) truncated power-law, $P(k) \sim k^{-\gamma} \exp(-k/k_x)$.

We measured the degree of network centrality using models of core/periphery structure (a measure borrowed from social network analyses: Borgatti & Everett 1999). The idea of network core/periphery structure in food webs is that there is a physical centre of the food web (species with high levels of interspecific interactions) and a periphery of a cloud of points in Euclidean space (species with fewer direct and/or indirect interactions). Given a plot of species interactions in space (such as one provided

by multidimensional scaling), those species that occur near the centre of the plot are those that are proximate not only to each other but also to all species in the network, while those species that fall on the outskirts are close only to those species in the centre (Laumann & Pappi 1976; Borgatti & Everett 1999). To estimate the core/periphery structure within each network we used UCINET 6 (Borgatti *et al.* 2002), which is based on a genetic algorithm (see Borgatti & Everett 1999). The algorithm seeks to find ‘partitions’ within the data set such that the correlation between the observed data and the pattern matrix induced by the partitions are maximized. We sorted all species into different classes using a continuous model that assigns each species a measure of ‘coreness’ that corresponds to the distance of a species to the centre of the network (Borgatti & Everett 1999).

These analyses were conducted on our topological food webs consisting of the predator(i)-prey(j) matrix. Consequently, the properties we observe are a consequence of the free-living trophic structure of each food web and are not confounded by the biased inclusion of parasites sampled from a limited number of host species.

Field collections

The abundance of a sentinel fish, *Fundulus heteroclitus*, and its helminth parasites were measured every three months starting in December 2005 and ending in December 2007 (eight contiguous seasons: two fall, two spring, two winter, two summer).

Fundulus heteroclitus was selected as a sentinel species because it is a highly abundant resident marsh species (Lotrich 1975) along the east coast of North America (Relyea 1983), likely plays an important role in marsh food webs and has a wide range of possible

helminth parasites (Harris & Vogelbein 2006). Fish were collected using a 4 mm seine and baited minnow traps; all habitats within each marsh were sampled for at least 5 days each season. From each seasonal collection, thirty fish were identified to species using a field guide to North American fishes, euthanized and immediately necropsied. Fish necropsy was done using standard parasitological techniques (see Hoffman 1999). Helminth parasites collected during necropsy were identified using keys (Yamaguti 1958; Schell 1970; Schmidt 1970; Anderson, Chabaud & Willmott 1974) and primary literature (see Harris & Vogelbein 2006).

To estimate species richness in each marsh, we used species accumulation curves (SACs), a technique common for estimating diversity in ecology. We used the bias-corrected Chao2 estimator in EstimateS 8.0.0 (Colwell 2006) to calculate the species richness of parasite component communities (the community of parasites associated with a regional subset of hosts) at each sample date. The Chao2 estimator has been shown to have excellent predictive power when sample sizes are relatively small and the bias-corrected model has been shown to perform well in host-parasite systems (reviewed in Dove & Cribb 2006). Sample order was randomized 150 times without replacement and mean species richness was estimated for each sample. We performed a Kruskal-Wallis one-way analysis of variance (ANOVA) on estimated species richness at each site to determine whether there were significant differences between sites; multiple pairwise comparison was conducted using Dunn's test.

We further analyzed relationships using general linear models (GLMs) with host community measures as predictor variables and mean parasite community diversity as the response variable. We also determined the effect of time since restoration on the parasite

community and whether patterns of parasite species richness were consistent between marshes. Consequently, initial GLM models included host community richness, marsh (Oritani Marsh, Secaucus High School Marsh, Harrier Meadow, Mill Creek Marsh) and the host*marsh interaction. Further, because we sampled each of the four marshes over 2 years, we also determined whether the effect of marsh was affected by season. The effect of marsh on host community (benthos, fishes, and birds) was consistent across years; there was no interaction between season and marsh (all $p > 0.25$). Thus, only the marsh and host community richness may be considered as potential cofactors of the parasite community richness. All p-values were conservatively two-tailed with a critical value of 0.05. We performed all analyses using the software platform JMP Version 7.0.1 (2007 SAS Institute).

Incorporating parasites into the networks

Information on parasites came from field sampling of the sentinel, *Fundulus heteroclitus*, and from a literature review of potential parasites of the free-living organisms present in the study system. We selected four representative parasites, in addition to our empirical parasite data, that ranged in life cycle strategy and host specificity, and that were likely to be found in each marsh site given the presence of particular hosts. Consequently, host-parasite links in these analyses were only included in the web when the parasite was known to have suitable hosts present for each life stage of the parasite species. Thus, our network is not a comprehensive host-parasite network, but a subset of parasites within a network of host interactions. This creates a somewhat idealised network of host-parasite links, however, when conservatively interpreted and

used as a preliminary step towards understanding the link between host trophic structure and parasite diversity it is a valid approach (see Lafferty *et al.* 2008). We sorted all life stages of parasite species into core classes based upon the classes of the potential host. Given that trophically transmitted parasites rely on stable trophic associations for successful transmission, we predicted that the life stages of each parasite species should be nested within distinct cores (i.e. if a parasite species has its adult stage in the central core then all life stages will also be located in the central core).

Results

Does host diversity determine parasite diversity?

In the restored salt marshes of the New Jersey Meadowlands, parasite diversity does not scale with host diversity. A total of 960 sentinel fish were studied: 30 collected in each of the eight seasons between 2006-07 in each of the 4 marshes. Eleven taxa of metazoan parasites were identified including nematodes *Dichelyne bullocki* and *Contracaecum* sp.; the digenean *Lasiotocus minutus* and metacercaria of *Ascocotyle diminuta*, *Mesostephanus appendiculatoides*, *Posthodiplostomum minimum*; monogeneans *Fundulotrema prolongis* and *Swingleus ancistrus*; acanthocephalans *Paratenuisentis ambiguous* and *Southwellina hispida* (cystacanth); the copepod *Ergasilus funduli*; these taxa infected more than 70% of the mummichogs examined. Parasite intensity per host ranged from 1 to 127.

The community similarity of birds ($r^2=0.81$, stress value=0.08), fishes ($r^2=0.82$, stress value=0.09) and benthic macroinvertebrates ($r^2=0.82$, stress value=0.07) showed distinct separation between each of the four marshes sampled. Despite the communities

varying significantly between sites there was no correlation with parasite species richness. Bird species richness was not associated with mean parasite species richness (Fig. 2.1A, $r^2=0.00$, $F=0.57$, $p=0.46$). Neither marsh, nor the interaction between marsh and the bird host community, were significant factors in determining parasite richness ($F=0.58$, $p=0.64$, and $F=0.32$, $p=0.81$). Fish species richness was not associated with mean parasite species richness (Fig. 2.1B, $r^2=0.084$, $F=0.53$, $p=0.48$). Marsh identity had a significant, positive association with parasite species richness ($r^2=0.51$, $F=6.51$, $p=0.0073$), but the interaction between marsh and host species richness was not significant ($F=1.09$, $p=0.39$). Our final grouping, benthos species richness, was also not associated with mean parasite species richness (Fig. 2.1C, $r^2=0.18$, $F=3.45$, $p=0.088$). Neither marsh, nor the interaction between marsh and the benthic host community, was a significant factor in determining parasite species richness ($F=0.13$, $p=0.94$, and $F=2.57$, $p=0.10$).

Structure of the free-living web

The Oritani marsh (unrestored) included 71 species and had 5041 potential links of which 629 were realized, resulting in a connectance of 0.125 (Table 2.1). The Secaucus Marsh (0 year) included 87 species and had 7569 potential links of which 627 were realized, resulting in a connectance of 0.083 (Table 2.1). The restored marshes, Harrier Marsh (10 year) and Mill Creek (20 year) included 112 and 122 species respectively; the resulting values of connectance were 0.096 for Harrier Marsh and 0.124 for Mill Creek Marsh (Fig 2.2: Table 2.1). All four of our trophic food webs displayed cumulative degree distributions that were different from what would be expected if the

link distribution were random (Fig. 2.3). In each food web, the data was well fit by power-law distributions but then had a sharp cut-off after a certain number of interactions (Amaral *et al.* 2000; Jordano, Bascompte & Olesen 2003). Each food web had data that were consistent with an exponential or truncated power-law distribution: there was no significant difference between the models. The identity of the best-fit model is secondary to our data departing from a power-law distribution; in our data, super-generalist species are more rare than would be expected if the networks were built using a scale-free distribution to describe the number of interactions per species. Like many aquatic ecosystems, the food web had high diversity in the low and high trophic levels and with relatively few species in the intermediate trophic levels. The linkage density increased, though not markedly so, across the gradient of time post-restoration (Table 2.1).

All four networks were tested for nestedness, i.e. a pattern where specialists interact with a subset of the species that the generalist species interact with. All networks were significantly nested in comparison to randomized matrices ($p < 0.001$). The presence of core and peripheral modules, a complementary concept to nestedness, was also analyzed for each network using a continuous model that partitioned the species in our networks based on a measure of ‘coreness’, if a species was assigned a value of 1 it was part of the predominant network module. The correlation between the data and the continuous coreness model was 0.294 (Oritani), 0.342 (Secaucus), 0.273 (Harrier) and 0.186 (Mill Creek), which indicates an adequate fit of the model (Borgatti & Everett 1999). Because our data is in the form of a binary matrix, it can be embedded in a Euclidean space of no more than $N - 1$ dimensions without distortion: thus, we can use metric multidimensional scaling (MDS) procedures to visualize the structure of each

matrix. Furthermore, each species within the network has a coreness value that may be phrased as an eigenvector; the magnitude of the eigenvector represents a measure of centrality and the species importance to the structure of the network. A MDS of each network is presented in Figure 2.4. It can be seen in the figure that as we consider successively wider concentric circles, beginning at the centroid, the average distance among points within the circles increases with the distance from the centre. This is a defining characteristic of core/periphery structure.

The results of the Mantel analyses on the species found in the predominant food web core are given in Table 2.2. All correlations were positively significant ($p < 0.001$) at 20,000 randomizations. Thus, each matrix is similar to each of the other three matrices, which reflects a relatively high species overlap in the core species. The two most similar cores were the modules in the newly restored marsh (Secaucus Marsh: 0 year) and the intermediate marsh (Harrier Marsh: 10 year). However, the two most dissimilar cores were the intermediate marsh (Harrier Marsh: 10 year) and the oldest restored marsh (Mill Creek Marsh: 20 year). The simplest explanation accounting for these data, as you would expect that restored marshes would be more similar, is that the structural differences among the four sites were not primarily related to the time post-restoration.

Where are the parasite life stages?

More than two thirds of the trophically transmitted parasite stages in our system were located in the predominant core of each food web. The core/periphery analysis we conducted assigns a coreness value, phrased as an eigenvector, to each species and

identifies the species that fall in the predominant core of each food web. The predominant core species represent approximately one third of the total species richness in each food web: Oritani Marsh has a core of 20 species (28% of species: concentration = 0.774), Secaucus Marsh has a core of 31 species (35% of species: concentration = 0.825), Harrier Meadow has a core of 27 species (24% of species: concentration = 0.822) and Mill Creek Marsh has a core of 40 species (33% of species: concentration = 0.786). Our *a priori* assumption was that parasite life stages would be evenly distributed across all species in each food web i.e. in Oritani Marsh, 28% of parasite life stages would fall in the core, 72% in peripheral species. Using data from our field collections and primary literature (Table 2.3) we find that: 70%, 65%, 64%, 82% of the parasite life stages fall in the predominant core in Oritani Marsh ($\chi^2 = 25.2, p < 0.001$), Secaucus Marsh ($\chi^2 = 13.7, p < 0.001$), Harrier Marsh ($\chi^2 = 36.0, p < 0.001$) and Mill Creek Marsh ($\chi^2 = 38.6, p < 0.001$) respectively.

Discussion

These data suggest that food web core/periphery structure plays a significant role in the persistence of complex parasite life cycles. The key insight provided by our analyses is that the core of a food web, along with nested network structure, provides a critical cluster of interactions that allow for higher transmission efficiency in trophically transmitted parasites. In our indicator species, we did not find a correlation between the diversity of the parasite infracommunity and the diversity of the free-living community, whereas previous studies, some in very similar systems, have described positive linear associations between the diversity of parasite species and the diversity of the free-living

communities resulting in the intuitive statement; diversity begets diversity (Smith 2001; Hechinger & Lafferty 2005; Fredensborg *et al.* 2006; Hechinger *et al.* 2007). The reason for this difference is twofold. First, the diversity of parasites in our sentinel species may not reflect the diversity of parasites in the entire system. In addition, we may have biased our finding by using a sentinel species (*F. heteroclitus*) that is located within the predominant core food web module. Second, this core module was replicated at each site (Table 2). Further, up to 85% of the parasite species life stages are transmitted within the same predominant food web module as the definitive host. Consequently, the host community measures that correlate with the diversity of parasites are not measures of system diversity but of the structure of the food web.

Graphical representations of our four estuarine food webs reveal network structure that contains link-dense and link-sparse areas (e.g. Figure 2A). We were able to designate these link-dense areas as cores that represent clusters of species that are linked more tightly together than they are to species in other areas of the network. Discussions of cores in ecological networks began in the 1960s, and despite some concerns (e.g. Pimm & Lawton 1980), the presence of distinct cores have been directly correlated with measures of system robustness (Gardner & Ashby 1970; May 1972; Krause *et al.* 2003; Melian & Bascompte 2004; Olesen *et al.* 2007). Furthermore, highly resolved data sets reveal that many networks are highly cohesive, with several small groups of species connecting to a single dense core which plays a central role in determining network structure (Melian & Bascompte 2002, 2004). A significant consequence of network cohesiveness is that the network may become more robust to perturbation, as changes are restricted to one area of the network. Similarly, if a disease or pathogen enters a

particular food web core, the spread of that disease may be enhanced within these cores of tightly interacting species (Pastor-Satorras & Vespignani 2001). It is therefore likely that core structures in food web networks provide a reliable resource for complex life cycle parasite species because it represents a cluster of repeatable trophic interactions.

A fundamental aspect of searching for clusters of interactions is describing the distribution of feeding links in food webs. The appearance of a characteristic single-scale distribution of feeding links in our networks may be related to how these salt marsh communities have assembled. It is likely that the mechanisms that produce the link distribution in our food webs differs from those that produce scale-free distributions observed in real world networks (Amaral *et al.* 2000). This is largely due to the violation of two assumptions in amenable models of real world networks: (i) the network grows at each time step through the addition of nodes and links and (ii) there is a preferential attachment of new nodes to other nodes with a higher number of links (Barabasi & Albert 1999). Predator-prey webs appear to violate the first assumption through the processes of immigration, extinction, and speciation (i.e. Whittaker, Triantis & Ladle 2008). Secondly, though there is yet to be a general consensus as to how new species link to existing species in food webs, it appears that immigrants do not always link to the most linked species (Piechnik *et al.* 2008; Olesen *et al.* 2008). In an explicit test of the preferential attachment model, Olesen *et al.* (2008) determined that the assembly process in a plant-pollinator network was intermediate between preferential attachment and random; with attachment constrained by the ecology (i.e. abundance, phenophase length) of the system. This is further supported by our data (Fig. 3), and a larger analysis of 16 food webs (Dunne *et al.* 2002) that suggest there are fewer super-generalists than would

be expected if new species preferentially attached to other highly linked species. The proposition that there are a few super-generalists that are driving the structure of the entire web is supported by the high degree of nestedness for each of our estuarine food webs (Fig. 4). These data imply that there is a distinct group of generalist species that interact amongst themselves and that there is a tendency for specialist species to interact with the most generalist species. This topological property is a standard measure in food web analyses because of the potential for core generalist species to drive the evolution of entire systems (Thompson 1994).

Complementing the distribution of feeding links, and the generalist-specialist dichotomy we observed in our networks, is the presence of a predominant food web core at each site (Figure 3 & Table 3). The presence of network modules may have a significant effect on the coevolutionary processes in plant-pollinator systems (Olesen *et al.* 2007) and as a potential stabilizing force in food webs (Krause *et al.* 2003). In the case of our estuarine food webs, the observed cores represent tight clusters of feeding interactions that act as transmission routes for trophically transmitted parasites. The interaction between parasite and host is often extremely intimate and persistent; survival is not possible without the host. Parasites, in continued selection of a particular environment (i.e. the definitive host), have facilitated the recognition of, and therefore response to, unique features that signal preferred habitat (Sukhdeo 1997). Combes (2001) has proposed a similar theory, stating that parasites need only develop specific responses to a narrow selection of host species, so enhancing their 'fitness'. Consequently, those highly connected species in our food webs provide a stable coevolutionary unit that complex life cycle parasites may exploit during their evolution

and persistence (Thompson 1994; Marcogliese & Cone 1997; Sukhdeo & Hernandez 2005).

The core/periphery structure we observe is particularly important for parasites with complex life cycles as they rely on feeding interactions between trophic levels, a strategy with a considerable failure rate (see Kuris *et al.* 2008). Failure for a parasite in this case, may occur when a predator that is not a suitable host consumes a parasite stage. Given that there is a remarkable diversity of parasite species found throughout all natural ecological systems (Poulin 2007; Dobson *et al.* 2008), it is likely that there has been considerable selection for parasite stages to fall in host species that increase the probability for life cycle success. In some cases, parasites have circumvented diffuse predator-prey interactions by modifying the behaviour of intermediate hosts to make them more susceptible to predation from specific definitive hosts (Lafferty 1992; Lewis *et al.* 2002). Though this is a fruitful approach to increasing transmission efficiency, it is not a predominant mechanism (reviews in Lewis *et al.* 2002) and it is more likely that it is the structure of the host food web that exerts a strong selective force on parasite life cycles (Combes 2001; Poulin 2007). Therefore, it is plausible to suggest that through evolutionary time, parasite species have become embedded in subsets of host food webs that ensure high transmission. Indeed, we find not only tight clusters of interacting species but trophically transmitted parasite life stages restricted by the structure of the cluster.

The demonstration of cores in these four estuarine food webs has implications for ecology and evolution outside of parasite transmission and life strategies. To our knowledge, there are only two studies that have found modularity in ecological networks

(Krause *et al.* 2003; Olesen *et al.* 2007), and this is likely the result of poorly resolved data and the lack of sufficiently strong algorithms to detect modules (Montoya, Pimm & Sole 2006). As the resolution of food web data improves (see Lafferty *et al.* 2008) and studies begin to incorporate module-detecting algorithms from the social sciences (i.e. Borgatti & Everett 1999) and physics (Guimera & Amaral 2005) it is likely that network modularity will be revealed as a critical component in the functioning of ecological networks, particularly with regards to the stability of ecological systems (May 1973). Further, the identification of modules of species within networks may reveal critical information about the effect of species extinctions on community dynamics (i.e. Sole & Montoya 2001), the impact of exotic species on native plants and animals (i.e. Lockwood, Hoopes & Marchetti 2007), the spread of infectious diseases within and between communities (Pastor-Satorras & Vespignani 2001; Lafferty *et al.* 2008) and potentially provide the critical units of tightly interacting species that could operate as coevolutionary units (Thompson 1994).

In conclusion, the concept of food webs was formally introduced in the early Twentieth century and has since developed into a widely appealing and accepted approach to describing species interactions that reflects the interconnectedness of all animal species (Elton 1927; Pascual & Dunne 2006). While debate continues about the utility of food webs as synthetic tools (e.g. de Ruiter *et al.* 2005; Pascual & Dunne 2006) it is plausible to suggest that at the very least, highly resolved food webs provide an opportunity to integrate processes operating at the level of the free-living community with those important for parasites. Parasites permeate entire ecosystems; positions derived from the frequency of complex life cycles with one parasite species interacting

with many free-living hosts, and substantially alter common food web metrics (Marcogliese & Cone 1997; Lafferty *et al.* 2008). More importantly, this study has demonstrated how food web structure strongly influences parasite diversity patterns, a result of the dependence of parasites upon their free-living hosts and the nature of the ecological network in which they reside.

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Figure 2.1: Parasite species richness correlations with host birds **(a)**, fishes **(b)**, and benthos **(c)** in the four marshes sampled. Oritani Marsh (unrestored - *open squares*), Secaucus Marsh (0 year - *open circles*), Harrier Meadow Marsh (10 year - *filled square*) and Mill Creek Marsh (20 year - *open triangles*). R^2 and p -values for the effect of host species richness are $r^2=0.00$, $p=0.46$ for **a**; $r^2=0.084$, $p=0.48$ for **b**; and $r^2=0.18$, $p=0.088$ for **c**.

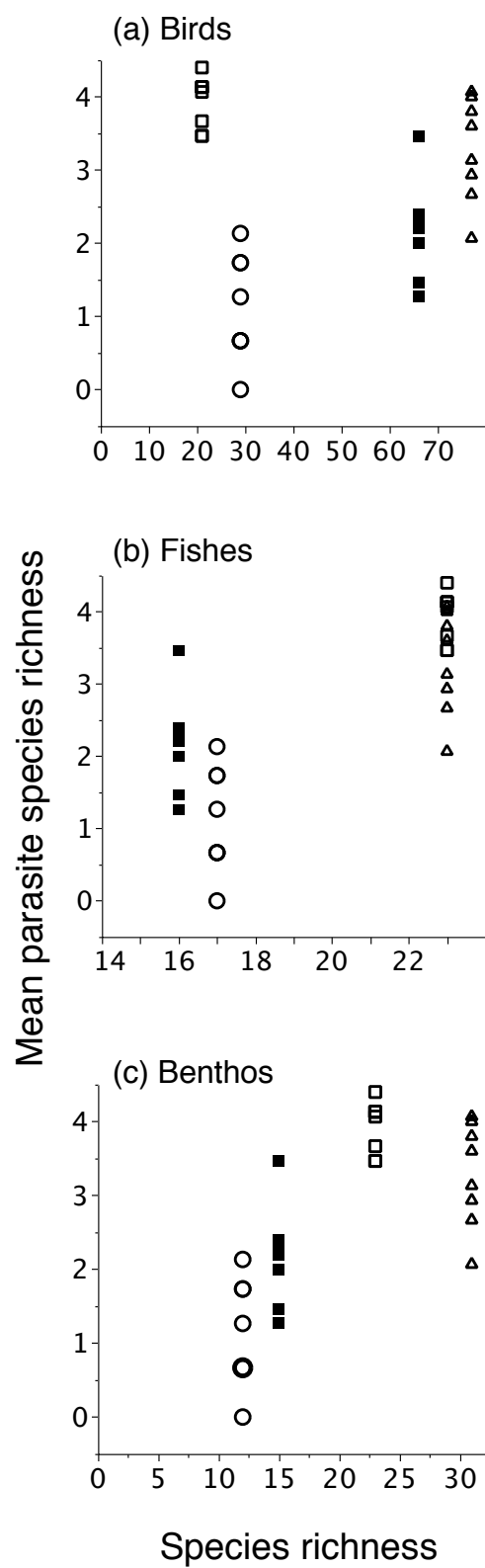


Figure 2.1

Figure 2.2: Sample-based species accumulation curve for parasite communities in Oritani Marsh (unrestored - *solid line*), Secaucus Marsh (0 year – *dashed line*), Harrier Meadow Marsh (10 year – *dotted line*) and Mill Creek Marsh (20 year – *dotted and dashed line*). Curves represent the result of the bias-corrected Chao2 estimator of species richness based on *Fundulus heteroclitus* samples.

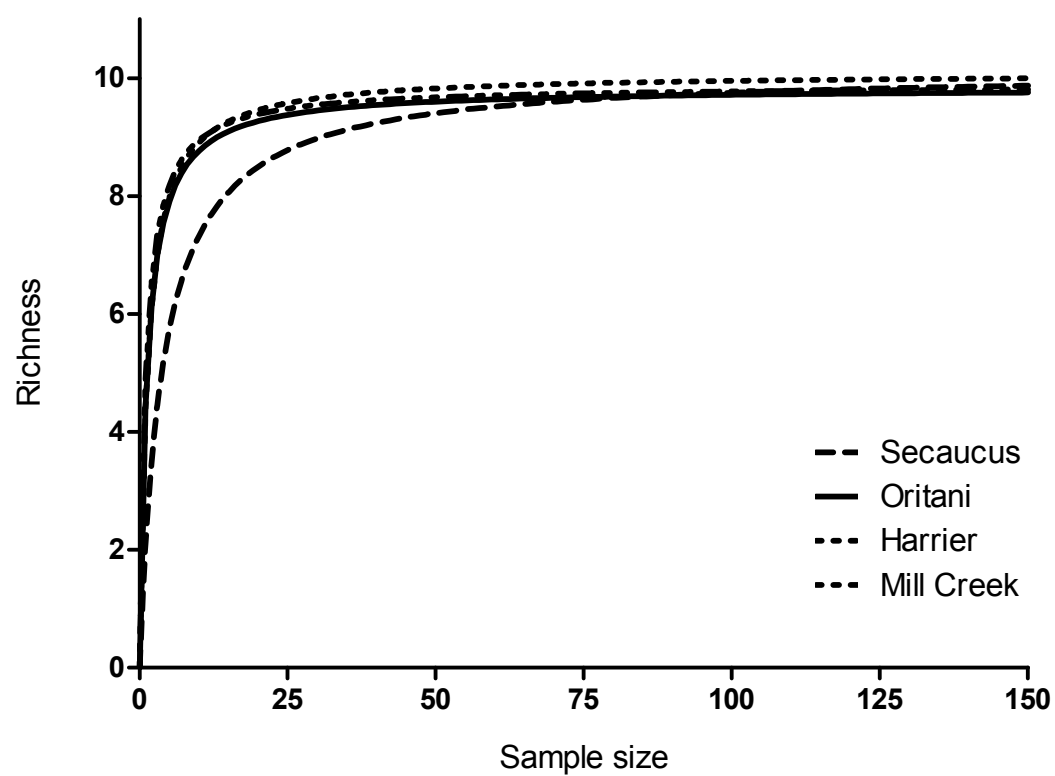


Figure 2.2

Figure 2.3: Multidimensional scaling analysis visualization of **(a)** Mill Creek Marsh (20 years post restoration) food web structure, and **(b)** Harrier Marsh (10 years post restoration) food web structure. Black lines indicate predator-prey links. The relative size of each species represents the eigenvector (a measure of network centrality) and core/periphery position. Species denoted by circles fall in the predominant food web core, those by triangles in the periphery: species in white are used by trophically transmitted parasites.

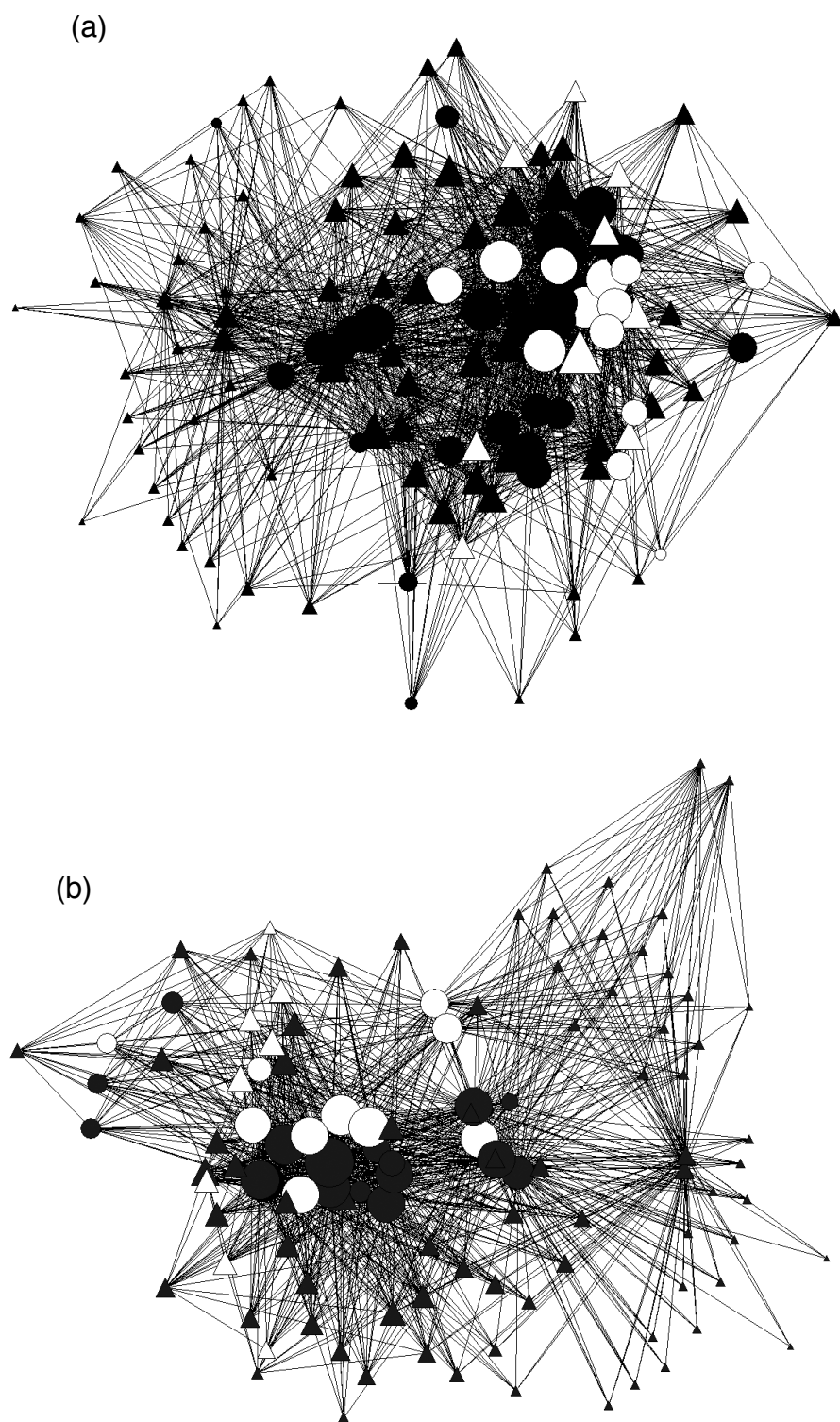


Figure 2.3

Figure 2.4: Log-log plots of cumulative distribution of links per species in **(a)** Oritani Marsh (unrestored), **(b)** Secaucus Marsh (0 year), **(c)** Harrier Marsh (10 year) and **(d)** Mill Creek Marsh. Cross marks represent observational data, lines and r^2 values represent the fit to the data of the best simple models: power-law distribution (straight line), truncated power-law distribution (downward curved dashed line), or exponential distribution (downward curved solid line).

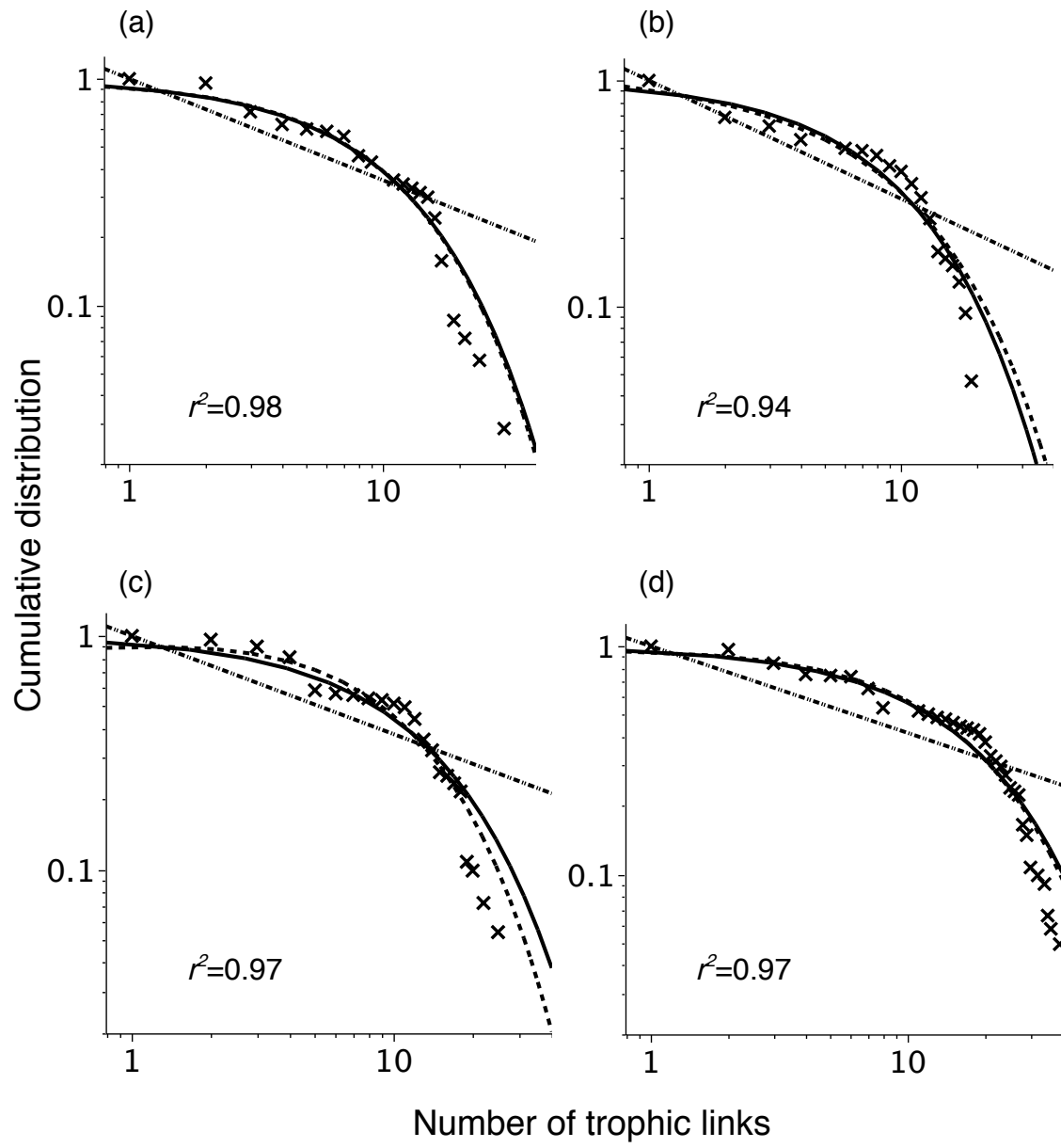
**Figure 2.4**

Figure 2.5: Multidimensional scaling analysis of core/periphery values for **(a)** Oritani Marsh (unrestored), **(b)** Secaucus Marsh (0 year), **(c)** Harrier Marsh (10 year) and **(d)** Mill Creek Marsh.

Figure 2.5

Table 2.1: Summary of food web metrics for each of the estuarine food webs. Statistics include species richness (S), potential links (S^2), observed links (L_o), linkage density (d), connectance (C), relative nestedness (n^*)

Parameters:	<i>Oritani Marsh</i>	<i>Secaucus</i>	<i>Harrier</i>	<i>Mill Creek</i>
	<i>(unrestored)</i>	<i>Marsh (0</i>	<i>Marsh (10</i>	<i>Marsh (20</i>
		<i>year)</i>	<i>year)</i>	<i>year)</i>
Number of species; S	71	87	112	122
Potential no. of links; S^2	5041	7569	12544	14884
Observed no. of links; L_o	629	627	1206	1846
Linkage density; d	8.86	7.21	10.77	15
Connectance; C	0.125	0.083	0.096	0.124
Relative nestedness; n^*	0.75	0.75	0.86	0.81

Table 2.2: Significant correlation coefficients from Mantel analyses on the similarity of the predominant core species between estuarine food webs.

	<i>Oritani Marsh</i> <i>(unrestored)</i>	<i>Secaucus</i> <i>Marsh (0</i> <i>year)</i>	<i>Harrier</i> <i>Marsh (10</i> <i>year)</i>	<i>Mill Creek Marsh</i> <i>(20 year)</i>
Secaucus Marsh	0.324			
Harrier Marsh	0.265	0.332		
Mill Creek Marsh	0.245	0.263	0.246	

Table 2.3: Life cycle characteristics of select parasites in the Meadowlands estuary complex. Parasite species marked with a star (*) represent those identified in field collections of *Fundulus heteroclitus*.

Parasite species	Type	Intermediate Host 1	Intermediate Host 2	Definitive Host
<i>Contracaecum</i> sp.*	Nematode	Copepods, Amphipods (2 spp.)	Fish (5 spp.)	Piscivorous birds (7 spp.)
<i>Eustrongylides</i> sp.	Nematode	Oligochaete (1 spp.)	Fish (1 spp.)	Piscivorous birds (6 spp.)
<i>Paratenuisentis</i> <i>ambiguous</i> *	Acanthocephalan	Amphipods (1 spp.)		<i>Anguilla</i> <i>rostrata</i>
<i>Leptorhynchoides</i> <i>thecatus</i>	Acanthocephalan	Amphipods (1 spp.)		Fish (3 spp.)
<i>Ascocotyle</i> <i>diminuta</i> *	Trematode	Gastropoda (2 spp.)	Fish (2 spp.)	Piscivorous birds (6 spp.)
<i>Posthodiplostomum</i> <i>minimum</i> *	Trematode	Gastropoda (2 spp.)	Fish (3 spp.)	Piscivorous birds (4 spp.)
<i>Schistocephalus</i> <i>solidus</i>	Cestode	Copepod (1 spp.)	Fish (1 spp.)	Piscivorous birds (8 spp.)
<i>Proteocephalus</i> sp.	Cestode	Copepod (1 spp.)		Eels, fish (6 spp.)

CHAPTER 3

Abiotic and biotic hierarchies in the assembly of parasite populations.

Abstract

The presence or absence of parasites within host populations is the result of a complex of factors, both biotic and abiotic. This study uses a non-parametric classification tree approach to evaluate the relative importance of key abiotic and biotic drivers controlling the presence/absence of parasites with complex life cycles in sentinel killifish *Fundulus heteroclitus*. Parasite communities were classified from 480 individuals representing 15 fish from 4 distinct marsh sites in each of four consecutive seasons between 2006-07. Abiotic parameters were recorded at continuous water monitoring stations located at each of the four sites. Classification trees identified the presence of benthic invertebrate species (*Gammarus* sp. and *Littorina* sp.) as the most important variables in determining parasite presence: secondary splitters were dominated by abiotic variables including conductance, pH and temperature. Seventy percent of hosts were successfully classified into the correct category (infected/uninfected) based on only these two criteria. The presence of competent definitive hosts was not considered to be an important explanatory variable. These data suggest that the most important determinant of parasite community assembly is the availability of diverse communities of benthic invertebrates.

Key-words: Complex life cycle; Definitive host; Intermediate host; Parasite establishment

Introduction

The presence or absence of parasites in host populations is the result of a complex of factors, some biotic and others abiotic. Although there is little consensus as to which of these factors are dominant, it is clear that the diversity and abundance of parasites differs from one host population to the next. This variation is to be expected, as habitat characteristics, biotic or abiotic, vary between locations and this can either facilitate or inhibit the establishment and persistence of parasites in host populations. For example, the critical importance of biotic factors on parasite populations has been demonstrated in salmonid fish (Kennedy and Bush, 1994), rocky reef fish (Holmes, 1990) and waterfowl (Bush and Holmes, 1986). On the other hand, it has been argued that the role of biotic factors have been greatly over-emphasized (i.e. Combes, 2001) and natural abiotic factors such as ‘harsh’ environmental conditions (Galaktionov, 1993; Marcogliese and Cone, 1996; Biserkov and Kostadinova, 1998) and anthropogenic perturbations (see MacKenzie *et al.* 1995; Marcogliese and Cone, 1998) may also have large impacts on parasite populations.

In heteroxenous parasite species (those with multiple hosts), it is thought that the dominant drivers of the parasite infracommunities are related to the diversity and abundance of the host community (Huspeni and Lafferty, 2004; Hechinger and Lafferty, 2005; Hechinger *et al.* 2007). The rationale being that as parasite lineages diversify over evolutionary time, they become embedded within the trophic interactions of host food webs, and host-feeding links provide repeatable and dependable interactions for parasites to use as ‘pathways’ for transmission (Marcogliese and Cone, 1997). The number and distribution of pathways within food webs is a direct consequence of the number of

species present, as diversity increases so to does the number of trophic connections (MacArthur, 1955). Thus, diverse communities of invertebrates, fishes and birds have the ability to support multiple parasite species with complex life cycles (Marcogliese, 2002, 2005; Hudson *et al.* 2006). This is because a typical parasite life cycle may include fish (or bird) definitive hosts and several intermediate invertebrate hosts, and for the parasite to survive, all hosts must co-occur in a stable community structure (Marcogliese and Cone, 1997). Consequently, it is generally accepted that the diversity and stability of the host community, primarily that of the definitive hosts, should impose significant restrictions on species composition of local parasite communities (Rohde, 1993; Combes, 2001; Poulin, 2007).

On the other hand, abiotic variables affect the biotic variables, and the interaction between abiotic and biotic variables may be the actual agent of parasite community composition. Indeed, variables such as lake size, water pH and distance between lakes have been associated with the diversity of parasite species in host populations, or with the mean abundance of parasites within given hosts (Kennedy, 1978; Karvonen *et al.* 2003; Simkova *et al.* 2003). Further, there is evidence that seasonal variability in water temperature drives parasite population cycles in temperate and tropical areas (Chubb, 1979; Rohde, 1993). At even smaller spatial scales, there is evidence that water flow rate in streams alters parasite populations in fish (Janovy *et al.* 1997; Marcogliese, 2001). Additionally, heteroxenous endoparasites are highly susceptible to abiotic conditions through the elimination or reduction of potential intermediate hosts (Poulin, 1992), and direct effects on the population dynamics of definitive hosts (Moller, 1987). However, there is no general consensus on the importance of abiotic effects on parasites, and the

majority of studies that consider abiotic variables show trends that are positive, negative or neutral depending on the abiotic variable and the parasite taxa (Khan and Thulin, 1991; Poulin, 1992; MacKenzie *et al.* 1995; Valtonen *et al.* 1997; Ondrackova *et al.* 2004; Marcogliese, 2004, 2005).

In this study, we compare the relative importance of abiotic and biotic factors that contribute to the presence of three complex life cycle parasites in a sentinel fish species, *Fundulus heteroclitus*, using a hierarchical classification tree analysis. We consider *F. heteroclitus* (common killifish) a sentinel fish because it is a highly abundant resident marsh species (Lotrich, 1975) along the east coast of North America (Relyea, 1983), and likely plays an important role in marsh food webs. Furthermore, the common killifish was selected for this study because its parasite fauna is well known in New Jersey (Anderson and Sukhdeo, unpublished data) and it is known to harbour multiple heteroxenous parasites (Harris & Vogelbein, 2006). Thus, the presence of parasite species within the common killifish is likely to be sensitive to both biotic and abiotic conditions.

To include a wide range of differences in biotic and abiotic parameters for our analyses, we used a system of estuarine salt marshes located in the Hackensack Meadowlands estuary complex in New Jersey USA, each with distinct host diversity, abundances and variation in abiotic conditions. Classification tree analysis is a non-parametric technique that hierarchically partitions a data set using dichotomous criteria based upon multiple predictor variables (Breiman *et al.* 1984; De'Ath and Fabricius, 2000) was used to separate the relative effects of biotic and abiotic variables. The output generated is similar to other regression techniques in that it explains the variation of a

single response variable through one or more explanatory variables with the added advantage of the predictor variables being assigned a hierarchical order. Trees are constructed by repeatedly splitting the data using a simple rule based on a single explanatory variable. The products of each split are two mutually exclusive groups, each of which as homogenous as possible. A major advantage of this analysis technique is that it does not rely on the assumptions that are required for the appropriate use of parametric statistics (i.e. Gaussian distribution of predictor variables). Further, regression tree analysis is not restricted by linearity in predictor and response variables or by multicollinearity in predictor variables. In doing this analysis we are able to construct a hierarchical tree that documents the relative importance of abiotic and biotic variables in the presence of parasite populations.

Our *a priori* hypothesis was that the presence of complex life cycle parasite populations would be dependent on the presence of competent host species. Specifically, we predicted that: (1) definitive host presence will be the most important factor (i.e. primary explanatory variable) in determining parasite presence; and (2) intermediate host presence will be assigned a secondary position in the analysis hierarchy.

Methods

Characterisation of study sites

Sampling occurred within four salt marshes in the New Jersey Hackensack Meadowlands. These marshes reflect a gradient in time since restoration and a gradient in community diversity: Mill Creek Marsh (20 years since restoration), Harrier Meadow (10 years since restoration), Secaucus High School Marsh (0 years) and Oritani Marsh

(unrestored). Mill Creek marsh (20 year) is a 57-hectare tidal marsh bordered by highways and residential land (40°47'45'' N, 74°02'30'' W). Harrier Meadow marsh (10 year) is a 32-hectare tidal marsh surrounded by tidal mudflats and urban development (40°47'12'' N, 74°07'3'' W). Secaucus High School marsh (0 year) is a 43-hectare tidal marsh bordered by a river and residential development (40°48'17'' N, 74°02'52'' W). Oritani marsh (unrestored) is a 224-hectare tidal marsh that has no record of human alteration or use (40°47'57'' N, 74°05'07'' W). Though this marsh is much larger than the others, more than 150 hectares are upland area, and a smaller area (~70 hectares) consists of high and low marsh with small tidal channels, making it of similar size to the other marshes.

Free-living community data including species abundances were collected from the literature for birds (Seigel *et al.* 2005; Seigel, 2006; pers. comm.), fishes (Bragin *et al.* 2005; pers. comm.) and benthos (Yuhas, 2001; Yuhas *et al.* 2005; pers. comm.). To control for the influence of abundant species relative to rare species, all species abundances were square root transformed. To determine variation in the compositional structure of the host community between sites, we used non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index. Ordination was implemented using the software PC-ORD version 5 (McCune and Mefford, 2002) with 500 iterations and 250 runs of both real and randomized data. Abiotic parameters for each marsh were recorded at continuous water monitoring stations located at each of the four marshes. Water monitoring stations consisted of Yellow Springs Instruments Model 6600 multiprobes: these probes were configured to measure abiotic water parameters, at approximately 1.0 m depth. The predictor variables used in this analysis are listed in

Table 1. Predictor variables included the square root transformed abundance of each potential host species in the marsh (benthic invertebrates, fishes, birds), dissolved oxygen, acidity, specific conductance, temperature, salinity, heavy metals and turbidity.

Fish sampling and examination for parasites

A sentinel fish, *Fundulus heteroclitus* (common killifish), and its helminth parasite community were measured every three months starting in December 2005 and ending in December 2007 (eight contiguous seasons: two fall, two spring, two winter, two summer). Fish were collected using a 4 mm seine and baited minnow traps; all habitats within each marsh were sampled for at least 5 days each season. From each seasonal collection, fifteen fish were euthanized and immediately necropsied. Fish necropsy was done using standard parasitological techniques. Helminth parasites collected during necropsy were identified using parasitological keys (Yamaguti, 1958; Schell, 1970; Schmidt, 1970; Anderson *et al.* 1974) and primary literature (Harris and Vogelbein, 2006).

Data analysis

Classification and regression tree analysis was performed using the software platform JMP Version 7.0.1 (2007 SAS Institute). We selected three representative parasite species (an acanthocephalan *Paratenuisentis ambiguous*, a nematode *Contracaecum* sp. and a trematode *Ascocotyle diminuta*) for this analysis based upon three factors: (1) we wished to address the abiotic and biotic factors important in the presence/absence of complex life cycle parasites; (2) these complex life cycle parasites

were prevalent enough to warrant statistical inference; and (3) these three species occurred at each of our sites. The criterion used for selecting the splits on the nodes was set to ‘Maximise Split Statistic’. This split selection examines all possible splits for each predictor variable at each node. Missing values in our data were assigned ‘Closest’ and the minimum split size was set to five. We used a k -fold cross-validation procedure to determine the optimal tree size. This process divides the data into a number of mutually exclusive subsets (k subsets) of approximately the same size and builds a series of trees using 90% of the available subsets and uses them to predict the response for the omitted subset(s). It subsequently calculates the error for each tree as the sum of the squared differences between observed trees and predicted trees; for each tree, we ran a series of 10-fold cross-validations and chose the best tree size using the 1-SE rule (Breiman *et al.* 1984; De’Ath and Fabricius, 2000). Trees are represented graphically, with the root node representing undivided data at the top, and the branches and leaves (each leaf represents a final grouping) beneath.

We further explored relationships within the data using alternative splits and surrogate variables. For each of the splits in the data, we compared the strengths of the split due to the selected variable with the best splits of each of the remaining predictor variables. A strongly competing alternative variable was substituted for the original variable to determine whether a tree could be simplified or the number of predictor variables be reduced. Often surrogate variables will give the best alternative split; consequently we generated trees using surrogate variables. Should surrogate variables generate trees in accordance with the tree generated by the primary splitting variable, it is

plausible to state that they are equally important in determining the presence/absence of the response variable.

Results

A total of 480 sentinel fish were necropsied: 15 collected in each of the eight seasons between 2006-07 in each of the 4 marshes. Host species richness was 71 spp. in Oritani marsh, 87 spp. in Secaucus marsh, 112 spp. in Harrier marsh and 122 spp. in Mill Creek marsh. These marshes had significantly different benthic, fish and bird communities with regards to abundance and similarity as measured by non-metric multidimensional scaling analyses. Non-metric multidimensional scaling analyses of birds ($r^2=0.81$, stress value=0.08), fishes ($r^2=0.82$, stress value=0.09) and benthic macroinvertebrates ($r^2=0.82$, stress value=0.07) showed distinct separation in communities between each of the four marshes sampled. Within our sentinel species, eleven taxa of metazoan parasites were identified including the nematodes *Dichelyne bullocki* and *Contracaecum* sp.; the digenean *Lasiotocus minutus* and metacercaria of *Ascocotyle diminuta*, *Mesostephanus appendiculatoides*, *Posthodiplostomum minimum*; monogeneans *Fundulotrema prolongis* and *Swingleus ancistrus*; acanthocephalans *Paratenuisentis ambiguous* and *Southwellina hispida* (cystacanth); the copepod *Ergasilus funduli*. These taxa infected more than 70% of the killifish examined and parasite intensity per host ranged from 1 to 127.

Of the aforementioned parasite species, only three complex life-cycle parasites, a trematode *A. diminuta*, an acanthocephalan *P. ambiguous*, and a nematode *Contracaecum* sp., were present in all four sites and of sufficiently high prevalence to warrant statistical

inference. Consequently, for these three parasite populations, we constructed classification trees that assigned each of the 480 host observations of parasite presence/absence to terminal leaf nodes: these terminal leaf nodes categorise broad-scale controls on the establishment of these parasite populations in our salt marsh system. Using a cross-validation procedure (*sensu* Breiman *et al.* 1984) we obtained estimates of prediction error for trees of a given size (Figures 1b, 2b, 3b). The best tree size was taken as the smallest tree such that its prediction error rate is within one standard error of the minimum (Breiman *et al.* 1984). For the trematode *A. diminuta*, cross-validation using the 1-SE rule determined the optimal tree size as a five-leaf tree (Figure 1b), and 9-leaf trees for the acanthocephalan *P. ambiguous* (Figure 2b) and the nematode *Contracaecum* sp. (Figure 3b). The tree selected for *A. diminuta* explained 31% of the variance in the data and the trees selected for *Contracaecum* sp. and *P. ambiguous* explained 36% and 30% of the variance respectively. These r^2 values are acceptable given that our initial analyses included 184 predictor variables.

The first split within the *A. diminuta* tree is the abundance of the amphipod, *Gammarus* sp. Receiver operating characteristic (ROC) curves, which plot the proportion of correct classifications, demonstrate that a test model including the predominant predictors classified 80.1% of the host observations as infected or uninfected correctly. Though the optimal tree size for *A. diminuta* (Figure 1a) included a series of abiotic parameters (pH and conductance) that split the data into progressively more homogenous leaf nodes, the discriminatory power of these secondary predictors was relatively low (less than 15%: Table 2). Surrogate variables were examined to better understand the relative effects of these biotic and abiotic variables. In the classification

of *A. diminuta*, a suite of benthic invertebrates (oligochaetes, *Hobsonia florida*, *Melampus bidentatus*, *Balanus improvisus*) and one fish species (the American shad *Alosa sapidissima*) were strong surrogates for *Gammarus* sp. and provided classification trees in accordance with Figure 1a. For example, dropping the abundance of *Gammarus* sp. from the *A. diminuta* model resulted in the same five-leaf tree with the same splitting criteria and it explained only marginally less of the variance in the data (31% vs. 30%).

The optimal tree selected for the acanthocephalan *P. ambiguous* (Figure 2a) partitioned the data into two main branches based on the abundance of harpacticoid copepods, followed by the abundance of an invasive mussel species (*Mytilopsis leucophaeta*) and then a series of abiotic variables (conductivity, pH, the heavy metals cadmium and chromium, and salinity). ROC curves, demonstrated that a test model including the predominant predictors classified 71% of the host observations as infected or uninfected correctly. The relative discriminatory power for the primary splitter variables (Table 2) used in *P. ambiguous* revealed an increased importance of abiotic parameters, with salinity (53.66%) and conductance (41.95%) playing a similarly important a role as the secondary biotic variable, *M. leucophaeta* (40.25%). In the classification of *P. ambiguous* host infection status, the primary splitter (harpacticoid copepod abundance) had strong surrogates in three families of fly larvae (Empididae, Ceratopogonidae and Tipulidae), a polychaete (*Glycera* sp.), and an unidentified species of amphipod. The surrogates for the secondary splitter, *M. leucophaeta*, were a diverse group of benthic invertebrates (*Littorina* sp., *Macoma* sp., *Corophium* sp. and *Nereis succinea*).

The optimal 9-leaf tree that described the presence of *Contracaecum* sp. (Figure 3a) partitioned the data on the common periwinkle, *Littorina* sp., and then a series of abiotic parameters (conductance, turbidity, pH, temperature and salinity). Relative discriminatory power (Table 2) ranked the important variables to *Littorina* sp. (100%), conductance (81%) and salinity (59%). Using ROC curves, the infection status of the common killifish was correctly determined 67% of the time. The primary predictor splitter in the *Contracaecum* sp. classification tree, *Littorina* sp., had surrogates of two polychaete species (*N. succinea*, *Streblospio benedecti*) and three benthic invertebrates (*Macoma* sp., Nemertea, *Palmacorixa* sp.): in the case of *P. ambiguous* and *Contracaecum* sp. the biotic surrogates provided classification trees in accordance with those presented in Figure 2a and 3a.

Where the surrogates and alternative splits for biotic variables were strong, the surrogates and alternative splits for abiotic parameters included in the models for each of the three species were considerably weaker and showed no consistent pattern when removed from analyses. The only consistent trend being that abiotic parameters seemed to be collinear i.e. temperature was collinear with dissolved oxygen and pH, conductance was collinear with salinity and pH.

Discussion

In this study, we constructed hierarchies of biotic and abiotic variables that contribute to the success of three representative complex life cycle parasite populations. The key insight provided by our analyses is that a diverse benthic community is more important in determining parasite presence within our sentinel fish than the presence of

competent hosts. This is not to say that parasites exist without hosts, but that free-living groupings of organisms are more likely to support competent hosts. Other studies have differed, reporting strong positive relationships between parasite community diversity and the diversity of bird definitive hosts (Smith, 2001; Hechinger and Lafferty, 2005) and large benthic host invertebrates (Hechinger *et al.* 2007). Our data does not support this pattern. Competent hosts were less important in determining parasite presence than non-host benthic invertebrates in our analyses. Thus, our data suggest that it is not simply the presence of competent host species, but the context in which the trophic interaction between fishes and birds, or crustaceans and fishes, occurs that is necessary for the successful completion of each parasite's life cycle.

Earlier studies, largely using digeneans, have elegantly demonstrated the effects of intermediate host density and contact rates on parasite population dynamics (Marcogliese *et al.* 2001; Sandland *et al.* 2001). These studies complemented earlier evidence that abiotic factors such as water flow rate and temperature may affect the success of parasite infective stages (Stables and Chappell, 1986; Janovy *et al.* 1997). Further, other studies have correlated the physical structure of the ecosystem (i.e. habitat characteristics such as character of the lake or river bottom, presence or absence of macrophyte vegetation) and the abundance of the digenean *Diplostomum* spp. in fish hosts (Marcogliese *et al.* 2001). However, there is only one study (Ondrackova *et al.* 2004) that attempted to explain the presence of a parasite species with all potential predictor variables (i.e. intermediate and definitive hosts, community structure of the fish community, and habitat characteristics). Much like Ondrackova *et al.* (2004), the advantage of our study is that it considers a broad suite of abiotic and biotic variables.

However, in addition to identifying predictor variables that correlate with the presence of certain parasite species, our method also provides a hierarchical ranking of the relative importance of each variable.

Classical regression techniques used in abiotic and biotic parasite studies (e.g. Ondrackova *et al.* 2004) assume that interactions are linear or additive and that the specified models describing interactions are realistic. In contrast, the classification analyses we use provides a flexible relationship between predictor variables, allows for missing values, is not sensitive to multicollinearity and controls for outliers in the data (Breiman *et al.* 1984; De'Ath and Fabricius, 2000). For instance, outliers have little influence on splitting because they are partitioned into unique subsets during analysis. In addition, missing values are estimated using surrogate predictor variables so that missing predictor data does not influence the decision tree output. Furthermore, the relative discriminatory power for each predictor may also be determined (Table 2) while the comparison of relative discriminatory power is not possible in classic multivariate analyses. Classification tree analysis flexibility and power has seen the technique become popular in environmental science studies (e.g. Rothwell *et al.* 2008), ecology (e.g. De'Ath and Fabricius, 2000) and has been implemented to describe risk factors in malaria transmission (Thang *et al.* 2008).

The analyses we present suggest that the presence of three complex life cycle parasites in *F. heteroclitus* is primarily the result of a diverse community of benthic invertebrates. In each of the hierarchical displays of dichotomous decision criteria the abundance of benthic invertebrates is the most important factor. It should be noted that the invertebrates need not be intermediate hosts, and each of the non-host invertebrates

had multiple non-host invertebrate surrogates (i.e. a diverse assemblage of benthic invertebrates), and this occurred with both autogenic and allogenic parasite species in our system. Autogenic parasite species complete their entire life cycle within the confines of an aquatic system, whereas allogenic species use hosts that are outside of the aquatic environment e.g. bird or mammal definitive hosts (Esch *et al.* 1988). Our results challenge a central tenet in parasite ecology, that the diversity and abundance of definitive and intermediate hosts determines the diversity and abundance of the parasite community (Smith, 2001; Hechinger and Lafferty, 2005), whereas we found these parasite populations were most dependent on the presence of a broad group of non-host benthic macroinvertebrates. From classic studies, evidence suggests that autogenic parasite species are strongly influenced by the trophic ‘condition’ of the ecosystem (Wisniewski, 1958; Chubb, 1963; Esch, 1971). As an example, Esch (1971) demonstrated that decreased trophic interactions in oligotrophic lakes resulted in an increase in the presence of adult parasites and fewer larval stages than in eutrophic lakes. On the other hand, in allogenic species where trophic limitation is not evident, the density of intermediate hosts, and frequency of contact between definitive and intermediate hosts (a function of population size of susceptible individuals) are thought to be the most important variables (Janovy *et al.* 1997; Marcogliese, 2001; Bagge *et al.* 2004; Ondrackova *et al.* 2004).

We found no association between the abundance of competent hosts and the success of complex life cycle parasites in our sentinel fish. Our data does not include competent intermediate or definitive hosts as primary splitters but it is likely that a high diversity of benthic invertebrates drives the diversity of fishes, which generates a high

diversity of birds. Whittaker (1972, 1975) presented two different mechanisms by which community diversity may be realized, either diversity begets diversity (e.g. Murdoch *et al.* 1972; Rosenzweig, 1995) or that diversity is limited by niche saturation (e.g. MacArthur and Levins, 1967; Lawlor, 1980; Wilson *et al.* 1987). Niche saturation is unlikely to be a consideration in our salt marsh system because host community species diversity increases with time post-restoration in our study. Diversity creating more diversity is a more likely mechanism operating within our system. If consumers are to some extent specialized on prey items, whether plant or animal, more consumers will occur in systems with more 'prey' species. Diversity at lower trophic levels providing resources and driving diversity at higher trophic levels has been demonstrated (Hutchinson, 1959) and positive correlations exist between the species richness of producers and consumers (e.g. Murdoch *et al.* 1972; Brown, 1995; Rosenzweig, 1995). It is then plausible that the diversity evidenced in our benthic invertebrate community, reflected in its status as a primary splitter and multiple strong invertebrate surrogates, might be a cause of diversity at higher trophic levels.

A cascading effect of free-living diversity at lower trophic levels supporting free-living diversity at higher trophic levels is of particular importance for complex life cycle parasites. This is because high diversity systems have a greater probability of including species necessary for the successful completion of the life cycle (Hudson *et al.* 2006; Lafferty *et al.* 2008). This situation is analogous to experiments on, and observations of, ecosystem productivity and community dynamics in relation to species diversity. In marine systems, highly diverse communities are more likely to include individual species that have disproportionate effects on community dynamics (Paine, 1966; Sala and

Knowlton, 2006). Further, the likelihood of encountering a competent host is similar to the sampling effect observed in biodiversity-ecosystem functioning studies (Loreau *et al.* 2001). It is therefore plausible to state that a diverse free-living community not only increases the diversity of parasite community because of simple addition of hosts that act as habitat and dispersal agents, but also because the probability of encountering a suitable host is increased.

It has been argued that complex life cycle parasites rely on stable trophic links (Marcogliese and Cone, 1997), and trophic stability is likely a consequence of a diverse, and functioning ecosystem (Hudson *et al.* 2006; Tilman *et al.* 2006; Allesina and Pascual, 2008). Thus, the presence of benthic invertebrates as the most important factor in determining the presence of parasites likely reflects a robust ecosystem that can support multiple parasite life cycles (Huspeni and Lafferty, 2004; Hudson *et al.* 2006). It is logical to assert that stable communities of free-living organisms provide parasites with predictable host resources to exploit (Rohde, 1993; Combes, 2001; Poulin, 2007) because host species will experience fewer fluctuations in abundance, or vary in a predictable manner (i.e. cyclically). For example, stable predator-prey trophic links between host species are a requirement in trophic transmission, and parasites with multiple hosts exploit the stability of ecosystems to ensure successful transmission (Marcogliese and Cone, 1997; Sukhdeo and Hernandez, 2005). There is a growing body of empirical data that suggests that diverse communities provide for more predictable dynamics. Studies of marine sessile invertebrates and seaweed (Stachowicz *et al.* 2002; Allison, 2004), crustaceans (Duffy *et al.* 2003) and predators (Byrnes *et al.* 2006) have suggested that a more diverse assemblage of species provides for higher ecosystem productivity and

greater resilience to perturbation. Recent evidence also suggests that highly diverse communities exhibit species redundancy (Levin, 1999) so that species richness provides a reservoir of biological options that ensure ecosystems can respond to perturbation without failure; this phenomenon has been empirically validated (Naeem and Li, 1997; Yachi and Loreau, 1999; Tilman *et al.* 2006). Although there is still debate on the mechanisms driving these patterns, it appears that a diverse mix of species in ecosystems reduces fluctuations of ecosystem properties (Loreau *et al.* 2001; Tilman *et al.* 2006).

The classification tree analyses also reveals that abiotic parameters act as a secondary filters, most probably because invertebrate communities are very susceptible to abiotic conditions (Gasith and Resh, 1999; Hart and Finelli, 1999; Yuhas *et al.* 2005). There is considerable evidence that abiotic variables can drive parasite population dynamics indirectly through their impact on benthic invertebrate communities (Zander and Reimer, 2002: see review in Marcogliese, 2005). An elegant example of this was reported by Esch and colleagues (Esch *et al.* 1986; Marcogliese *et al.* 1990), whereby the factors driving the abundance and prevalence of a digenean parasite in its mayfly intermediate host were analysed. These data revealed that superficially the spatial coincidence of competent hosts (mayflies and sphaeriid clams) determined the prevalence and intensity of infection. However, it was determined that the patterns of spatial coincidence of hosts were determined by lake eutrophication. Though our data do not show a causal relationship between abiotic parameters and the presence of benthic invertebrates, it does suggest that abiotic conditions act as a secondary filter in the presence of three parasite populations.

In our study, we used a non-parametric classification tree technique to hierarchically link biotic and abiotic factors to the presence of three complex life cycle parasites. In doing so, we demonstrate that the most important predictor in the presence of a parasite species is the benthic invertebrate community. We suggest that this occurs because a diverse community is more likely to contain competent host species. Further, we suggest that a consequence of a highly diverse community is an increased likelihood for the existence of stable trophic links that parasite species may exploit.

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Figure 3.1 (a) Classification tree and decision criteria for predicting the presence or absence of *Ascocotyle diminuta* in the killifish, *Fundulus heteroclitus*. Decision criteria, split size and infection status (percentage infected in black, uninfected in white) are identified. (b) Cross-validation relative error plots for a single 10-fold cross-validation including 1-SE estimates for each tree size. Under unstratified cross-validation, a tree size of five is selected using the 1-SE rule: the best tree size was taken as the smallest tree such that its prediction error rate is within one standard error of the minimum.

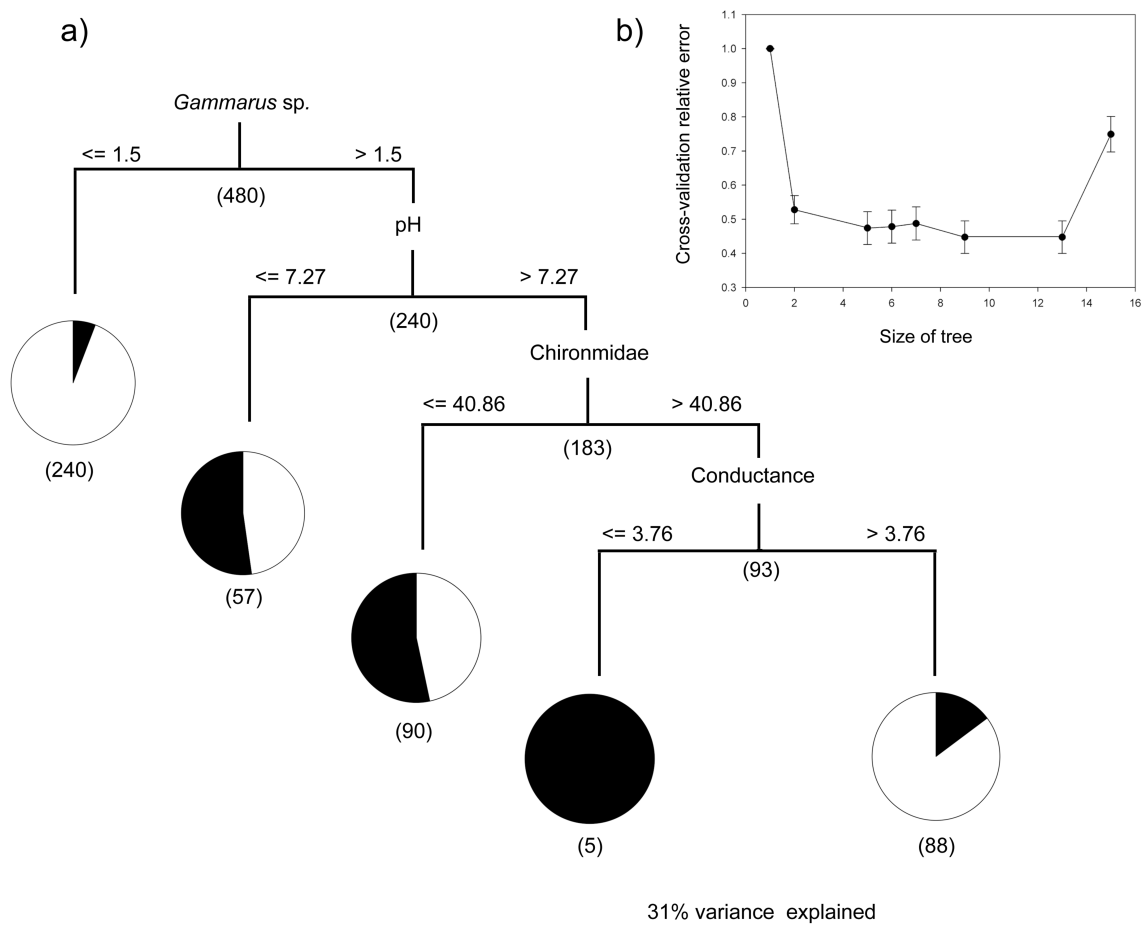


Figure 3.1

Figure 3.2: (a) Classification tree and decision criteria for predicting the presence or absence of *Paratenuisentis ambiguous* in the killifish, *Fundulus heteroclitus*. Decision criteria, split size and infection status (percentage infected in black, uninfected in white) are identified. (b) Cross-validation relative error plots for a single 10-fold cross-validation including 1-SE estimates for each tree size. Under unstratified cross-validation, a tree size of nine is selected using the 1-SE rule: the best tree size was taken as the smallest tree such that its prediction error rate is within one standard error of the minimum.

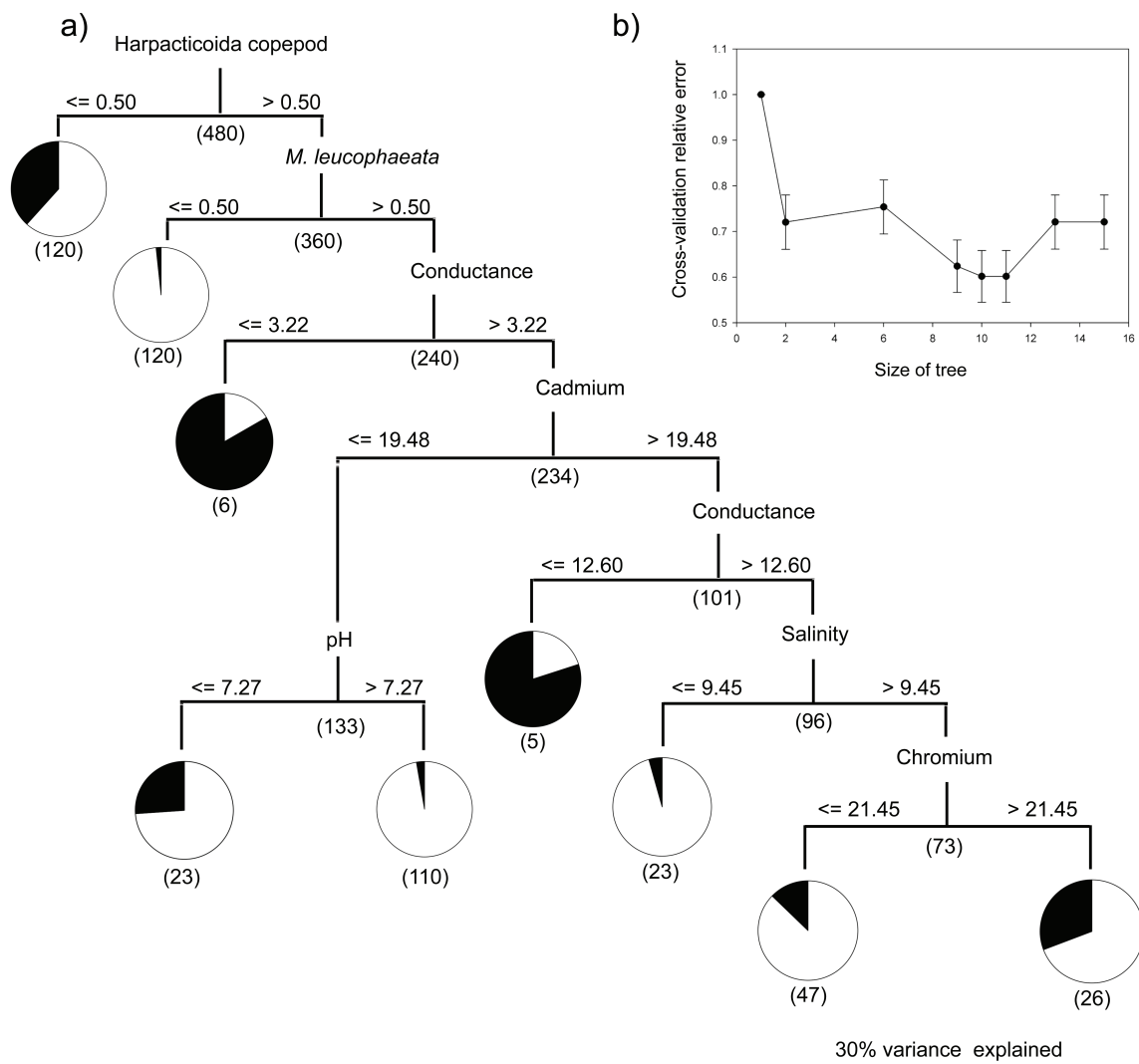


Figure 3.2

Figure 3.3: (a) Classification tree and decision criteria for predicting the presence or absence of *Contracaecum* sp. in the killifish, *Fundulus heteroclitus*. Decision criteria, split size and infection status (percentage infected in black, uninfected in white) are identified. (b) Cross-validation relative error plots for a single 10-fold cross-validation including 1-SE estimates for each tree size. Under unstratified cross-validation, a tree size of nine is selected using the 1-SE rule: the best tree size was taken as the smallest tree such that its prediction error rate is within one standard error of the minimum.

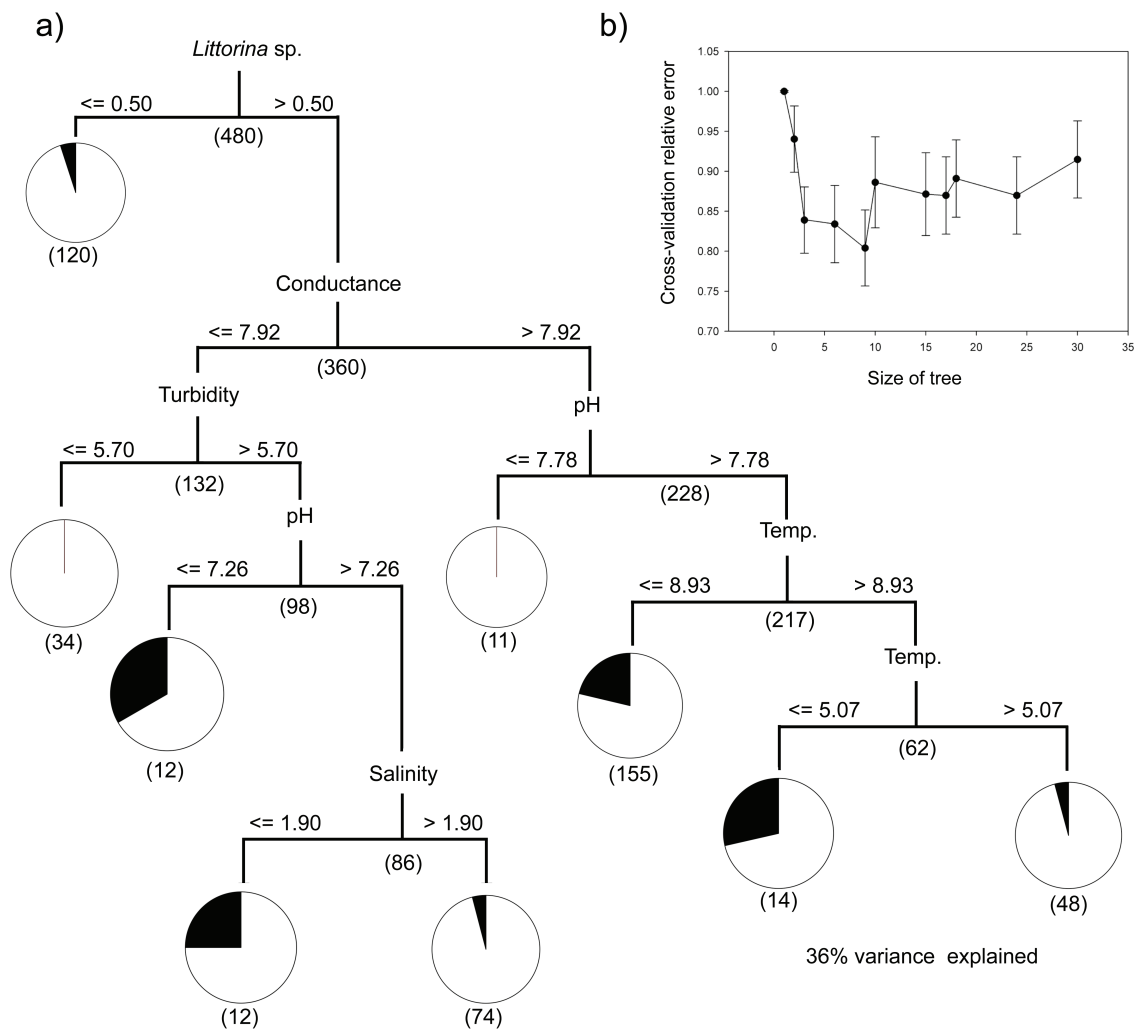


Figure 3.3

Table 3.1: Predictors used in model building

Code	Description	Units	Range
Benthos	Species of benthic invertebrates by site	Square root of species abundance	0 – 233.31
Fishes	Species of fishes by site	Square root of species abundance	0 – 44.07
Birds	Species of birds by site	Square root of species abundance	0 – 84.60
Season	Fall, Winter, Spring, Summer	None	
Site	Parasite presence/absence	Oritani, Secaucus, Harrier, Mill Creek	
DO	Dissolved oxygen	mg/L	1.10 – 15.40
Conductance		mS/cm	0.47 – 28.30
Temperature		Deg C	1.80 – 35.10
Salinity		ppt	0.40 – 17.40
pH		SU	5.88 – 8.02
Turbidity		NTU	3.00 – 42.40
Lead		µg/L	7.18 – 581.20
Zinc		µg/L	14.40 – 693.00
Cadmium		µg/L	0.10 – 73.90
Chromium		µg/L	2.53 – 229.70
Copper		µg/L	3.20 – 99.90
Iron		µg/L	0.00 – 2402.00

Table 3.2: Ranking of factors contributing to infection status of *Fundulus heteroclitus* for complex life cycle parasites by overall discriminatory power. Only variables representing primary splitters are presented.

Parasite taxa	Variables	Power
<i>Ascocotyle diminuta</i>	<i>Gammarus</i> sp.	100.0
	Chironomidae	15.96
	Conductivity oxygen	13.33
	Salinity	10.28
	pH	8.03
<i>Paratenuisentis ambiguous</i>	Harpacticoida	100
	Salinity	53.66
	Conductivity	41.95
	<i>Mytilopsis leucophaeata</i>	40.25
	pH	28.41
	Cadmium	35.29
	Chromium	12.49
<i>Contracaecum</i> sp.	<i>Littorina</i> sp.	100.0
	Conductivity	80.72
	Salinity	58.86

CHAPTER 4

Community stability threshold in parasite establishment and persistence in estuarine marshes.

Abstract

This study investigates the relationship between stability of host communities and the establishment and subsequent diversity patterns of parasite communities. The colonization of naïve killifish, *Fundulus heteroclitus*, by parasites was measured in caged killifish within four distinct salt marsh areas. These sites represented a gradient in host species diversity ($H = 0.29, 0.31, 0.33, 0.37$) and time since major disturbance (unrestored, 0 year, 10 year, 20 year respectively). Killifish were held in cages for 14 weeks at each site to allow parasite infracommunities to establish: cages were sampled weekly ($n = 600$ over the study). Species accumulation curves demonstrate that the diversity of the parasite community and the rate at which species are accumulated were similar for the unrestored and two restored marsh sites (10 and 20 years). The killifish parasite community in the 0 year marsh site was restricted to directly transmitted parasite species. To explain the paradox of a low diversity, highly invaded salt marsh having the same parasite community as highly diverse restored marsh sites we constructed community matrices with randomly determined interaction coefficients to assess community stability. We find a correlation between system stability and parasite species richness in our sentinel fish species. This suggests a role for host community stability in parasite community assembly because stable trophic relationships are required for complex parasite life cycle persistence.

Key-words: Complex life cycle; Food web; Stability; Species accumulation curves

Introduction

Parasites are considered to be ubiquitous components of ecosystems and it is estimated that the trophic strategy represents more than 50% of potential interactions in food webs (Price 1980; de Meeus & Renaud 2002; Lafferty *et al.* 2006). The recognition of their importance has led to studies on their role in regulating competition and predation (Hatcher *et al.* 2006), community structure (Dobson & Hudson 1986; Wood *et al.* 2007; Hernandez & Sukhdeo 2008), trophic relationships (Marcogliese 2002) and ecosystem energy flow (Mouritsen & Jensen 1994; Kuris *et al.* 2008). These studies are nested within a growing body of evidence (Thomas *et al.* 2005; Collinge & Ray 2006) that suggests that parasite species diversity is positively related to ecosystem functioning. It is generally accepted that ‘stable’ ecosystems that have a structured organization and which are resilient to change are those that are rich in parasites (Hudson *et al.* 2006; Dobson *et al.* 2008). In this study, we address whether complex life cycle parasites require a stable system in order to persist.

Complex parasite life cycles are dependent on trophic interactions, and appear to rely on the stability of those interactions (Marcogliese 2002; Sukhdeo & Hernandez 2005). Though ecosystems are thought to be constantly in flux (Holling 1973; May 1977; Heffernan 2008), the continuum of species compositions and alternate states that exist are likely the consequence of long evolutionary and co-evolutionary processes between plants and animals (May 1973; Thompson 1994). It is plausible that over time, the component parts of communities result in configurations that endow systems with long-term stability, provide systems with predictable dynamics, and that are shaped by a limited number of biological processes (May 1973; Pimm 1982). For parasites, the

structured and stable nature of host communities is an essential resource (Combes 2001; Thompson *et al.* 2005; Poulin 2007). The selective pressure to ensure transmission has resulted in parasite life strategies that are integrally coupled with host species and which are dependent upon the long-term stability of systems (Marcogliese & Cone 1997; Sukhdeo & Hernandez 2005; Poulin 2007). The host, thus, is not only exploited as an energy source but as an essential habitat (Poulin 2007). As a result the dynamics of the host population will necessarily be reflected in the dynamics of the parasite population. A logical extension of this premise is that complex life cycle parasites will only be present when a system is in a stable configuration (Marcogliese & Cone 1997; Sukhdeo & Hernandez 2005; Lafferty *et al.* 2008).

Parasite and host population dynamics are tightly entwined (Grenfell & Dobson 1995; Poulin & Thomas 1999), and this has been exploited in the use of parasites as biological tags (e.g. Manel *et al.* 2002; Criscione *et al.* 2006) and indicators of system restoration (Huspeni & Lafferty 2004). However, very few studies consider the impact of host community dynamics upon the parasite community (reviewed in Lafferty *et al.* 2008). In addition, community level studies largely restrict themselves to the nature of the relationship between the diversity of hosts and the diversity of the parasite community (Smith 2001; Hechinger & Lafferty 2005; Chen *et al.* 2008). Thus, there is no empirical evidence to support the stability of the host community as a requirement for the persistence of parasite communities (Combes 2001; Thompson *et al.* 2005; Dobson *et al.* 2008).

Stable states in ecological systems are likely the result of feedbacks that result in compositions of species that correspond to stable equilibria (Petraitis & Latham 1999;

Didham *et al.* 2005). These systems may arise from differences in the sequence of species colonization (reviewed in Samuels & Drake 1997; Chase 2003) or differences in a series of factors including productivity (Chase 2003; Fukami & Morin 2003), predation (Morin 1984; Louette & De Meester 2007), dispersal rate (Lockwood *et al.* 1997), or ecosystem size (Fukami 2004). A more consistent pattern in alternate stable states is the effect of disturbance (Scheiffer *et al.* 2001; Chase 2003; Heffernan 2008), and it has been argued by Didham *et al.* (2005) that systems with severe abiotic disturbance regimes are more likely to exhibit multiple states. Though much of this work has been observational with confounding factors, work conducted in areas that experience significant disturbance regimes such as salt marshes (e.g. Srivastava & Jefferies 1996; van de Koppel *et al.* 2005) presents compelling evidence for alternate community stable states.

To understand the consequence of system stability on complex parasite life cycles, we report the results of a field experiment that manipulated the infection status of a sentinel fish species within four salt marshes. We addressed the following questions: (1) Are complex life cycle parasites a ubiquitous component of food webs in sites along a gradient of time after major disturbance? (2) How does the rate and trajectory of parasite accumulation vary across host diversity gradients? (3) Does host stability provide insight into the dynamics of the parasite community? To address these questions, our field experiment was based in the salt marshes of New Jersey that represented a natural disturbance regime; this was reflected in time post restoration and a gradient in species diversity. We report that complex life cycle parasites are not an ever-present component of salt marsh systems. Second, we demonstrate that stability in the network of host trophic interactions limits the establishment and persistence of complex life cycle

parasites. These data reveal how parasite transmission may respond to changing environmental conditions, a pressing concern in ecology given increasing environmental stress and human-mediated perturbation of ecosystems (Lafferty 2009).

Methods

Defining the study system

We conducted our study of parasite establishment in a sentinel host species within an area where over 90% of estuarine marshes are heavily impacted due to decades of anthropogenic disturbances (Tiner *et al.* 2002). Recent large-scale restoration projects with the goal to recreate ‘pristine’ New-England type salt marshes have created spatially delineated habitats reflecting a gradient in time since restoration: Mill Creek Marsh (20 years), Harrier Meadow (10 years), Secaucus High School Marsh (0 years) and Oritani Marsh (unrestored). Data on the host community data was extracted from the literature for birds (Seigel *et al.*, 2005; Seigel 2006; pers. comm.), fishes (Bragin *et al.* 2005; pers. comm) and benthos (Yuhas 2001; Yuhas *et al.* 2005; pers. comm). To determine variation in the compositional structure of the host community between sites, we used non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index. Bray-Curtis coefficients were based on host species abundances; to control for the influence of abundant species relative to rare species all species abundances were square-root transformed. Ordination was implemented using the software PC-ORD version 5 (McCune & Mefford 2006) with 500 iterations and 250 runs of both real and randomized data. NMDS checks for the structure of the matrix in a two-dimensional ordination space

producing a measure of goodness-of-fit: the adequacy of NMDS is contingent upon stress values <0.3 .

Field collections

We use a sentinel species, the common marsh killifish *Fundulus heteroclitus*, and its parasite community to assess the impact of community stability on parasite establishment. In our marshes, the host community (birds, fishes, mammals) potentially transmits 11 species of helminth parasites to the killifish (Anderson & Sukhdeo, unpublished data). Further, this fish is a highly abundant resident marsh species (Lotrich 1975) along the east coast of North America and likely plays an important role in marsh food webs (Relyea 1983). We collected approximately 2000 fish from Kingsland Impoundment, a marsh area abutting our Harrier Meadow site. Upon capture, killifish were held in plastic cattle watering tanks (1.52 m in diameter and 0.61 m deep: containing ~1000 L of water pumped from Kingsland Impoundment) for 7 days and we subjected the killifish to a series of anthelmintic treatments. Fish were treated for 5 consecutive days with the addition of metronidazole, praziquantel, levamisole and piperazine in standard concentrations to the cattle watering tanks (Bishop 2004). Following treatment, fish were held in recovery tanks for 2 days. Prior to stocking field cages at each site, 30 fish ($n = 120$ total necropsied) were removed from the recovery tank and dissected to ensure the treatment process was effective and establish a time zero parasite community value.

Three cages (2.4 m long, 2.4 m wide, and 1.5 m deep) were placed in each of the four marsh sites. Each cage was made of plastic-coated galvanized wire panels with 1 cm

mesh, this allowed for water flow and benthic macroinvertebrate colonization but excluded predators. Cages were placed in marsh sites two weeks prior to stocking them with fish. Following our fish treatment and recovery regime, we stocked each cage with 150 ‘cleaned’ killifish. The resulting density (17 fish/m³) was well within the natural variation exhibited by local killifish populations. We placed the cages in water that ranged from 1.0 m - 1.5 m in depth; there was no halocline in the range in which the cages were placed. To eliminate the possibility that differences in cage placement or construction may affect the results, cage location within each marsh was determined randomly. Fish cages were sampled weekly for four weeks; at each sampling date 10 fish were removed from each cage (n = 30 per site each week). After the first 4 weeks, cages were sampled every two weeks (n = 30 per site) until cages were exhausted. Fish were necropsied immediately following sampling using standard parasitological techniques (see Hoffman 1999). Helminth parasites collected during necropsy were identified using the keys of Hoffman (1999), Anderson *et al.* (1974), Schell (1970) and Harris & Vogelbein (2006).

Analysis of parasite community establishment

To document the accumulation of parasite richness in the killifish during the course of our field study we use species accumulation curves (SACs), a technique common for estimating diversity in ecology (Gotelli & Colwell 2001). We use the bias-corrected Chao2 estimator in EstimateS 8.0.0 (Colwell 2006) to calculate the species richness of parasite component communities (the community of parasites associated with a regional subset of hosts) at each sample date. The Chao2 estimator has been shown to have

excellent predictive power when sample sizes are relatively small and the bias-corrected model has been shown to perform well in host-parasite systems (reviewed in Dove & Cribb 2006). Sample order was randomized 100 times without replacement and mean species richness was estimated for each sample. We also calculated the fit of the asymptotic Michaelis-Menten equation $y = ax/(b + x)$, where y is observed richness, x is sample size, a is the asymptote or predicted richness and b is a measure of the rate at which the curve approaches the asymptote. We performed a Kruskal-Wallis one-way analysis of variance (ANOVA) on mean species richness to determine whether there were significant differences between sites; multiple pairwise comparison was conducted using Dunn's test. We performed analyses using the software platform JMP Version 7.0.1 (2007 SAS Institute): all p-values were conservatively two-tailed with a critical value of 0.05.

Host community stability analyses

Food web stability was assessed using the framework provided by May (1973) and extended by Allesina & Pascual (2008). It is based on the concept of food web matrices and the dynamics of species densities in the network, determined by the equations:

$$\frac{dX_i}{dt} = F_i(X_1(t), X_2(t), X_3(t), \dots, X_n(t)). \quad (1)$$

where X_i is the abundance of species i and n is the total number of species. The steady state of the system, in which all growth rates are zero, occurs when:

$$0 = F_i(X_1^*(t), X_2^*(t), X_3^*(t), \dots, X_n^*(t)). \quad (2)$$

Expanding about this equilibrium, for each population:

$$x_i(t) = X_i(t) - X_i^*. \quad (3)$$

where x_i measures a small perturbation to the i th population and $*$ denotes the steady state. The dynamics and stability in the neighborhood of the steady-state point may be determined by expanding (1) in a Taylor series about the steady state, discarding all terms that are of second or higher order in the population perturbations x . A linearized approximation may be obtained, in matrix notation:

$$\frac{d \mathbf{x}(t)}{dt} = A \mathbf{x}(t). \quad (4)$$

where $\mathbf{x}(t)$ is an $n \times 1$ column vector of the deviations from the steady state. May (1973) demonstrates that the eigenvalues for A reveal the stability properties of the system. Specifically, if matrix A is stable, its eigenvalues will all have negative real parts.

To compute the eigenvalues for our sites we generate community matrices from adjacency matrices that describe the trophic interactions from the marshes in which we work (Anderson & Sukhdeo, unpublished data). In order to convert these matrices into the matrices described by May (1973) we follow the methods of Allesina & Pascual (2008) and impose that if $a_{ij} > 0$ then $a_{ji} < 0$ for each $i \neq j$, in doing so creating an antisymmetric matrix. The diagonal coefficients of the matrix were set to -1 (self-regulation). Coefficient strengths were assigned by extracting values from a standard normal distribution ($\mu = 0$, $\sigma^2 = 1$), taking the absolute value, and multiplying the antisymmetric community matrices with the randomly determined interaction coefficient. For each of the matrices we calculate the percentage of eigenvalues with a negative real parts; further, we randomize the assignment of coefficients 100,000 times in order to determine whether the eigenvalues we obtain were due to combinations of coefficients or a property of the trophic structure of the food webs.

We also calculate the connectance of our food web matrices where connectance ($C = L_o/S^2$) is the number of realized links (L_o) divided by the number of possible links (S^2). Measured in this way, C is the average fraction of species in a community consumed by the average species, i.e. when $C = 0$ no species consume each other and when $C = 1$ all species consume all other species and themselves. In order to allow for between network comparisons of connectance we normalize following the method of Gilbert (2009):

$$C_{norm(S)} = \frac{C_{(S)} - C_{min(S)}}{1 - C_{min(S)}} \quad (5)$$

where $C_{norm(S)}$ = normalized connectance for S species; $C_{(S)}$ = connectance for S species; and $C_{min(S)}$ = the minimum value of connectance for S species.

Results

A total of 600 sentinel fish were studied: 15 fish were necropsied from each of the collections (a subsample from the 30 fish collected) that occurred at each of the 4 sites over 10 samples, covering 14 weeks during the summer of 2008. Eight taxa of metazoan parasites were identified including nematodes *Dichelyne bullocki* and *Contracaecum* sp.; the digenean metacercaria of *Ascocotyle diminuta* and *Posthodiplostomum minimum*; monogeneans *Fundulotrema prolongis* and *Swingleus ancistrus*; the acanthocephalan *Paratenuisentis ambiguous*; the copepod *Ergasilus funduli*; these taxa infected more than 70% of the killifish examined. Parasite intensity per host ranged from 1 to 2146 for the directly transmitted monogeneans and copepod: parasite intensity per host ranged from 1 to 806 for the complex life cycle acanthocephalans, nematodes and digeneans.

The Oritani marsh (unrestored) included 71 species and had 5041 potential links of which 629 were realized, resulting in a normalized connectance of 0.113 (Fig. 4.1a; Table 4.1). The Secaucus Marsh (0 year) included 87 species and had 7569 potential links of which 627 were realized, resulting in a normalized connectance of 0.072 (Fig. 4.1a; Table 4.1). The restored marshes, Harrier Marsh (10 year) and Mill Creek (20 year) included 112 and 122 species respectively; the resulting values of normalized connectance were 0.088 for Harrier Marsh and 0.117 for Mill Creek Marsh (Fig. 4.1a; Table 4.1). The community similarity of birds ($r^2=0.81$, stress value=0.08), fishes ($r^2=0.82$, stress value=0.09) and benthic macroinvertebrates ($r^2=0.82$, stress value=0.07) showed distinct separation between each of the four marshes sampled. A NMDS plot of the benthic, fish and bird communities ($r^2=0.83$, stress value=0.15) is present in Figure 4.1b.

Secaucus marsh (0 year) had a parasite community consisting of the directly transmitted monogenean *S. ancistrus* and the copepod *E. funduli* (Fig. 4.2b). The remaining three marsh sites recorded observations of all 8 species of metazoans parasites (direct and complex life cycle) discovering during this study: Oritani Marsh (Fig. 4.2a), Harrier Marsh (Fig. 4.2c) and Mill Creek Marsh (Fig. 4.2d). The mean species richness and parasite community displayed significant pairwise correlations between Oritani Marsh, Harrier Marsh and Mill Creek Marsh (Table 4.2). The accumulation of parasite species in each marsh was consistent with the asymptotic Michaelis-Menten equation: a steep slope with an early asymptote (Fig. 4.3). The goodness-of-fit was adequate for: Oritani Marsh (Fig. 4.3: $df = 149$, $r^2 = 0.53$, $SS = 58.64$, $S_{yx} = 0.63$); Secaucus Marsh (Fig. 4.3: $df = 149$, $r^2 = 0.95$, $SS = 0.51$, $S_{yx} = 0.058$); Harrier Marsh (Fig. 4.3: $df = 149$, $r^2 =$

0.93, $SS = 7.86$, $S_{yx} = 0.23$); and Mill Creek Marsh (Fig. 4.3: $df = 149$, $r^2 = 0.76$, $SS = 20.31$, $S_{yx} = 0.37$). Overall mean species richness differed significantly between the four marsh sites (Fig. 4.3: Kruskal-Wallis one-way ANOVA: $H = 350.5$, $df = 3$, $p < 0.0001$), with the mean species richness at Secaucus marsh (0 year) significantly lower than the species richness observed at the other three sites (Fig. 4.3: Dunn's multiple comparison test: $p < 0.01$; Secaucus mean = 1.1919 ± 0.018 SE; Oritani mean = 7.447 ± 0.055 SE; Harrier mean = 7.735 ± 0.046 SE; Mill Creek mean = 7.662 ± 0.034 SE). There was no significant difference between the mean species richness observed at Oritani, Harrier and Mill Creek marshes (Fig. 4.3: Dunn's multiple comparison test: $p > 0.05$).

For 100,000 randomizations of the community matrices generated from our four food webs, Figure 4.4 shows the number of eigenvalues with a negative real part. None of the food webs appear to satisfy the criteria of May (1973) for stability: given the random interaction coefficients we imposed, no community matrix has 100% of the eigenvalues with negative real parts. However, there were significant differences in the mean fraction of eigenvalues with negative real parts between each of the marshes (One-way ANOVA with Tukey's pairwise comparison: all $p < 0.001$). The Secaucus Marsh (0 year) exhibits the lowest likelihood of achieving stability with a 77% mean fraction of eigenvalues with a negative real part (meanE), the maximum (maxE) and minimum (minE) fraction of eigenvalues attained for this food web were 78% and 75% respectively (Table 4.1). Mill Creek marsh, our oldest restoration (20 year) and highest diversity site, has a mean fraction of eigenvalues with negative real parts of 80.3%. Oritani Marsh (unrestored) has a mean fraction of eigenvalues with negative real parts of 83.9%. Harrier Marsh (10 year) has a mean fraction of eigenvalues with negative real parts of

85.1%. We further analyzed the relationship between the mean species richness of the helminth community and the stability of the host community assemblages. We used a bivariate plot (Fig. 4.5), and determined that the best nonlinear model fit was in the form of the logistic Richards equation ($df = 595$, $r^2 = 0.5849$, $SS = 1579$, $S_{yx} = 1.629$):

$$\text{Log}X_b = \text{Log}E_{50} + \left(\frac{1}{HS}\right) \times \text{Log}(2^{1/S} - 1) \quad (6)$$

where X_b is the inflection point, X_{50} is the midpoint, HS is the slope factor, and S is the symmetry parameter. This analysis had an infection point (X_b) at 0.8162, and a midpoint (X_{50}) of 0.7930.

Discussion

These data suggest that the stability of the host community and not just host diversity (*sensu* Smith 2001; Hechinger & Lafferty 2005) may play a significant role in the establishment of complex parasite life cycles. The key insight provided by our analyses is that complex life cycle parasites are not a ubiquitous component of all ecological food webs. Further, in our indicator species, there appears to be a threshold in the stability of trophic interactions that must be exceeded for complex life cycle parasites to establish. This is plausible given that stable trophic interactions provide the critical connections that allow for transmission in trophically transmitted parasites. Dobson *et al.* (2008) demonstrated variation in the relationship between host diversity and parasite diversity across wide scales, highlighting the difficulty in making predictions about parasite diversity patterns across geographical boundaries. We suggest that the reason for this difficulty is that the host community metrics that correlate with the diversity of

parasites are not independent measures of system diversity but also of the structure (cohesiveness) and stability of the food web, an inherently local phenomenon.

The traditional approach to estimating the species richness of communities has resulted in an α - β dichotomy that links local and regional patterns of diversity (Gering & Crist 2002). This dichotomy has allowed for broad scale inferences about the mechanisms driving the patterns evident in species richness patterns, in particular, whether the community is the result of local or regional processes and whether community assembly is determined by niche or dispersal dynamics (Gotelli & Colwell 2001; Dove & Cribb 2006). In α -dominated communities, richness is concentrated in individual samples, whereas β -dominated communities have dissimilar individual samples with most species richness existing as regional turnover among samples. These patterns are characterized by certain species accumulation curve (SAC) shapes: α -dominated communities have a steep slope that rapidly reaches asymptote, and β -dominated communities have a more gradual slope and much later asymptotes. My data follows the shape exhibited in α -dominated communities. This suggests interactive processes that exist on a local scale determine the parasite community in killifish (Dove & Cribb 2006). Further, α -dominated parasite communities are niche assembled, rather than being limited by dispersal (Dove & Cribb 2006). Thus, it seems plausible that patterns of complex life cycle parasites in our sentinel species are the result of local processes such as the structure and stability of trophic interactions.

In general, diverse communities are more stable than comparably depauperate ones (Cottingham *et al.* 2001). However, abiotic variables affect the biotic variables, and thus the interaction between abiotic and biotic variables may be the real agent of

community stability (Ives & Carpenter 2007). This interaction, and interactions between diversity and stability, has been explored experimentally (e.g. Petchey *et al.* 2002; Vogt *et al.* 2006) revealing a positive effect of diversity on stability. However, long-term datasets seem to suggest that this relationship holds little traction in natural systems (Valone & Barber 2008). This has led to the contention that a positive relationship between diversity and stability may be an artifact of the level of ecological realism in the system studied (Romanuk *et al.* 2009). Thus, despite a growing consensus about the effects of diversity on ecosystem functioning (i.e. Palumbi *et al.* 2009) there seems little evidence to suggest that it is appropriate to make the *a priori* assumption that a diverse system will be a stable system (Ives & Carpenter 2007; Romanuk *et al.* 2009).

For a parasite, this is of critical concern, since stable, predictable communities of organisms provide the foundational resource for complex life cycle parasites (Poulin 2007). The rationale being that in order to increase transmission, parasite life strategies become integrally coupled with host species and rely on stable populations of hosts in the life cycle (Combes 2001; Poulin 2007). Indeed, the interaction between the parasite and its host is so vital that the death or absence of that host will result in the death of the parasite. As a result, the dynamics of the host population will be reflected in the dynamics of the parasite population (Lafferty *et al.* 2008). A logical extension of this premise is that parasite species with complex life cycles will be present only when stable predator-prey trophic links exist in ecosystems (Marcogliese & Cone 1997; Sukhdeo & Hernandez 2005). Our data appears to support this thesis, our lowest diversity site (unrestored marsh) achieved the same parasite species richness as the more pristine, highly diverse marsh sites (10 and 20 year marshes): further, these three sites had similar

system stability, as measured by the fraction of eigenvalues that had negative real parts. The deviation in parasite species richness occurred in our 0 year marsh site. This site was colonized by only directly transmitted parasites, and had a significantly lower fraction of eigenvalues with negative real parts. We think it likely that the range of local stability documented by our food webs provides insight into a potential critical threshold in the stability of the host community that is required for the persistence of complex life cycle parasites.

The ideas of threshold levels in the invasion or persistence of infectious diseases are central to the theory and practice of disease ecology (Grenfell & Dobson 1995). These ideas have been derived from epidemiological theory and have focused primarily on the threshold population size for invasion (N_T) and the critical community size (CCS) required for disease persistence (Diekmann *et al.* 1995; Heesterbeek 2002). A central result of research in this field is that though abrupt thresholds appear to be rare (e.g. Davis *et al.* 2004), a consequence of limited replication and data, they have considerable traction in the pursuit of understanding the transmission of disease in wildlife populations (Lloyd-Smith *et al.* 2005). The best example of these ideas comes from analysis of a 30-year time series that definitively showed a threshold density of great gerbils, *Rhombomys opimus*, below which infection by plague, *Yersinia pestis*, was not present (Davis *et al.* 2004). The data in our study suggest a similar scenario, the likelihood of complex life establishment is much higher once of measure of local stability exceeds 0.81 i.e. 81% of the eigenvalues in a community matrix have negative real parts.

The view that parasites are attached to stable community interactions is slowly becoming a central theme in parasite ecology (Marcogliese & Cone 1997; Sukhdeo &

Hernandez 2005; Lafferty *et al.* 2008). This plays into a growing body of evidence that has begun to address whether there are critical clusters of interactions within free-living communities. Beginning with the work of Gilbert (1977, 1979), and continued by Thompson (1982, 1994, 2005), it has been suggested that the identification of interacting unit groups of species, in which natural selection acts upon all participants significantly, will likely to provide considerable insight into community dynamics. It has been argued that these unit groups, termed ‘stable evolutionary units’, co-adapt and co-evolve as a direct result of their interactions (Thompson 1982, 1994). This argument stems from theory that has demonstrated that two populations of natural enemies (or mutualists) can co-adapt and will become dynamically stable over evolutionary time. Indeed, the existence of such stable two-species interactions within communities of interactions has been shown to facilitate a third species that is able to adapt to, and exploit, the pre-existing interaction (Thompson 1982, 1994). Over time, it is this dynamic that has become canalized and provides for the fundamental unit of community evolution. For a parasite, the initial interaction between two natural enemies and the subsequent formation of a ‘vortex’, provides the critical unit in its establishment and persistence. In essence, the structure of the host food web, likely made of multiple evolutionary vortices, exerts a strong selective pressure on the evolution of parasite transmission strategies and the subsequent patterns of parasite diversity observed in extant systems (Marcogliese & Cone 1997; Sukhdeo & Hernandez 2005; Hernandez & Sukhdeo 2008).

Parasites permeate entire ecosystems; positions derived from the frequency of complex life cycles with one parasite species interacting with many free-living hosts, and substantially alter common food web metrics (Marcogliese & Cone 1997; Lafferty *et al.*

2008). More importantly, this study has demonstrated how food web structure strongly influences parasite diversity patterns, a result of the dependence of parasites upon their free-living hosts and the nature of the ecological network in which they reside.

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Figure 4.1: (a) Comparison of the community (benthos, fishes, birds) species richness in the four marshes in our study. (b) Nonmetric multidimensional scaling (NMDS) ordination of benthos (*squares*), fishes (*circles*) and bird species (*triangles*). A second categorical overlay of site is represented by: Oritani Marsh (*O*), Secaucus Marsh (*S*), Harrier Meadow Marsh (*H*) and Mill Creek Marsh (*M*).

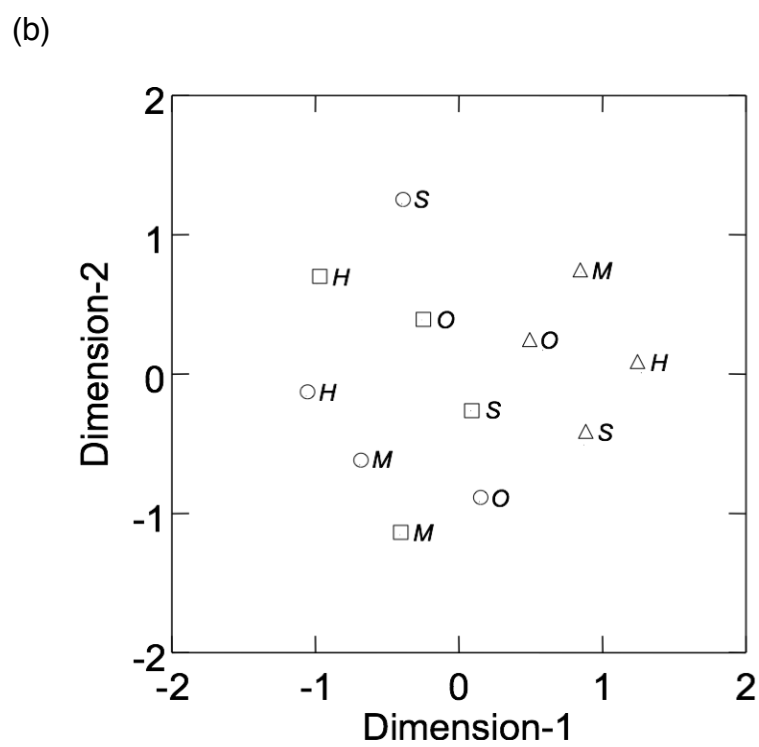
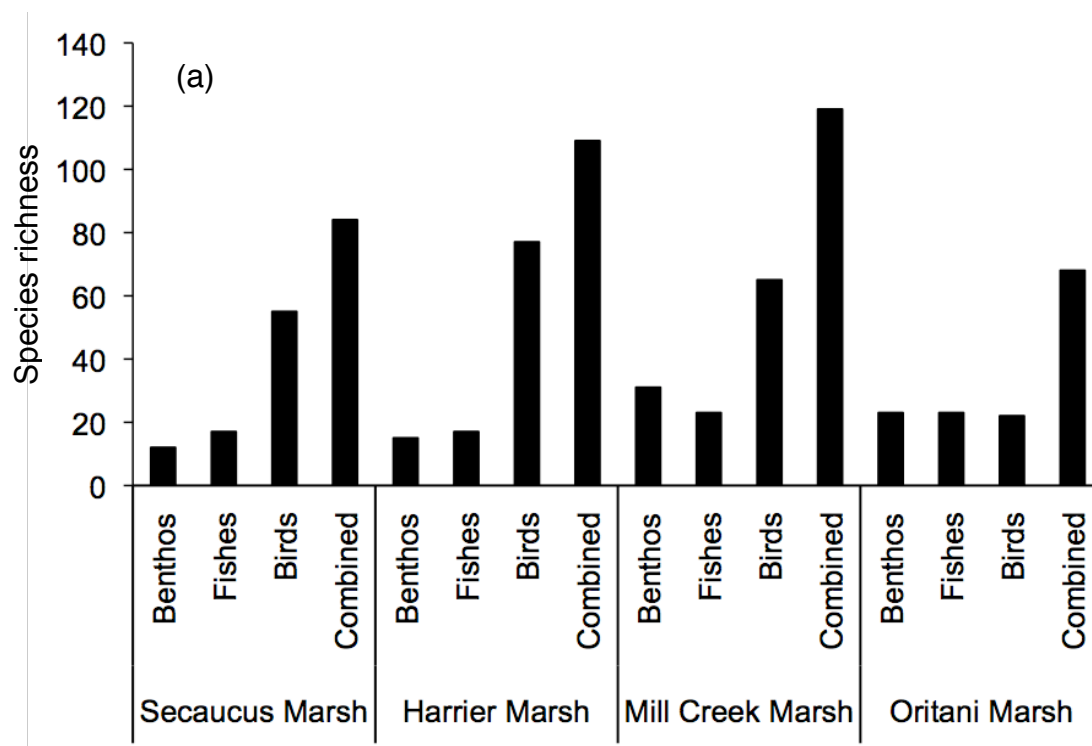


Figure 4.1

Figure 4.2: Sample-based species accumulation curves for parasite communities in (a) Oritani Marsh, (b) Secaucus Marsh, (c) Harrier Meadow Marsh and (d) Mill Creek Marsh. Curves represent the result of the bias-corrected Chao2 estimator of species richness based on *Fundulus heteroclitus* samples collected weekly from fish cages. For each curve, each point represents the mean of 100 estimates using randomized accumulation order.

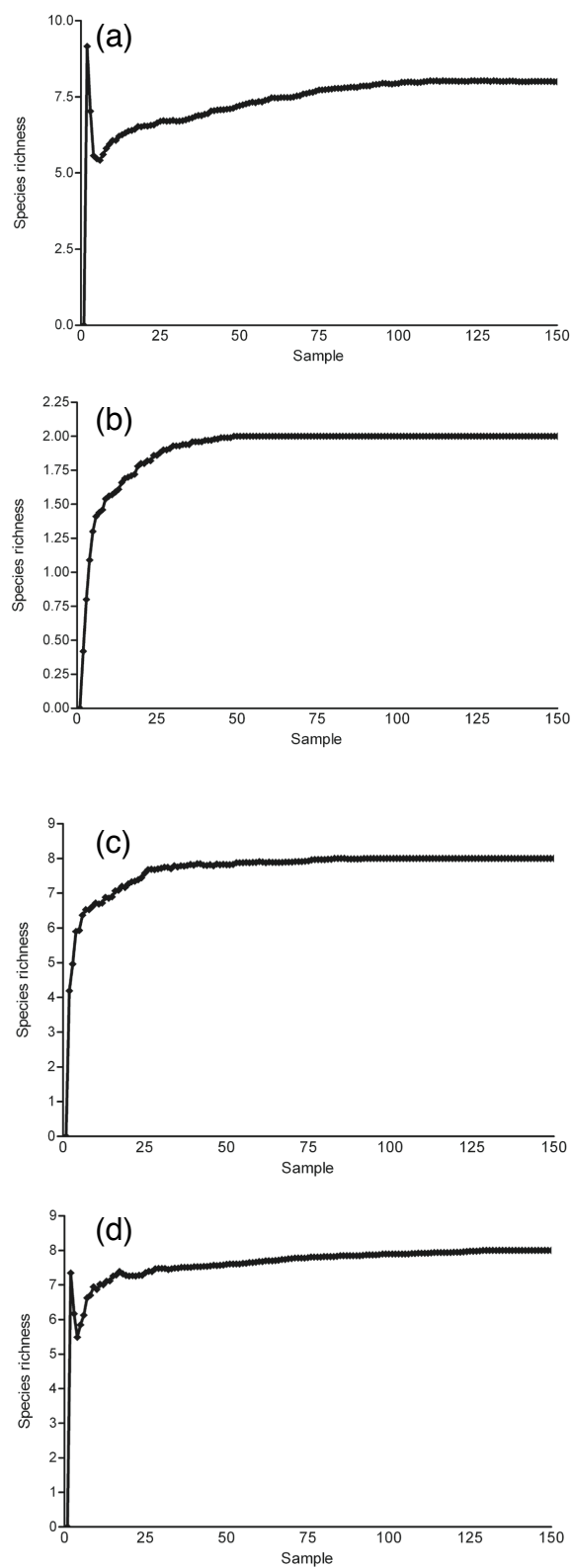
**Figure 4.2**

Figure 4.3: Asymptotic randomized sample-based species accumulation curves for Oritani Marsh, Secaucus Marsh, Harrier Meadow Marsh and Mill Creek Marsh.

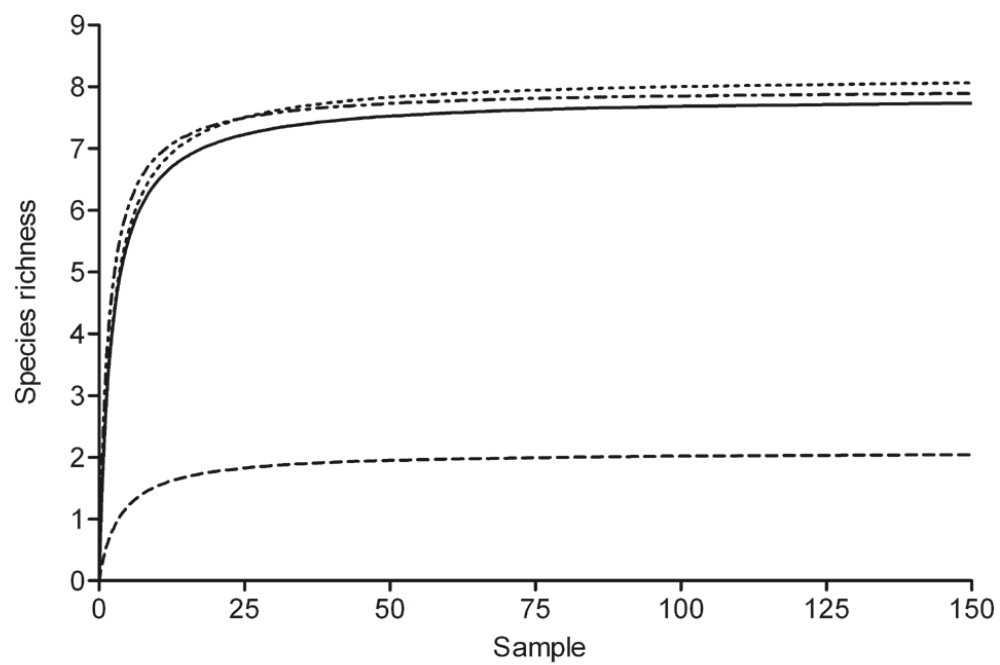


Figure 4.3

Figure 4.4: Percentage of eigenvalues with a negative real part out of 100,000 simulations for: Oritani Marsh (Oritani); Secaucus Marsh (SHS); Harrier Marsh (Harrier); Mill Creek Marsh (MC).

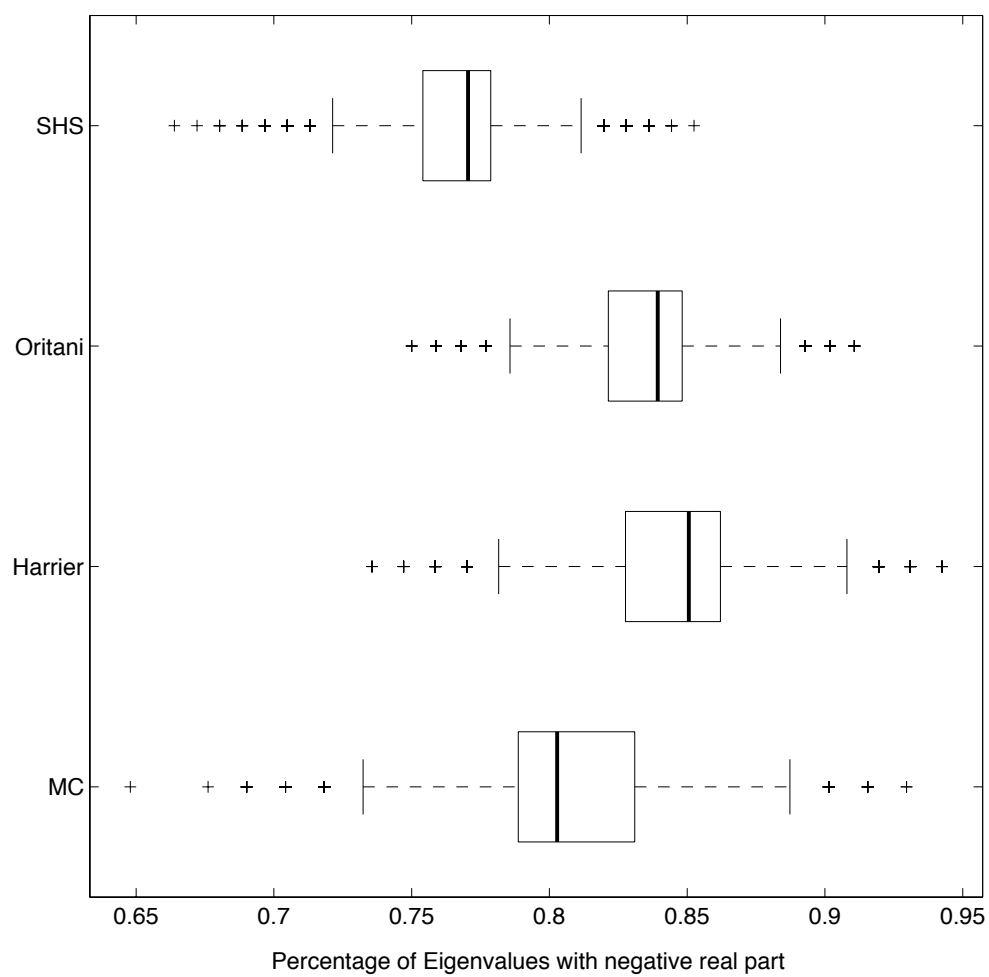
**Figure 4.4**

Figure 4.5: Bivariate plot of mean parasite species richness and fraction of eigenvalues with negative real parts. Dashed line represents best nonlinear model fit, a five parameter logistic equation with $r^2 = 0.5849$.

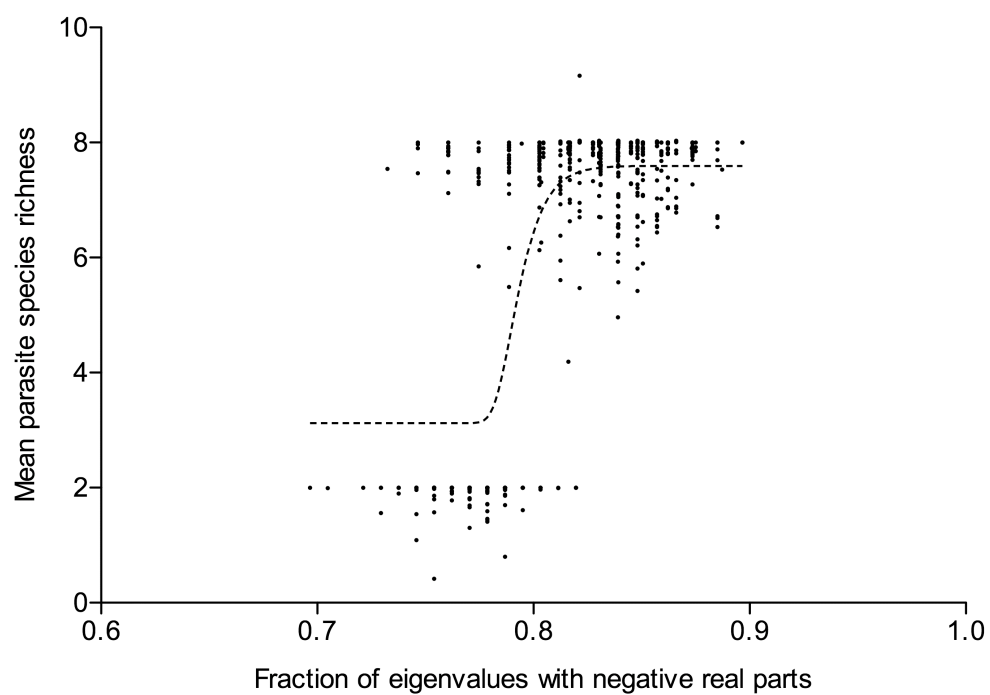


Figure 4.5

Table 4.1: Summary of food web stability metrics for each of the estuarine food webs.

Statistics include species richness (S), potential links (S^2), observed links (L_o), linkage density (d), connectance (C), normalized connectance (C_{norm}), minimum fraction of eigenvalues with negative real part (minE), average fraction of eigenvalues with negative real part (meanE), and maximum fraction of eigenvalues with negative real part (maxE).

Parameters:	<i>Oritani Marsh</i> (unrestored)	<i>Secaucus Marsh</i> (0 year)	<i>Harrier Marsh</i> (10 year)	<i>Mill Creek Marsh</i> (20 year)
Number of species; S	71	87	112	122
Potential no. of links; S^2	5041	7569	12544	14884
Observed no. of links; L_o	629	627	1206	1846
Linkage density; d	8.86	7.21	10.77	15
Connectance; C	0.125	0.083	0.096	0.124
Normalized connectance; C_{norm}	0.113	0.072	0.088	0.117
MeanE	0.839	0.771	0.851	0.803
MaxE	0.911	0.852	0.943	0.930
MinE	0.750	0.664	0.736	0.650

Table 4.2: Pairwise Spearman nonparametric correlation coefficients on mean parasite species richness observed in the killifish, *Fundulus heteroclitus* in each of the marsh sites. Values marked with a * represent significant correlation at the $p < 0.05$.

	<i>Oritani Marsh</i> <i>(unrestored)</i>	<i>Secaucus</i> <i>Marsh (0</i> <i>year)</i>	<i>Harrier</i> <i>Marsh (10</i> <i>year)</i>	<i>Mill Creek Marsh</i> <i>(20 year)</i>
Secaucus Marsh	0.772			
Harrier Marsh	0.913*	0.851		
Mill Creek Marsh	0.935*	0.822	0.957*	

CHAPTER 5

General discussion

The field of parasite ecology has flourished over the last 30 years, with studies addressing parasite community assembly (Guegan *et al.* 2005), the role of parasites in population regulation (Cattadori *et al.* 2004; Moller 2005), and the evolutionary and ecological implications of parasite mediated trophic interactions (Esch 1977; Anderson & May 1979; May & Anderson 1979; Minchella & Scott 1991; Marcogliese & Cone 1997; Hudson *et al.* 1998; Lafferty *et al.* 2000; Thomas *et al.* 2005; Hechinger & Lafferty 2005; Wood *et al.* 2007). Although these studies support a strong influence of parasitism on community structure, the specific roles of parasites in community dynamics remains a hotly debated topic (see Sukhdeo & Hernandez 2005; Thomas *et al.* 2005). This is a question that has yet to be answered, primarily because of difficulties in quantifying critical theoretical parameters, such as R_0 , in empirical systems and in describing the structure and dynamics of parasites within entire host communities. As a consequence, understanding the role of the free-living community on parasite dynamics, and how parasites can be integrated with food web theory remains problematic (Sukhdeo & Hernandez 2005; Hernandez & Sukhdeo 2008; Lafferty *et al.* 2008).

My thesis investigates how parasites establish and persist within host food webs. I report results from four independent observational studies conducted over 2 years in a New Jersey salt marsh. These results demonstrate that: 1) a diverse community of primary consumers (non-host benthic invertebrates) lays the foundation for parasite establishment; 2) a diverse community of host species will support complex life cycle

parasites, but only when those host species exist in a stable configuration; 3) there is not a strict positive correlation between the diversity of parasites and the diversity of hosts; and 4) complex parasite life stages are restricted by topological phenomena (core/periphery structure) within food web networks, a likely consequence of evolutionary pressure to enhance trophic transmission between hosts. These data suggest that it is possible, using network analysis tools, to identify structural regularities within estuarine food webs, which provide critical insight into the mechanisms underlying metazoan parasite establishment and persistence.

The interaction between host diversity and parasite diversity

In parasites with multiple hosts, the dominant drivers of the parasite infracommunities are generally considered to be the diversity and abundance of the host community (Huspeni & Lafferty 2004; Hechinger & Lafferty 2005; Hechinger *et al.* 2007). This is a reflection of the nature of transmission observed in parasites with complex life cycles; host-feeding links provide repeatable and dependable interactions for parasites to use as ‘pathways’ for transmission (Marcogliese & Cone 1997). The number and distribution of pathways within food webs is a direct consequence of the number of species present, as diversity increases so to does the number of trophic connections (MacArthur 1955; Lafferty *et al.* 2006). Thus, diverse communities of invertebrates, fishes and birds have the ability to support multiple trematode life cycles (Marcogliese 2002, 2005). Consequently, it is generally accepted that the diversity and stability of the host community, primarily that of the definitive hosts, should impose significant restrictions on species composition of local parasite communities (Rohde 1993; Combes

2001; Poulin 2007). On the other hand, abiotic variables affect the biotic variables, and thus it is the interaction between abiotic and biotic variables that may be the agent of parasite community composition taxa (Moller 1987; Khan & Thulin 1991; Poulin 1992; MacKenzie *et al.* 1995; Valtonen *et al.* 1997; Ondrackova *et al.* 2004; Marcogliese 2004, 2005).

In this study, I constructed hierarchies of biotic and abiotic variables that contributed to the success of three representative complex life cycle parasites. The key insight provided by my analyses was that a diverse non-host benthic community was more important in determining the parasite communities within my sentinel species than the presence of competent definitive hosts. Further, I did not find any correlation between the diversity of the parasite community and the diversity of the free-living community (benthic invertebrates, fishes or birds). These data do not support the pattern evident in other studies that have identified positive relationships between parasite communities and the diversity of bird definitive hosts (Smith 2001; Hechinger & Lafferty 2005) and large benthic host invertebrates (Fredensborg *et al.* 2006; Hechinger *et al.* 2007). The reason for this difference, and the patterns observed in my data, are likely because of the evolutionary history of complex life cycle parasites. These parasite species rely on stable trophic links (Marcogliese & Cone 1997; Hudson *et al.* 2006) and trophic stability in my system is likely a consequence of a diverse benthic community. Thus, the presence of non-host benthic invertebrates as the most important factor in determining the presence of parasites probably reflects a robust ecosystem that can support multiple parasite life cycles (Huspeni & Lafferty 2004; Hudson *et al.* 2006). Further, it is likely that the absence of correlation between measures of host diversity and

parasite diversity in my analyses is because the truly informative measures of parasite diversity are measures of system structure (cohesiveness).

Food web networks provide insight into parasite dynamics

In 1927 Charles Elton championed the idea that complex biological systems may be understood through simplification. The strategy he suggested was to create webs of trophically interacting populations of species. Elton (1927) argued that in order to truly comprehend a system, an understanding of the dynamics of each population, including each pair-wise interaction between species, and the direct and indirect influences of the whole community is required. The strategy Elton proposed, with its inherent simplification of biological complexity, has been supported by modern empirical studies on simple food chains (e.g. Gause 1934; Lawler 1993; Lawler & Morin 1993). For example, Kaunzinger & Morin (1998) demonstrated that trophic cascades, a general feature of ecosystems, may be replicated in model microcosm communities. Further, simple rule-based theoretical models that use simplified species traits have revealed fundamental mechanisms underlying the formation of complex communities (e.g. Brown *et al.* 2004; Petchey *et al.* 2008).

The success of food webs to inform ecological questions has seen them become commonly used as predictors of the dynamics of host populations and the diversity of host communities (Belgrano *et al.* 2005; de Ruiter *et al.* 2005; Thomas *et al.* 2005; Pascual & Dunne 2006). These studies have provided the foundation for unifying many disparate fields in ecology through the emergence of patterns in empirical and theoretical studies (see reviews in Pascual & Dunne 2006). These patterns may be grouped as: how

consumer-resource interactions cascade across trophic levels; how web structure alters the outcome of competition and predation; and the complex interactions between diversity and stability (Winemiller & Polis 1996). Though subject to debate as to their universality (de Ruiter *et al.* 2005; Pascual & Dunne 2006), simple biological explanations to these patterns have been proposed and can be broadly limited to: biological constraints on population dynamics; physical limitations of energy flow; and the inherent nature of animal diversity (Pimm 1982). Thus, it has become apparent over the last century that a ‘simple’ approach describing trophic interactions on the level of individual species can result in the recognition of regularity and predictably structured communities (May 1973; Pimm 1982; Pascual & Dunne 2006; Petchey *et al.* 2008).

It is of note that the structure we observe in food webs is the product of long evolutionary and co-evolutionary processes operating between plants and animals (May 1973; Pianka 2000). In seminal work, May (1973) and Pimm (1982) have suggested that over time, the component parts of communities have ended up in configurations that endow systems with long-term stability and that provide systems with predictable dynamics. For a parasite, the structured and predictable nature of host communities is likely to provide a fertile resource (Poulin 1998; Combes 2001). The rationale being that in order to increase transmission, parasite life strategies become integrally coupled with host species and rely on stable populations of hosts critical in the life cycle (Rohde 1993; Combes 2001; Poulin 2007). Indeed, the interaction between the parasite and its host is so critical that the death or absence of that host will result in the death of the parasite. The host, thus, is not only exploited as an energy source but as an essential habitat (Esch *et al.* 1990). As a result, the dynamics of the host population will necessarily reflect in

the dynamics of the parasite population (Lafferty *et al.* 2008). Accordingly, I argue that the study of food webs and patterns of host interactions within them should strongly correlate with patterns of parasite species diversity and community structure.

Identifying critical structures in ecological networks

Over the past 50 years, a growing body of evidence has begun to address whether there are critical clusters of interactions within communities, the presence of which parasites are likely to be dependent upon. Beginning with the work of Gilbert (1977, 1979), and continued by Thompson (1982, 2005), it has been suggested that the identification of interacting unit groups of species, in which natural selection acts upon all participants significantly, will likely to provide considerable insight into community dynamics. It has been argued that these unit groups, termed ‘stable evolutionary units’, co-adapt and co-evolve as a direct result of their interactions (Thompson 1994, 2005). This argument stems from theory that has demonstrated that two populations of natural enemies (or mutualists) can co-adapt and will become dynamically stable over evolutionary time. Indeed, the existence of such stable two-species interactions within communities of interactions has been shown to facilitate a third species that is able to adapt to, and exploit, the pre-existing interaction (Thompson 2005). Over time, it is this dynamic that has become canalized and provides for the fundamental unit of community evolution. These units have subsequently been referred to as ‘coevolutionary vortices’ (Thompson 1994, 2005). For a parasite, the initial interaction between two natural enemies and the subsequent formation of a ‘vortex’, provides the critical unit in its establishment and persistence. In essence, the structure of the host food web, likely made

of multiple evolutionary vortices, exerts a strong selective pressure on the evolution of parasite transmission strategies and the subsequent patterns of parasite diversity observed in extant systems (Marcogliese & Cone 1997; Poulin & Morand 2000; Sukhdeo & Hernandez 2005; Hernandez & Sukhdeo 2008).

I argue that clusters of species that have a critical place in the topology of the host network (core species) provide insight into the diversity of parasites in ecosystems for two reasons. First, those host species that fall into the core cluster of an ecological network are likely to experience fewer fluctuations in abundance relative to those that fall in the periphery of a network (Allesina *et al.* 2006) providing a reliable resource for parasites. Second, clusters of tightly interacting species that drive nestedness and modularity in food webs yield stable predator-prey trophic links (Wasserman & Faust 1994; Jordano *et al.* 2006) and exploiting these stable links may ensure successful completion of the parasite life cycle. The potential for the structure of free-living communities to change local parasite dynamics is supported by studies that demonstrate the effects of climate-mediated physiological stress on host resistance to pathogens and the relationship between host range shifts and the emergence of new or known pathogens in local populations (Harvell *et al.* 1999). Additionally, system dynamics driven by predator-prey interactions have been shown to cause bacterial epidemics in an aquatic system (Lafferty 2004; Berhens & Lafferty 2004). Consequently, identifying patterns in the topology of ecological networks and linking regularities in the networks to parasite community dynamics is central to understanding how parasites establish and persist in host communities.

A final consideration in thinking of patterns in food webs is the metric in which to describe the interactions of interest. The food web statistics that have been developed over the last 50 years, that have provided the foundation for much of the theoretical and empirical food web research do little to help ‘visualize’ the biological patterns that are critical for parasites. Indeed, it has been argued that the typical measures (i.e. connectance, link density) may be too arbitrary to be useful in informing on patterns in community ecology (Paine 1988; Polis 1991, 1999; Tavares-Cromar & Williams 1996; Raffaelli 2002). As an example, when parasitism is included in the metrics used to analyze the topology of food webs, food chain length increases, omnivore links increase, and connectance tends to decrease (Huxham *et al.* 1995, 1996; Leaper & Huxham 2002; Hernandez & Sukhdeo 2008). An increase in the number of links makes intuitive sense because more species have been added to the food web network. Omnivore links increase because many parasites depend upon multiple hosts within their life cycles. A decrease in connectance, the number of links observed relative to the total number of possible links (Cohen 1978), is more difficult to interpret. Thus, there are reservations about the utility of research that focuses on these ‘traditional’ statistics because patterns in real communities generally do not support the predictions arising from models of food web structure that are parameterized using these values (Paine 1988; Polis 1991; Martinez 1991; Leibold & Wootton 2001). As the field has begun to reassess the meaning of the metrics used in theory behind food webs, there have been strong arguments for the use of mechanistic frameworks and whole network models (Ings *et al.* 2009).

The use of mechanistic models to generate predictions on the structure and function of food webs is fast becoming a productive avenue in understanding ecological

networks (reviewed in Ings *et al.* 2009). The recent model of Petchey *et al.* (2008), which uses optimal foraging theory and allometric scaling relationships, accurately describes the structure of real food webs more than 65% of the time. Brown *et al.* (2004) propose a similar mechanistic approach; the principles of kinetics, stoichiometry, body size, temperature and basal metabolic rate are applied to ecological systems. In doing so, Brown *et al.* (2004) generate a metabolic theory that encompasses all levels of biological organisation that may have significant impact upon the way in which we view ecological systems. These studies develop explicit and robust predictions about the structure and function of ecological networks, a critical concern given the preponderance of evidence that suggests our world is rapidly changing (e.g. Dobson *et al.* 2008; Lafferty 2009).

A concurrent thrust, alongside individual-based mechanistic models, is the use of whole network algorithms that search for groups of interactions (e.g. Allesina & Pascual 2008, 2009). It is my contention that this approach, and the search for groups within ecological networks, will provide considerable insight into the function of ecological networks. The identification of groups within food webs is not new, and a series of different definitions of ‘group’ have been bandied around the ecological literature for 40 years. Beginning in the 70s (Pimm & Lawton 1980; Yodzis 1982), several papers have attempted to identify clusters of highly interacting species that interact with the majority of other species in food webs weakly. These approaches have revealed some unique groups, based largely upon pre-existing differences in spatial, temporal and habitat distributions (e.g. benthic vs. pelagic communities: Krause *et al.* 2003; Melian & Bascompte 2004; Allesina *et al.* 2005). Though these have been important in our consideration of diversity and stability in ecological systems, I contend that algorithms

commonly in use in physics can provide a much better understanding of critical units in networks. Specifically, I believe that the core/periphery analyses can identify ‘communities’ of organisms that may be the main driver of network structure. The algorithm detects groups based upon dense within-group interactions and parses them out from other weakly interacting groups, providing a hierarchy of species importance to network topology, and thus, the analysis identifies the physical centre of the food web. I would suggest that in considering the ‘function’ of food webs one must start with the consideration of groups of critical species and the location of those species relative to the rest of the network.

In my estuarine food webs, link distributions suggest that there are fewer super-generalists than expected by chance. Further, I provide evidence that intimates that generalists interact amongst themselves, and that these generalists support groupings of specialist species. Of more interest from a parasites perspective is the presence of a predominant food web cores in each of networks I have generated. I have argued that these cores represent tight clusters of feeding interactions that act as transmission routes for trophically transmitted parasites. This does not deviate from traditional thinking in parasitology. Parasites, in continued selection of a particular environment (i.e. the definitive host), have facilitated the recognition of, and therefore response to, unique features that signal preferred habitats (Sukhdeo 1997). Consequently, those highly connected species in my food webs provide a stable coevolutionary unit that complex life cycle parasites may exploit during their evolution and persistence.

The core/periphery structure of food webs is particularly important for parasites with complex life cycles as they rely on feeding interactions between trophic levels, a

strategy with a considerable failure rate (see Kuris *et al.* 2008). Failure for a parasite in this case, may occur when a predator that is not a suitable host consumes a parasite stage. Given that there is a remarkable diversity of parasite species found throughout all natural ecological systems (Poulin 2007; Dobson *et al.* 2008), it is likely that there has been considerable selection for parasite stages to fall in host species that increase the probability for life cycle success. In some cases, parasites have circumvented diffuse predator-prey interactions by modifying the behaviour of intermediate hosts to make them more susceptible to predation from specific definitive hosts (Lafferty 1992; Lewis *et al.* 2002). Though this is a fruitful approach to increasing transmission efficiency, it is not a predominant mechanism (reviews in Lewis *et al.* 2002), and it is more likely that it is the structure of the host food web that exerts a strong selective force on parasite life cycles. Therefore, it is plausible to suggest that through evolutionary time, parasite species have become embedded in subsets of host food webs that ensure high transmission.

General conclusion

The central goal of my dissertation was to identify structures within host food web networks and describe their importance in the establishment and persistence of complex life cycle parasites. During the course of this work, using network theory tools, I have identified critical clusters of host species that provide the foundation for parasite persistence. I have argued that complex life cycle parasites are restricted by the nature of these clusters of interactions because parasite transmission strategies that increase the parasite's fitness have become fixed over the course of evolutionary time. The

observation that parasites preferentially exploit hosts that interact in critical clusters of interactions, and that these clusters of interactions exist in stable systems is by no means surprising, but is important in furthering our understanding of the ecology of parasitism and how parasites play a role in our view of nature.

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APPENDIX A

Running Head: RAFFEL & ANDERSON- NEW *HYSTEROETHYLACIUM* SPECIES IN
NEWTS

**A NEW SPECIES OF *HYSTEROETHYLACIUM* (NEMATODA: ANISAKIDAE)
FROM THE STOMACH OF THE RED-SPOTTED NEWT, *NOTOPHTHALMUS*
VIRIDESCENS, FROM PENNSYLVANIA FISHLESS PONDS**

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ABSTRACT: Species of the anisakid genus *Hysterothylacium* Ward & Magath, 1917 (Nematoda: Anisakidae) have previously only been reported from marine and freshwater fishes. Here, we describe a new species that infects red-spotted newts (*Notophthalmus viridescens*), a North American amphibian species with fully aquatic adults. Aside from the unique characteristic of infecting an amphibian host, the new species differs from congeners by the presence of lateral alae, the length of intestinal caecum (0.54-0.73 mm, 39.67-49.09% of oesophageal length), the number and arrangement of the caudal papillae (10 precloacal pairs, no adcloacal or postcloacal pairs), the size of the spicules (0.33-0.39 mm, 2.75-3.25% of body length) and the absence of tail tip ornamentation. The absence of fish in the ponds from which these specimens were obtained suggests that newts are the normal definitive host for this species. We suggest that this species may have diverged from a *Hysterothylacium* parasite of freshwater fishes, which often live in close proximity with newts.

The anisakid genus *Hysterothylacium* Ward & Magath, 1917 currently includes 65 described species worldwide, all from marine, brackish, or freshwater fishes (Bruce et al., 1994; Gopar-Merino et al., 2005; Li et al., 2008). Three species of *Hysterothylacium* have been reported from freshwater fishes in North America: *H. brachyurum* Ward & Magath, 1917 from North American fishes (Ward and Magath, 1917; Rye and Baker, 1984), *H. dollfusi* in *Polyodon spathula* (Walbaum) from Lake Sakajawea, North Dakota (Schmidt et al., 1974), and *H. analarum* Rye & Baker, 1984 in pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus) from Canada and the USA (Rye and Baker, 1984). No species of this genus have previously been described from an amphibian host, although larvae of *Contracaecum* spp., another anisakid genus (Anderson, 2000), have been reported from 4 amphibian species (McAllister and McDaniel, 1992; Kuperman et al., 2004). During a study of amphibian parasite ecology in central Pennsylvania, 9 adult specimens of a previously unknown ascaridoid nematode species with characteristics of *Hysterothylacium* were obtained from the digestive tracts of red-spotted newts (*Notophthalmus viridescens* Rafinesque). The purpose of the present paper is to describe a new species of *Hysterothylacium* found in *N. viridescens* from Pennsylvania.

MATERIALS AND METHODS

As part of a larger study of newt parasite ecology (Raffel, 2006), 105 newts were collected from Little Acre Pond (95 newts; N 40° 48' 5.8", W 77° 56' 36.5") and Greenbriar 1 Pond (10 newts; N 40° 46' 41.3", W 78° 0' 27.4"), both landlocked and fishless woodland ponds in the Scotia Barrens (PA State Game Lands #176), Centre County, Pennsylvania. Little Acre newts were collected from March 2003 to June 2005; Greenbriar 1 newts were all collected on 27 May 2004. Newts were killed within 3 hr of

capture, and intestines and their contents were fixed and preserved in 70% ethanol (30% water) until further dissections could be performed. Upon removal from the digestive tract, worms were transferred to 10% glycerol in 70% ethanol. Worms were cleared for study in 100% glycerol by evaporating the ethanol out overnight. Measurements in micrometers (unless otherwise indicated), using light microscopy.

A JSM-6490 scanning electron microscope (Jeol, Peabody, MA) was used to photograph the tail of a female worm under low vacuum (15 Kv, Spot 40, 30 Pa pressure), allowing imaging of wet specimens without critical point drying. All nine specimens were deposited as type specimens in the US National Parasite Collection (USNPC), Beltsville, Maryland.

DESCRIPTION

Hysterothylacium burtti n. sp.

(Figs. 1-2)

Diagnosis: Medium-sized worms, cuticle annulated. Anterior end with 3 equal-sized labia, length similar to width. Interlabia medium-sized, each composed primarily of 2 hook-like protrusions and approximately half the length of the labia. Dorsal labium with 2 lateral double papillae. Subventral labia each with 1 double and 1 single papillae. Esophagus cylindrical, 8.8-14.6% of body length. Amphids not located. Ventricular appendix and caecum usually similar in length (appendix-to-caecum ratio 1: 0.63-2.52). Ventriculus not distinguished from appendix. Lateral alae along entire body length but reduced towards anterior of worm. Nerve ring located one fifth down the esophagus. Single excretory pore immediately posterior to nerve ring. Tail tip smooth, lacking spines or protuberances.

Male (based on 1 mature specimen): Body 12.0 mm long, maximum width 0.69 mm at second third of body. Head 130 long, 155 wide at base. Length of esophagus 1.40 mm, representing 11.7% of body length. Nerve ring and excretory pore 310 and 610 from base of head, respectively. Ventricular appendix 800 long, caecum 620 long (ratio 1: 0.78). Spicules subequal, length 330 and 390. Tail length 110, tail tip lacking spines and protuberances. Ten pairs of precloacal caudal papillae; no adcloacal or postcloacal papillae located. Phasmid not seen.

Female (based on 8 mature specimens, holotype in parentheses): Body 9.5-19.8 (11.7) mm long, maximum width 0.50-1.00 (0.85) mm at second third of body. Head 113-203 (165) long, 140-210 (193) wide at base. Length of esophagus 1.10-1.84 (1.29) mm, representing 8.8-14.6% (12.9%) of body length. Nerve ring and excretory pore 240-320 (280) and 260-520 (400) from base of head, respectively. Ventricular appendix 290-940 (920) long, caecum 540-730 (580), with ratio 0.40-1.59 (1.59). Tail length 110-290 (245); tail tip cylindrical with no spines or protuberances. Vulva position at 27.4-38.1% (27.4%) of body length from anterior end. Uterus 3.8-4.9 (4.3) mm long. Eggs 93-104 (99) long and 90-98 (93) wide.

Taxonomic summary

Type host: *Notophthalmus viridescens* (Rafinesque).

Site of infection: Stomach and duodenum.

Type locality: Little Acre Pond (40° 48' 5.8" N, 77° 56' 36.5" W) and Greenbriar 1 Pond (40° 46' 41.3" N, 78° 0' 27.4" W), Pennsylvania.

Type locality habitat: Landlocked, fishless freshwater woodland ponds.

Date of collection: March 2003 – June 2005 (specifics in Methods)

Number of specimens studied: Nine

Prevalence: 4% (4/95) in Little Acre and 30% (3/10) in Greenbriar 1.

Mean intensity: Mean = 1.3

Specimens deposited: Holotype female, USNPC 102001; Allotype male, USNPC 102002; Paratype females, USNPC 102003-102008 (total of nine specimens; two from the same newt are stored together).

Etymology: The specific epithet is given in honor of Edward H. Burt of Ohio Wesleyan University, who advised T. R. Raffel during his undergraduate studies.

Remarks

There have been 65 species of *Hysterothylacium* Ward & Magath, 1917 described from marine, brackish, or freshwater fishes worldwide (Li et al., 2008). Twenty-one of these occur in North and South America and the Hawaiian Islands, including 12 species in marine fishes, 7 in freshwater fishes and 2 in estuarine fishes (Gopar-Merino et al., 2005).

General morphology clearly places the species within the genus *Hysterothylacium*. The triradiate head morphology, prominent labia, and cylindrical esophagus place this worm in Ascaridida (Chabaud, 1974), and the presence of interlabia coupled with both an intestinal caecum and an appendix limits the possible genera to *Contracaecum* Railliet and Henry, 1912, *Hysterothylacium*, *Iheringascaris* Pereira, 1935, or *Maricostula* Bruce and Cannon, 1989 (Hartwich, 1974; Bruce and Cannon, 1989). The unilateral excretory pore at the level of the nerve ring and relatively small interlabia are characteristic of *Hysterothylacium* and distinguish this worm from *Contracaecum* (Anderson, 2000). The lack of plicated annulations and well-defined posterior borders to

the labia and interlabia distinguish it from the single species of *Iheringascaris* (Deardorff and Overstreet, 1980). The short caecum relative to the esophagus (not always >50% length of esophagus) distinguishes this species from species of *Maricostula* (Bruce and Cannon, 1989). The location of these worms in the stomach or between the stomach and duodenum is unusual for ascarid nematodes in general, but not uncommon in species of *Hysterothylacium* (Anderson, 2000).

Hysterothylacium burtti differs from all other species described for the genus in having an amphibian host (Gopar-Merino et al., 2005). Outside of a unique host record, the new species may be readily distinguished from 30 species based on the presence of lateral alae (Lakshmi, 2005; Li, An et al., 2007; Li, Xu et al., 2007). Moreover, the new species may be differentiated from 20 of the remaining 35 species based on the absence of clear ornamentation on the tail (Bruce, 1990; Torres et al., 1998; Shih and Jeng, 2002; Li, An et al., 2007). We compare the new species to congeners that cannot be readily distinguished by lateral alae or tail tip ornamentation: *H. magnum* Smedley, 1934; *H. sebae* Bruce, 1990; *H. auctum* Rudolphi, 1802; *H. ilishae* Yamaguti, 1941; *H. arii* Yamaguti, 1954; *H. epinepheli* Yamaguti, 1941; *H. coiliae* Yamaguti, 1941; *H. cenaticum* Bruce and Cannon, 1989; *H. pagrosomi* Yamaguti, 1935; *H. zenis* Baylis, 1929; *H. cornutum* Stossich, 1904; *H. trichiuri* Thwaite 1927; *H. incurvum* Rudolphi, 1819; *H. eurycheilum* Olsen, 1952; and *H. ogcocephali* Olsen, 1952. We also compare species that share similar habitat (infecting fresh-water fishes) and type locality (North America).

Only 3 species of *Hysterothylacium* have previously been reported from freshwater fish hosts in North America. The head morphology and relative dimensions of

H. burtti closely resemble *H. analarum*, a parasite found in pumpkinseed sunfish (Rye and Baker, 1984). However, the presence of lateral alae, lack of tail tip spines, smaller body length (9.5-19.8 mm vs. 19.8-25.6 mm), shorter spicules (390 vs. 450-625), and short caecum relative to the appendix (1: 0.4–1.6 vs. 1: 0.33) distinguish this species from *H. analarum* (Rye and Baker, 1984). *Hysterothylacium burtti* can be distinguished from *H. brachyurum*, a common parasite of North American freshwater fishes, by smaller lateral alae in the anterior third of the body and lack of tail tip spines (Rye and Baker, 1984). It can be distinguished from *H. dollfusi*, the only other *Hysterothylacium* species found in N. American freshwater fishes, by its shorter spicule length (0.39 mm vs. 1.07-1.45 mm), smaller size (9.5-9.8 mm vs. 45-65 mm), shorter ventricular appendix (0.29-0.94 mm vs. 4.5-6.0 mm) and presence of lateral alae (Schmidt et al., 1974; Li, An et al., 2007).

The presence of lateral alae and absence of ornamentation on the tail tip distinguish *H. burtti* from all but 4 of the 22 described *Hysterothylacium* species from North and South America and Hawaii (Gopar-Merino et al., 2005; Li, An et al., 2007). *Hysterothylacium burtti* can be distinguished from *H. eurycheilum* by its smaller size (9.5–19.8 mm vs. 26.2–41 mm), larger ratio of head length to width (1: 0.77–0.99 vs. 1: 1.5–1.7), and shorter spicules (0.33–0.39 mm vs. 0.86 mm) (Deardorff and Overstreet, 1981). *Hysterothylacium burtti* can be distinguished from *H. ogcocephali* by its wider head, smaller length (9.5–19.8 mm vs. 25.5–48.1mm) and larger ratio of cecum to appendix length (1: 0.4–1.6 vs. 1: 2.7–7.3), and from *H. incurvum* by the narrower shape of its interlabia, shorter spicule length (0.33–0.39 mm vs. 2.6-8.7 mm) and smaller spicule length relative to body length (2.7–3.3% vs. 12–25%, Deardorff and Overstreet,

1980) *Hysterothylacium magnum* infects marine fishes off the coast of Nanaimo, British Columbia, Canada (Bruce et al., 1994), and can be further distinguished from *H. burtii* by its larger spicules (3.6 mm vs. 0.33-0.39 mm) and much larger body length of 35-102 mm (Smedley, 1934).

The remaining 11 species for comparison infect marine fishes outside the Americas, except for *H. arii* which is restricted to catfish (*Arius* sp.) located in Borneo (Bruce et al., 1994). This makes them unlikely to be closely related to *H. burtii*, which was isolated from red-spotted newts living in fishless ponds in Pennsylvania. Nevertheless, *H. burtii* is readily distinguished from *H. auctum* and *H. ilishae* based on vulval position (Li, An et al., 2007). In *H. burtii* the vulva is located pre-equatorially (27.4-38.1% from the anterior end) whereas in *H. auctum* the vulva is located post-equatorially (58.7-66.7% from the anterior end). A pre-equatorial vulva also differentiates the new species from *H. ilishae*; in addition, *H. ilishae* has spicules that are much larger (2.4-2.5 mm long, 12.0-12.9% of body length vs. 0.33-0.39 mm long, 2.75-3.25% of body length in *H. burtii*). *Hysterothylacium arii*, *H. epinepheli*, *H. sebae*, and *H. zenis* all have absolute spicule lengths of 0.6-3.7 mm (Yamaguti, 1941, 1954; Bruce, 1990), in contrast to the smaller 0.33-0.39 mm spicules of *H. burtii*. Finally, *H. cenaticum*, *H. coiliae*, *H. cornutum*, *H. incurvum*, and *H. pagrosomi* all have relative spicule lengths of 4.7-15.3% of body length {Li, 2007 #1805}, in contrast to relative spicule length in *H. burtii* (2.75-3.75% of body length)..

We have presented a morphological argument to exclude 30 congeners based on the presence of lateral alae. These congeners include 9 species for which the presence or absence of lateral alae is not reported (Li, An et al., 2007). *Hysterothylacium baylisi*

Yamaguti, 1941; *H. salvelini* Fujita, 1940; *H. okadai* Fujita, 1940; *H. sebae* Bruce, 1990; *H. seriola* Yamaguti, 1941; *H. bidentatum* Linstow, 1899; *H. rhacodes* Deardorff and Overstreet, 1978; *H. melichthysi* Olsen, 1952; and *H. melanogrammi* Smedley, 1934. *Hysterothylacium baylisi*, *H. salvelini*, *H. okadai*, and *H. melichthysi* have spicules representing 6.0-13.8% of total body length (Li, An et al., 2007), in contrast to 2.75-3.25% in *H. burtii*. *Hysterothylacium burtii* may be distinguished from 4 of the remaining 5 species using absolute spicule length: *H. sebae*, *H. bidentatum*, *H. melanogrammi*, and *H. seriola* have spicules 0.66-4.23 mm in length (Smedley, 1934; Bruce, 1990; Li, An et al., 2007), in contrast to 0.33-0.39 mm in *H. burtii*. Finally, *H. burtii* lacks the elongated lips with equatorially notched flanges characteristic of *H. rhacodes* (Deardorff and Overstreet, 1980). Only two of these species are found in hosts in the Americas, both in marine fishes: *H. melichthysi* in *Melichthys bunica* (Lacepede) from Honolulu, Hawaii (Olsen, 1952), and *H. melanogrammi* in *Melanogrammus aeglefinus* (Linnaeus) from St. Andrews, New Brunswick, Canada (Smedley, 1934; Bruce et al., 1994).

DISCUSSION

The presence of a *Hysterothylacium* species in an amphibian is unusual, given that no worm of this genus, or adult worms from closely related species of *Contracaecum*, have ever been found in an amphibian host (Kuperman et al., 2004; Gopar-Merino et al., 2005). Moreover, these specimens were obtained from newts living in fishless ponds, reducing the probability that these worms represent spillover from conspecific fish and suggesting that newts are the normal definitive host for this parasite species. However, the presence of a *Hysterothylacium* species in newts may be due to

the close ecological association of newts with freshwater fishes during recent evolutionary history. Red-spotted newts have mostly aquatic adults and often live in close proximity to freshwater fishes, particularly sunfish (T. R. Raffel, person. obs.). *Hysterothylacium* species typically use invertebrates as intermediate hosts, which must then be ingested for infection of the definitive host to occur (Anderson, 2000; Klimpel and Ruckert, 2005; Luque et al., 2007). Since sunfish and newts share a variety of invertebrate prey (Crowder and Cooper, 1982; Petranka, 1998), it seems plausible that an anisakid nematode parasite of freshwater fish such as *H. analarum* or *H. brachyurum* (Rye and Baker, 1984) might have spilled over to newts and eventually diverged into a new species.

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FIGURE 1. Line drawings of *Hysterothylacium burtti*. (A) Lateral view of the holotype specimen. (B) En face view of a female paratype. (C) Ventral view of the head of a female paratype. (D) Posterior end of the male showing caudal papillae and spicules, lateral view.

FIGURE 2. Photomicrographs of *Hysterothylacium burtti*. (A) Anterior section of the holotype specimen including the head (light micrograph). (B) Egg from a paratype specimen (light micrograph). (C) Scanning electron micrograph the tail tip of a female paratype. (D) Scanning electron micrograph of the head of a female paratype, showing the dorsal papillae and anterior lateral alae. Note that the overall head shape changed during specimen processing.

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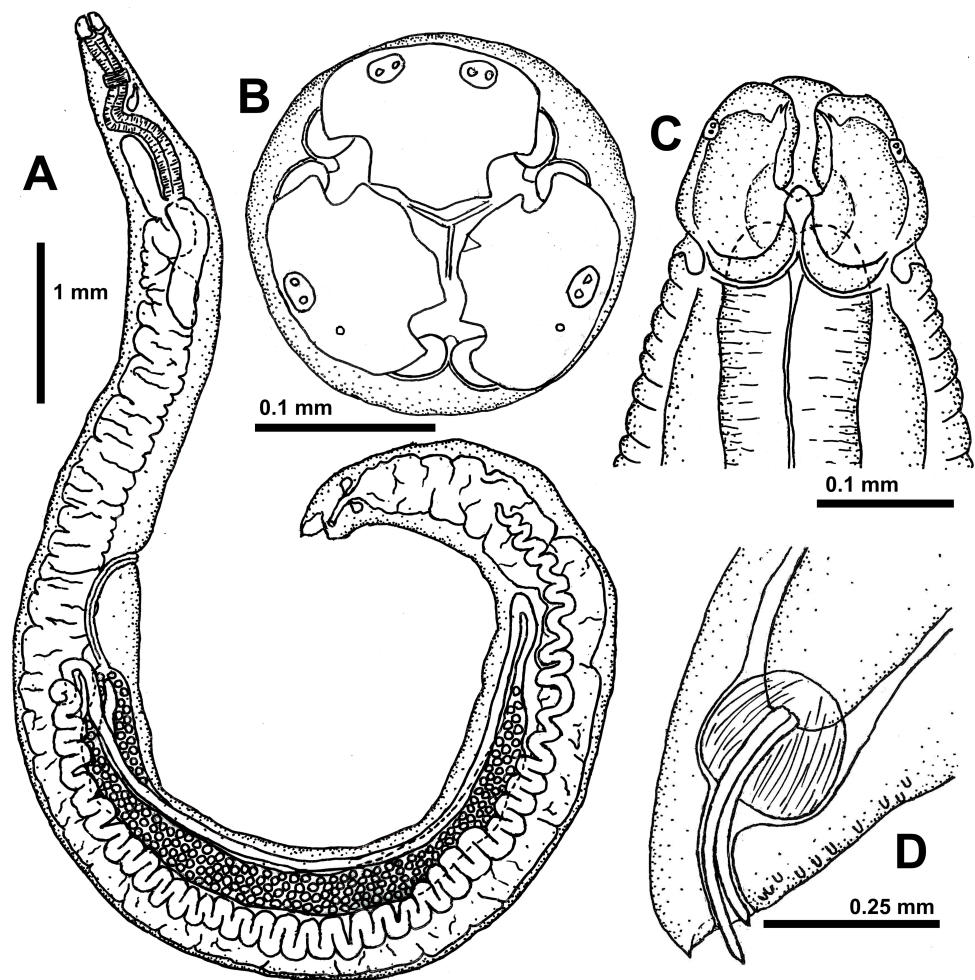


Figure 1.

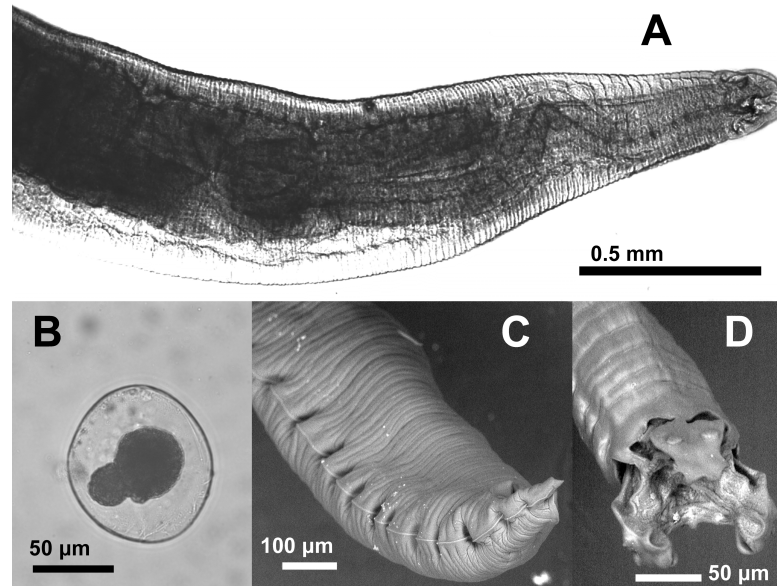
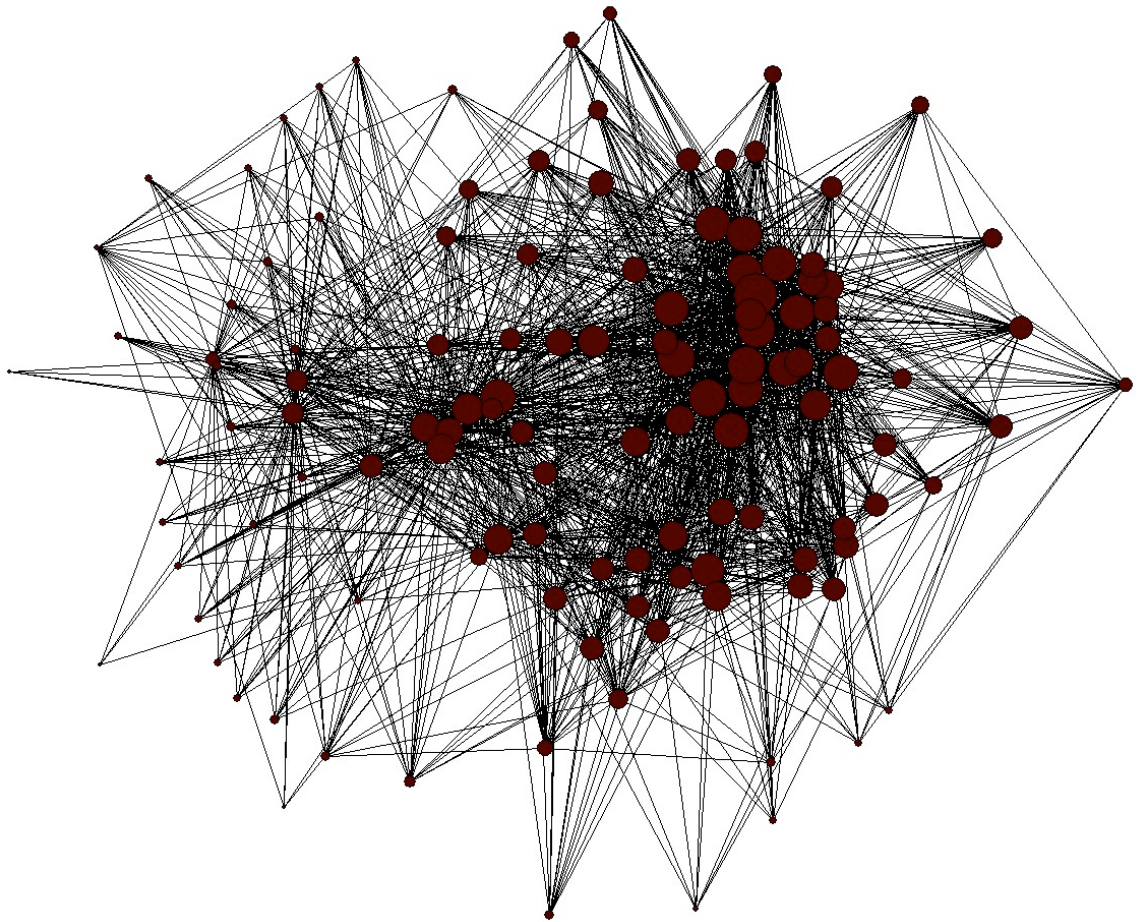


Figure 2.

APPENDIX B

NONMETRIC MULTIDIMENSIONAL SCALING VISUALIZATION OF THE MILL CREEK FOOD WEB



MILL CREEK SPECIES LIST

Benthic invertebrates

1. <i>Anisolaris maritime</i>	2. <i>Amphipoda</i> spp.	3. <i>Annura maritime</i>
4. <i>Aranae</i> sp.	5. <i>Balanus improvisus</i>	6. <i>Bryozoan</i> sp.
7. <i>Callinectes sapidus</i>	8. <i>Chironomidae</i> sp.	9. <i>Congerina leucopheata</i>
10. <i>Coleoptera</i> sp.	11. <i>Corophium</i> sp.	12. <i>Crangon septemspinosa</i>
13. <i>Cyathura</i> spp.	14. <i>Cyathura polita</i>	15. <i>Dulichopidae</i> sp.
16. <i>Gammarus</i> sp.	17. <i>Harpacticoid</i> sp.	18. <i>Hobsonia florida</i>
19. <i>Hydrobia minuta</i>	20. <i>Melampus bidentatus</i>	21. <i>Nematoda</i> spp.
22. <i>Oligochaeta</i> spp.	23. <i>Orchestia</i> sp.	24. <i>Ostracoda</i> sp.
25. <i>Palaeomonetes pugio</i>	26. <i>Philoscia</i> sp.	27. <i>Philoscia vittata</i>
28. <i>Polydora ligni</i>	29. <i>Rhithropanopeus harrisii</i>	30. <i>Spionidae</i> spp.
31. <i>Tabanidae</i> spp.		

Fishes

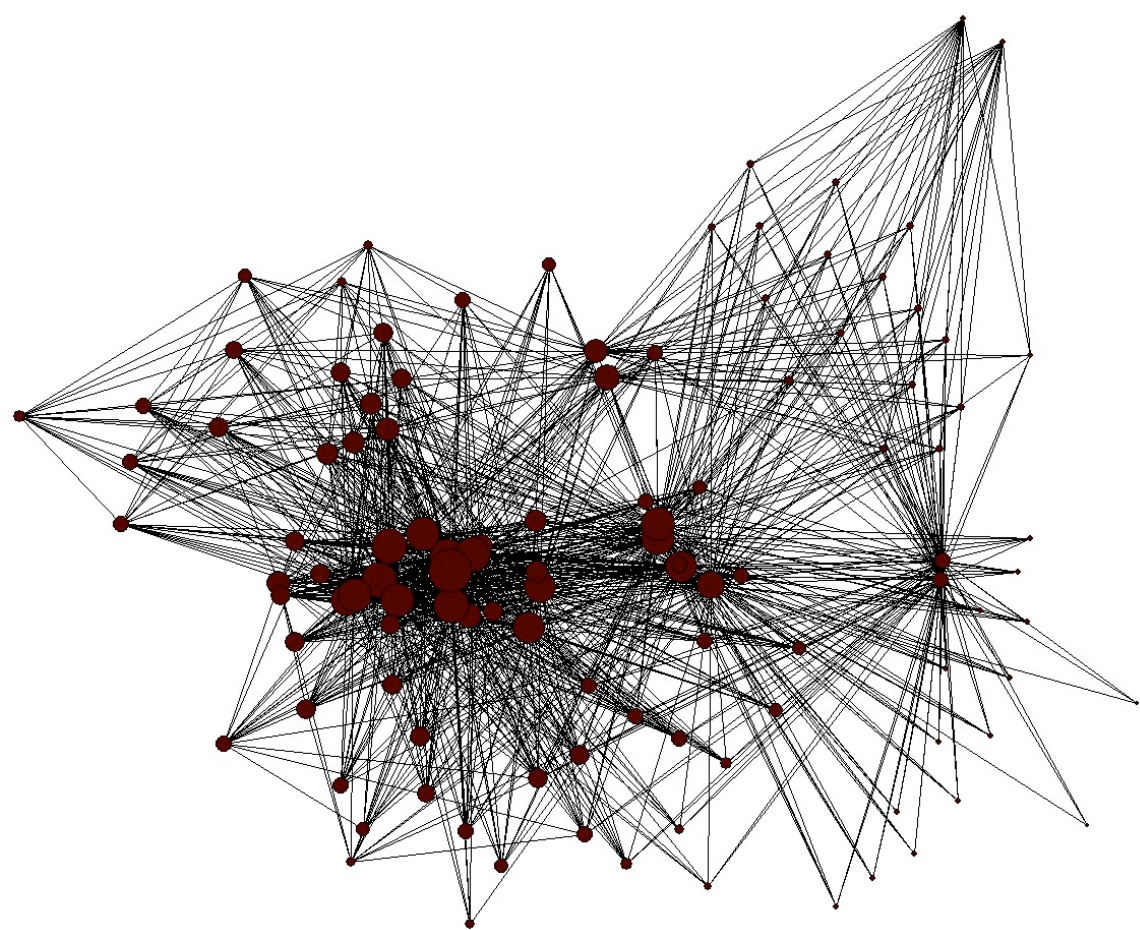
32. Alewife	33. American Eel	34. American Shad
35. Atlantic menhaden	36. Atlantic silverside	37. Bay anchovy
38. Black crappie	39. Blueback herring	40. Bluefish
41. Brown bullhead	42. Carp	43. Gizzard shad
44. Inland silverside	45. Mummichog	46. Northern pipefish
47. Pumpkinseed	48. Spot	49. Striped killifish
50. Striped bass	51. Threespine stickleback	52. Weakfish
53. White perch	54. Winter flounder	

Birds

55. American black duck	56. American goldfinch	57. American kestrel
58. American robin	59. American wigeon	60. American tree sparrow
61. Barn Swallow	62. Black-bellied plover	63. Belted kingfisher
64. Brown-headed cowbird	65. Bank swallow	66. Black skimmer
67. Brant	68. Canada goose	69. <i>Calidris</i> sp.
70. Cedar waxwing	71. Chimney swift	72. Common grackle
73. Common merganser	74. <i>Corvus</i> sp.	75. Common yellowthroat
76. Double-crested cormorant	77. Dunlin	78. European starling
79. Forster's tern	80. Gadwall	81. Great black-backed gull
82. Great blue heron	83. Gray catbird	84. Great egret
85. Green heron	86. Green-winged teal	87. Herring gull
88. Hooded merganser	89. House sparrow	90. Killdeer
91. Laughing gull	92. Mallard	93. Marsh wren
94. Mourning dove	95. Northern cardinal	96. Northern harrier
97. Northern mockingbird	98. Northern shoveler	99. Northern rough-winged swallow
100. Osprey	101. Palm warbler	102. Peregrine falcon
103. Ring-billed gull	104. Ruby-crowned kinglet	105. Ring-necked pheasant
106. Red-tailed hawk	107. Red-winged blackbird	108. Savannah sparrow
109. Semipalmated plover	110. Snowy egret	111. Song sparrow
112. Spotted Sandpiper	113. Swamp sparrow	114. <i>Tringa</i> spp.

115. Tree swallow	116. Willow Flycatcher	117. White-throated sparrow
118. Yellow warbler	119. Yellow-rumped warbler	

**NONMETRIC MULTIDIMENSIONAL SCALING VISUALIZATION OF THE
HARRIER MEADOW FOOD WEB**



HARRIER MEADOW SPECIES LIST

Benthic Invertebrates

1. <i>Callinectes sapidus</i>	2. <i>Idotea</i> sp. (Isopod)	3. <i>Rhithropanopeus harrissii</i>
4. Oligochaete	5. Nematoda	6. <i>Manayunkia aestuarina</i>

7. Chironomidae larvae	8. Copepods	9. Anthozoa
10. <i>Capitella</i> sp.	11. Ostracoda	12. <i>Conger</i> sp.
13. <i>Corophium</i> sp.	14. <i>Crangon</i> sp.	15. <i>Palaeomonetes</i> sp.

Fishes

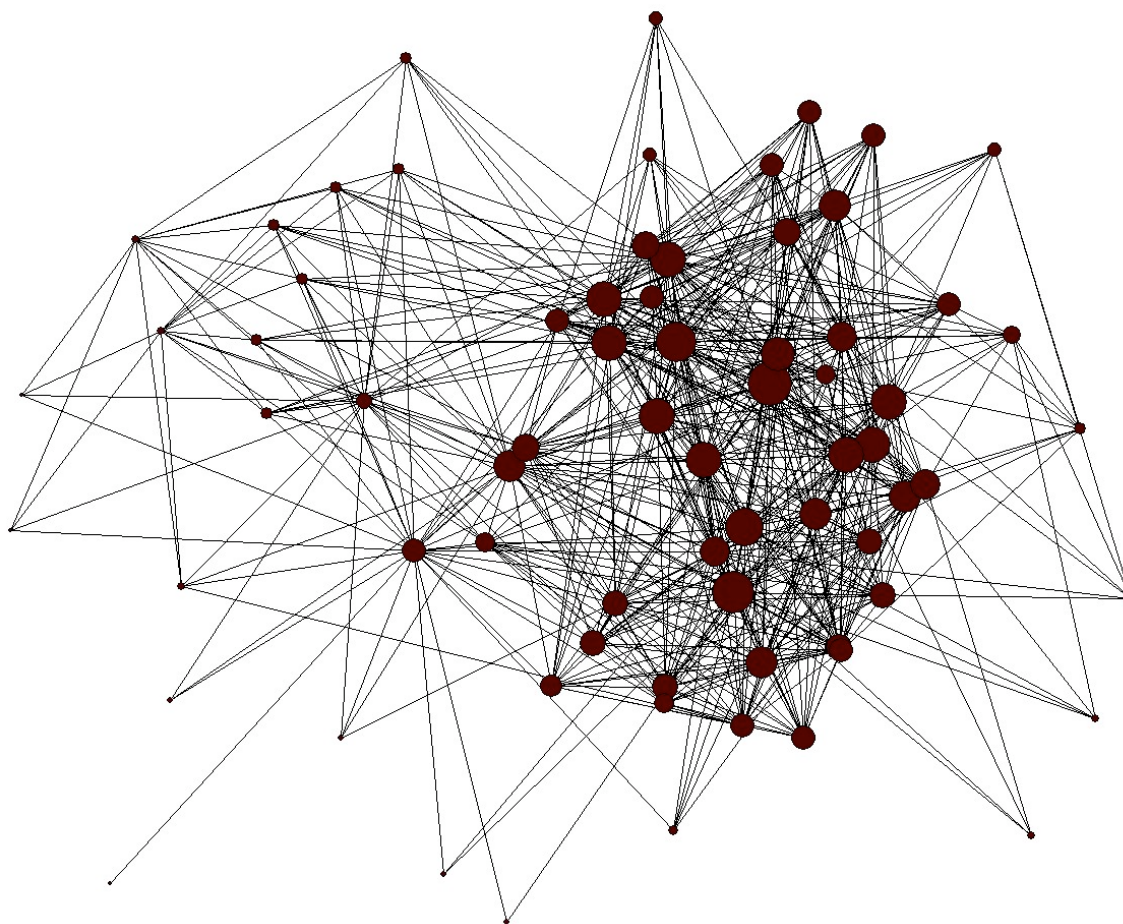
16. Alewife	17. American eel	18. Atlantic menhaden
19. Atlantic Silverside	20. Blueback herring	21. Bluefish
22. Carp	23. Crevalle Jack	24. Gizzard Shad
25. Lookdown	26. Mummichog	27. Spotted Hake
28. Striped Bass	29. Striped Killifish	30. Weakfish
31. White perch	32. Winter flounder	

Birds

33. American goldfinch	34. American black duck	35. American coot
36. American kestrel	37. American robin	38. Barn swallow
39. Black-crowned night heron	40. Baltimore oriole	41. Blackcapped chickadee
42. Belted kingfisher	43. Brownheaded cowbird	44. Bluejay
45. Black skimmer	46. Brown thrasher	47. Blue winged teal
48. Canada goose	49. Calidris species (knots)	50. Common grackle
51. Common merganser	52. Corvus spp.	53. Common yellowthroat
54. Double-crested cormorant	55. Dark-eyed junco	56. European starling
57. Eastern phoebe	58. Forster's tern	59. Gadwall

60. Great black-backed gull	61. Great blue heron	62. Gray catbird
63. Green heron	64. Green-winged teal	65. Great egret
66. hooded merganser	67. House sparrow	68. Herring gull
69. Killdeer	70. Laughing gull	71. Limnodromus spp.
72. Mallard	73. Marsh wren	74. Mourning dove
75. Mute swan	76. Northern cardinal	77. Northern flicker
78. Northern harrier	79. Northern pintail	80. Northern shoveler
81. Northern rough-winged swallow	82. Northern mockingbird	83. Osprey
84. Peregrine falcon	85. Ring-billed gull	86. Rock pigeon
87. Ring-necked duck	88. Ring-necked pheasant	89. Red-tailed hawk
90. Ruddy duck	91. Red-winged blackbird	92. Semipalmated plover
93. Savannah sparrow	94. Snow goose	95. Sora
96. Snowy egret	97. Song sparrow	98. Spotted sandpiper
99. Swamp sparrow	100. Tringa species (shanks)	101. Tri-colored heron
102. Tree swallow	103. Virginia rail	104. White-crowned sparrow
105. Willow fly-catcher	106. Wilson's phalarope	107. Wood duck
108. Yellow warbler	109. Yellow-rumped warbler	

NONMETRIC MULTIDIMENSIONAL SCALING VISUALIZATION OF THE ORITANI FOOD WEB



ORITANI SPECIES LIST

Benthic invertebrates

1. <i>Hobsonia florida</i>	2. <i>Streblospio benedicti</i>	3. <i>Scolecopides virides</i>
4. <i>Nereis succinea</i>	5. Oligochaeta	6. <i>Palmarcorixa</i> sp.(adult)
7. Chironomidae (larvae)	8. <i>Balanus improvisus</i>	9. <i>Cyathura polita</i>

10. <i>Idotea</i> sp.	11. <i>Rhithropanopeus</i> <i>harisii</i>	12. <i>Uca minax</i>
13. <i>Gammarus</i> sp.	14. <i>Littorina</i> sp.	15. <i>Melampus bidentatus</i>
16. <i>Macoma balthica</i>	17. Sipunculoidea	18. Nematoda
19. Nemertea	20. <i>Callinectes sapidus</i>	21. <i>Crangon septemspinosa</i>
22. <i>Palaemonetes</i> sp.		

Fishes

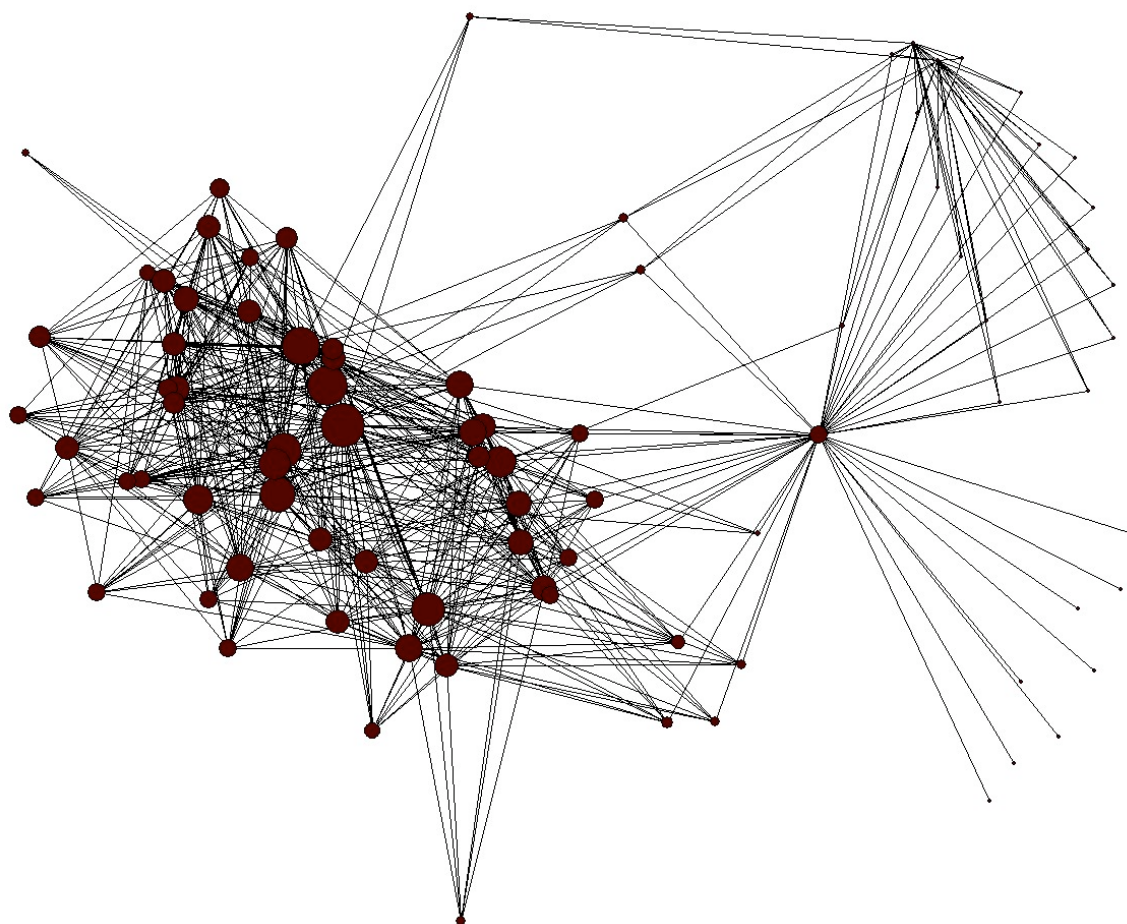
23. American shad	24. Alewife	25. American Eel
26. Atlantic Menhaden	27. Atlantic silverside	28. Bay anchovy
29. Blueback herring	30. Bluefish	31. Brown bullhead
32. Carp	33. Crevalle jack	34. Gizzard Shad
35. Hogchoker	36. Inland silverside	37. Mummichog
38. Spotted Hake	39. Spot	40. Striped bass
41. Striped killifish	42. Threespined stickleback	43. Weakfish
44. Winter flounder	45. White perch	

Birds

46. Tree Swallow	47. Chipping Sparrow	48. Ring-necked Pheasant
49. American Robin	50. Great Egret	51. Mallard
52. Northern Harrier	53. Song Sparrow	54. Swamp Sparrow
55. Common Yellowthroat	56. Herring Gull	57. Marsh Wren
58. Red Winged Blackbird	59. American Kestrel	60. Common Grackle

61. Northern Cardinal	62. American Crow	63. Blue-Winged Teal
64. Double-crested Cormorant	65. European Starling	66. Blue Jay
67. Savannah Sparrow		

NONMETRIC MULTIDIMENSIONAL SCALING VISUALIZATION OF THE SECAUCUS FOOD WEB



SECAUCUS SPECIES LIST

Benthic invertebrates

1. Oligochaeta	2. Nemoatoda	3. Chironomidae, <i>Chironomus</i> sp.
4. Polychaeta, <i>Glycera</i> sp.	5. Empididae	6. Ceratopogonidae
7. Tipulidae	8. Amphipoda, <i>Corophium</i> sp.	9. <i>Callinectes sapidus</i>
10. <i>Rhithropanopeus</i> <i>harisii</i>	11. <i>Crangon septemspinosa</i>	12. <i>Palaemonetes</i> sp.

Fishes

13. Alewife	14. American Eel	15. Atlantic menhaden
16. Atlantic silverside	17. Blueback herring	18. Brown bullhead
19. Carp	20. Gizzard shad	21. Inland silverside
22. Mummichog	23. Pumpkinseed	24. Striped bass
25. Striped killifish	26. Threespine stickleback	27. Weakfish
28. White perch	29. Winter flounder	

Birds

30. American Black Duck	31. Canada Goose	32. Gadwall
33. Mallard	34. Greater Black-backed Gull	35. Greater Yellowlegs
36. Herring Gull	37. Least Sandpiper	38. Ring-billed Gull
39. Sanderling	40. Black-crowned Night	41. Great Blue Heron

	Heron	
42. Great Egret	43. Green Heron	44. American Bittern
45. Least Bittern	46. Snowy Egret	47. Mourning Dove
48. Belted Kingfisher	49. American Kestrel	50. Northern Harrier
51. Osprey	52. Virginia Rail	53. American Crow
54. American Goldfinch	55. American Robin	56. American Tree Sparrow
57. Barn Swallow	58. Blackpoll Warbler	59. Blue Jay
60. Chipping Sparrow	61. Common Grackle	62. Common Yellowthroat
63. European Starling	64. Field Sparrow	65. Grey Catbird
66. House Sparrow	67. Junco	68. Marsh Wren
69. Northern Mockingbird	70. Northern Oriole	71. Palm Warbler
72. Pine Warbler	73. Red-winged Blackbird	74. Rufous-sided Towhee
75. Savannah Sparrow	76. Sharp-tailed Sparrow	77. Song Sparrow
78. Swamp Sparrow	79. Tree Swallow	80. White-throated Sparrow
81. Yellow Warbler	82. Yellow-rumped Warbler	83. Double-crested Cormorant
84. Northern Flicker		

Curriculum Vitae

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Education

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| 2000, December | B.Sc. in Parasitology |
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Publications

1. Raffel, T.R., & Anderson, T.K. (in press). A new species of *Hysterothylacium* (Nematoda: Anisakidae) from the stomach of the red-spotted newt, *Notophthalmus viridescens*, from Pennsylvania fishless ponds. *Journal of Parasitology*.
2. Anderson, T.K., & Sukhdeo, M.V.K. (in press). Abiotic versus biotic hierarchies in the assembly of parasite populations. *Parasitology*.
3. Anderson, T.K., & Sukhdeo, M.V.K. (in revision). Core/periphery structure in food web networks constrains parasite diversity. *Journal of Animal Ecology*.
4. Anderson, T.K., & Sukhdeo, M.V.K. (in prep). A community stability threshold in estuarine marshes informs parasite establishment and persistence. *Oecologia*.