**The effects of habitat connectivity and regional heterogeneity on artificial pond
metacommunities**

by

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Abstract

While much evidence suggests that ecosystem functioning is closely related to biodiversity, present rates of biodiversity loss are high. With the emergence of the meta-community concept ecologists have become increasingly aware that both local processes (e.g. competition, predation), and regional processes (e.g. dispersal and regional heterogeneity) affect ecological communities at multiple spatial scales. I experimentally investigated the effects of habitat connectivity and regional heterogeneity on biodiversity, community composition, and ecosystem functioning of artificial pond metacommunities of freshwater invertebrates at the local (α), among-community (β), and regional (γ) spatial levels.

There was a significant effect of habitat connectivity on mean local richness, but mean local Simpson diversity, mean local functional diversity (FD), and all the three indices of ecosystem functioning investigated (regional abundance, invertebrate biomass, and chlorophyll *a* concentration) were unaffected by connectivity levels. Regional heterogeneity had no effect on local diversity, but enhanced both among-community richness and among-community Simpson diversity. Conversely, connectivity reduced among-community Simpson diversity. All indices of regional diversity were unaffected by either connectivity or heterogeneity. Despite expectations that there would be strong interactions between the effects of connectivity and heterogeneity on species richness, there were no interactions for any index of biodiversity at any spatial scale.

Invertebrate community composition was unaffected by either connectivity or heterogeneity, though there was a significant effect of heterogeneity on its variance. Neither connectivity nor heterogeneity had significant effects on any index of ecosystem functioning, nor among-community coefficients of variation of ecosystem functioning.

Connectivity appears to act mainly as a force homogenizing habitat patches in a region, as opposed to having strong effects in and of itself on communities. Conversely, heterogeneity acts largely as a diversifying force, maintaining differences between communities within a region, but, similar to connectivity, it does not have clear effects on communities at the local scale. Despite the different processes expected to act in homogeneous and heterogeneous regions, it does not appear that connectivity and heterogeneity interact strongly.

Co-Authorship

This thesis conforms to the manuscript format as outlined by the School of Graduate Studies and Research. The manuscript that is a direct result of this thesis and its coauthors is:

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Chapter 1

General Introduction

A major goal of ecology is uncovering the processes that govern biological communities. Increasingly, understanding the factors that underlie biodiversity, relative species abundances, and ecosystem functioning is not merely a matter of academic concern, but rather one of grim urgency. While we have yet to fully understand the relationship between biodiversity and ecosystem functioning, it is clear that biodiversity plays an important role in maintaining ecosystem functioning, especially during periods of disturbance (Loreau et al. 2001; Worm et al. 2006). Yet even as we have come to understand this, present rates of species loss are phenomenally high (Pimm et al. 1995; Thomas et al. 2004; Worm et al. 2006). It is essential that humanity understands not only the likely consequences of our situation, but also how these consequences might be minimized. An important first step in gaining such comprehension is determining on a basic level which processes affect ecological communities.

Since MacArthur and Wilson published their theory of island biogeography (MacArthur and Wilson 1963, 1967) it has become increasingly clear that ecological communities are subject to both local and regional processes. While earlier researchers had considered dispersal and the spatial organization of habitats (e.g. Skellam 1951; Andrewartha and Birch 1954; Huffaker 1958), the effects of these processes were largely ignored by community ecologists until the advent of MacArthur and Wilson's theory, and the subsequent introduction of the metapopulation concept (Levins 1969), propelled these concepts into the ecological mainstream. As a result, it has become clear that the spatially discrete nature of biological habitats and inter-habitat dispersal play important roles in ecological communities.

Prior to the incorporation of regional processes into the study of community ecology the impressive biodiversity of communities presented a problem for ecologists. The competitive exclusion principle, which had been well established by both theoretical and empirical studies (Gause 1934), suggested that only one species should be able to exist for any given niche or limiting resource, yet even in communities that seemed to offer relatively few niches there remained high levels of biodiversity (Hutchinson 1961). Hutchinson (1961) originally termed this the paradox of the plankton, and it has since been generalized to the biodiversity paradox (Clark et al. 2007).

The theory of island biogeography (MacArthur and Wilson 1963, 1967) represented a significant departure from the competitive exclusion principle by postulating that the biodiversity of a habitat was not necessarily a function of the number of niches present in that habitat, but rather a function of its relationship to other habitats from which other species could immigrate. This incorporation of regional processes into community ecology was furthered by the metapopulation concept. Levins (1969) developed a model describing the dynamics of species patch occupancy in a collection of dispersal-connected, but discrete, habitat patches as a function of colonization and local extinction. Levins termed this collection of dispersal-connected, but spatially discrete, populations a “metapopulation,” and demonstrated that while populations in individual patches might go extinct, regional persistence was permitted as long as all local populations did not simultaneously go extinct and persisting local populations could colonize empty patches. Levins’ metapopulation model marked a synthesis of local processes (which ostensibly

underlay local extinctions), and regional processes (which controlled the colonization of new habitats) in determining regional species persistence.

The elegant simplicity of Levins' model inspired a boom in theoretical development around the metapopulation concept. A great deal of research can be argued to find roots in the "patch-dynamic" nature of the model, among them a number of studies investigating the effects of discrete habitats and dispersal (or its landscape analogue, habitat connectivity, which defines the propensity for inter-patch exchange of organisms and materials (Taylor et al. 1993)) on competition, predation, and relative species abundances. These last studies form the beginnings of the metacommunity concept, a term which would later be developed by Wilson (1992) and Leibold et al. (2004) (among others), as a set of communities linked by dispersal of some constituent species.

The Metacommunity Concept

Metacommunity theory has served as the focal point for the study of ecological communities at multiple spatial scales, however, it is not a conceptually homogeneous field. Indeed, Leibold et al. (2004) highlighted four metacommunity perspectives that have had significant influence on research: the patch-dynamic perspective, the species-sorting perspective, the mass-effects perspective, and the neutral perspective. All of the perspectives are concerned with how space and dispersal affect ecological communities, but they have distinct histories and vary in the relative importance attributed to dispersal and regional heterogeneity (among other things). Patch-dynamic metacommunity models are often concerned with species presence/absence in a set of connected identical patches. As such, the patch dynamics perspective is a direct extension of Levins' (1969) meta-

population model. Patch-dynamic models often assume dispersal levels to be relatively limited to maintain spatial asynchrony and allow for regional coexistence by life-history trade-offs, often a competition-colonization trade-off (Holyoak et al. 2005). The species-sorting perspective highlights the importance of local environmental heterogeneity, which is assumed to be reflected in heterogeneity of competitive ability. Here the major effects of dispersal are the introduction of species to suitable patches, and allowing community composition to track environmental change (Leibold et al. 2004), and therefore the assumption is that dispersal is not high enough to maintain species in patches where their long-term growth would be negative (Holyoak et al. 2005). Conversely, the mass-effects perspective (Shmida and Wilson 1985) describes a situation in which dispersal rates are high enough that species are maintained in environments where they could not persist in the absence of dispersal. As such, the mass effects perspective assumes that levels of both dispersal and regional heterogeneity are significant enough to create source-sink dynamics. Leibold et al. (2004) have suggested that this emphasizes the role of spatial dynamics in that patch-occupancy is more reliant upon habitat connectivity than local environmental conditions (but note that this is not necessarily true for relative species abundances). Finally, neutral models view all individuals or species as possessing equal fitness, with the end result that communities are controlled completely by speciation, migration, and ecological drift (Hubbell 2001; Leibold et al. 2004).

While actual metacommunities are unlikely to strictly conform to any of the above perspectives, there has been considerable interest in determining which metacommunity perspectives are empirically valid. Cottenie (2005) conducted a meta-analysis on

empirical data which suggested that the most common type of metacommunity resembled the species-sorting perspective, with mass-effects being the second most common, and relatively few systems resembling patch-dynamic and neutral perspectives. Interestingly, Cottenie (2005) also found that system characteristics such as dispersal mode (e.g. passive, active), habitat type, and spatial scale could explain much of the variation in the relative importance of local environmental conditions and space to metacommunities.

Metacommunity theory has become the primary locus for investigating the simultaneous effects of local and regional processes on community composition, and has produced a wealth of theoretical and empirical results. Below I review some of these results, with particular attention to the effects of habitat connectivity and heterogeneity on biodiversity and processes that are considered to play an important role in biodiversity: population dynamics, competition, and predation. I further review how local and regional processes are likely to affect ecosystem functioning.

Biodiversity in Metacommunities

As metacommunity theory deals with biodiversity at multiple spatial scales it is often of interest to investigate not only the biodiversity of a given habitat patch (local or α -diversity), but also the total diversity of a group of patches (regional or γ -diversity), as well as the extent to which patches within the region differ (among-community or β -diversity). These various levels may be related to each other by a multiplicative relationship (Whittaker 1972), or more commonly by an additive relationship (Lande 1996): $\bar{\alpha} + \beta = \gamma$, (mean local diversity + among community diversity = regional diversity).

Empirical and theoretical evidence strongly suggests that low to moderate levels of habitat connectivity increase local diversity (Warren 1996a; Warren 1996b; Gilbert et al. 1998; Mouquet and Loreau 2002; Loreau et al. 2003; Mouquet and Loreau 2003; Cottenie and De Meester 2004; but see Shurin 2000; Forbes and Chase 2002), though this effect may be dependent upon other factors such as predation (Shurin 2001; Kneitel and Miller 2003), initial among-community richness (Cadotte 2006a), or the time at which richness is examined (Cadotte and Fukami 2005). Conversely, the effects of habitat connectivity on regional diversity are more ambiguous, with some studies finding no effects (Warren 1996b; Cadotte et al. 2006a), positive effects (Kneitel and Miller 2003), or negative effects (Forbes and Chase 2002; Mouquet and Loreau 2003; Cadotte and Fukami 2005; Cadotte 2006a; France and Duffy 2006). Accordingly, in a meta-analysis Cadotte (2006b) found that while the effects of connectivity on local diversity were significantly positive, there was a trend for connectivity to decrease regional diversity, but this was not significant. The effects of connectivity on among-community diversity seem to be clearly negative (Warren 1996a; Mouquet and Loreau 2003; Cadotte and Fukami 2005), but again this effect may depend on the amount of among-community richness initially present in the metacommunity (Cadotte 2006a).

The effects of regional heterogeneity on biodiversity have been less studied empirically, however as noted above, heterogeneity plays an important role in the most common metacommunity perspectives. Theoretical evidence has suggested that heterogeneity has a positive effect on local richness, especially at intermediate levels of connectivity (Mouquet and Loreau 2003), a finding supported by Cadotte (2006a) who investi-

gated microcosms with heterogeneity of initial community composition. The effects of regional heterogeneity on both among-community diversity and regional diversity are clearly positive (Mouquet and Loreau 2003; Cadotte 2006a).

Effects of Connectivity and Heterogeneity in Single Species Systems

Dispersal between spatially discrete habitat patches has many implications for single species systems, the most obvious of which is that it allows individuals to colonize patches in which the species is absent, or recolonize patches in which the species has become extinct. In this way, dispersal can ensure indefinite regional coexistence of a species in the face of local extinctions, assuming that patch dynamics are not overly synchronous (Levins 1969). Dispersal may also increase patch population size and fitness, making it less likely that they will go extinct, a process that is termed “the rescue effect” (Brown and Kodric-Brown 1977). Along these lines dispersal can maintain genetic variation in a population by preventing genetic drift from fixing alleles (Slatkin 1987) and by rescuing maladapted populations by introducing adapted individuals (“the genetic rescue effect”) (Antonovics et al. 1997; Urban and Skelly 2006).

There are, however, also potential negative effects of dispersal on metapopulations. For example, high levels of dispersal could prevent populations from adapting to local environments (Slatkin 1987), synchronize patch dynamics (Gyllenberg et al. 1993), or cause reduced abundance or extinction by depleting habitat patches where the population is doing well (Holt 1985).

Spatial heterogeneity is likely to play an important role in metapopulation dynamics by fostering asynchronous local dynamics, a factor important in metapopulation per-

sistence. Furthermore, while variation in population fitness might seem to exert negative effects on metapopulations, sink populations can stabilize systems with unstable source populations (Holt 1985), and metapopulations consisting entirely of sink populations have been shown to experience long term persistence with sufficient spatiotemporal variation and dispersal (Matthews and Gonzalez 2007). In addition, spatial heterogeneity plays an important role in maintaining genetic diversity by sheltering it from the homogenizing effects of selection, “the genetic storage effect” (Gandon et al. 1996; Urban and Skelly 2006).

Competitive Coexistence in Metacommunities

Perhaps because of its clear relationship to the biodiversity paradox, the coexistence of competing species has received much attention from metacommunity researchers. Two major mechanisms for competitive coexistence have emerged from this work: coexistence due to life-history trade-offs such as the competition-colonization trade-off, and coexistence due to heterogeneity of competitive ability (Hoopes et al. 2005).

An important finding of patch-dynamic models of competition was that an inferior competitor could coexist in a region with a superior competitor as long as the inferior species was sufficiently better at colonizing empty habitat patches (Hastings 1980). These models typically examine strictly hierarchical competition among two or three species, however they can allow for regional coexistence of an indefinite number of competitors as long as each inferior competitor is sufficiently better at dispersing compared to superior competitors (Hastings 1980). This ability for inferior competitors to coexist regionally by being superior in colonization ability has been termed the competition-

colonization trade-off, and is remarkable in that it permits for regional coexistence in a competitively homogeneous space.

While the competition-colonization trade-off is well established theoretically, empirical confirmation has proven more elusive. Evidence that stronger competitors are weaker colonizers has been found for some animal and protozoan communities (Hanski and Ranta 1983; Cadotte et al. 2006b), but studies of plant communities have not found such a relationship (Jakobsson and Eriksson 2003; Clark et al. 2004). Further criticism has come due to the unrealistic assumption of strict competitive hierarchies employed in most trade-off models, however Calcagno et al. (2006) have demonstrated that coexistence is still possible where the trade-off is not absolute and where preemptive competition is allowed.

Coexistence of competing species can also result from spatiotemporal heterogeneity of relative competitive abilities. Chesson (1985) has suggested, for example, that temporal heterogeneity in competitive ability can permit coexistence of competing species if generation times are long enough that species can coexist based on population increases made in “good” times, a mechanism he has called “the Storage Effect.” Spatial heterogeneity in competitive ability can allow for regional coexistence of species by regional niche differentiation, and can allow for local competitive coexistence if dispersal maintains species in patches where they could not otherwise persist (Levin 1974; Shmida and Wilson 1985; Amarasekare and Nisbett 2001; Mouquet and Loreau 2002, 2003), the so-called Mass-Effect. High dispersal rates, however, can have negative effects on competitive coexistence under conditions where species are not globally competitively equivalent

(Amarasekare and Nisbett 2001; Mouquet and Loreau 2002): as dispersal between patches reaches high levels the individual communities within metacommunities begin to resemble one super-patch and locally dominant competitors from each patch are replaced by a regionally dominant competitor, preventing local and regional coexistence (Mouquet and Loreau, 2002, 2003).

Both major spatial mechanisms for competitive coexistence require that dispersal rates not exceed certain levels. In terms of the competition-colonization trade-off, colonization of empty habitat by the weaker competitor is essential to regional coexistence, but coexistence is more likely where the colonization rate of the dominant competitor is low (as this imposes less stringent demands on the colonization rate of the weaker competitor). Similarly, when coexistence depends upon heterogeneity of competitive ability, moderate levels of connectivity permit local competitive coexistence by mass effects, but high levels of connectivity decrease the chances for local and regional coexistence as the region effectively becomes a super-patch (Mouquet and Loreau 2003).

Trophic Interactions in Metacommunities

Theoretical and empirical evidence about the effects of predation on biodiversity is ambiguous. While there is some evidence that predators may facilitate competitive coexistence by limiting the ability of any one species to monopolize a community's resources (Paine 1966; Shurin and Allen 2001), there is also considerable evidence that predation can reduce local or regional biodiversity (Schoener and Spiller 1996; Shurin 2001; Kneitel and Miller 2003; Cadotte et al. 2006a). The ultimate effects of predation on local and regional community composition likely depend on a suite of factors, such as the

generality of the predator in question (Jiang and Morin 2005), the diversity of non-prey species present (Kratina et al. 2007), the presence of prey-refuges (Gause 1934), levels of disturbance or resources (Kneitel and Chase 2004), and the opportunity for either the predator or the prey species to disperse.

The discrete spatial nature of biological habitats can stabilize otherwise unstable predator-prey interactions (Huffaker 1958; Walde 1994; Holyoak and Lawler 1996), a fact likely tied to dispersal opportunities that alleviate predation pressure or that provide needed food resources. Holt (1997) has suggested that food chain length may be constrained by habitat connectivity, as higher-level predators require large patch networks in which to persist, and Huxel and McCann (1998) have shown that low levels of allochthonous inputs can stabilize food web dynamics, though high levels of allochthonous inputs can destabilize foodwebs, leading to species loss. The ways in which dispersal modifies the relationship between predation and biodiversity clearly depend on a variety of factors, such as the relative dispersal abilities of predator and prey species (Huffaker 1958), predator identity (Shurin 2001), and the presence of a regional colonist pool to replace predator-excluded species (Shurin 2001). While dispersal may increase the diversity of competing species (see above), if the increased connectivity also allows travel of predators then the positive effects of dispersal on biodiversity may be overcome by the negative effects of predation (Kneitel and Miller 2003; Cadotte and Fukami 2005).

The role of spatial heterogeneity in metacommunity trophic interactions appears to be stabilizing. Variation among prey individuals in the probability of predation can increase the stability of predator-prey interactions (Gause 1934; Hassell 1978), and disper-

sal only enhances regional persistence of predator-prey systems when local dynamics are asynchronous, which is more likely to occur in heterogeneous regions (Taylor 1988).

Ecosystem Functioning and Metacommunities

Studies explicitly dedicated to the relationship between connectivity and ecosystem functioning largely focus on the effects of connectivity on productivity and the spatiotemporal variability of productivity. Mouquet and Loreau (2003) found a monotonic negative response of local productivity to connectivity in their theoretical metacommunity as competitive dominants were replaced with less productive species by mass effects. Conversely, Loreau et al. (2003) found a unimodal relationship between connectivity and productivity due to a positive relationship between biodiversity and productivity. Furthermore, in communities where richness increases monotonically with connectivity one might expect that productivity would also share a monotonic positive relationship with connectivity.

In accordance with such ambiguous theoretical predictions, empirical results on the relationship between connectivity and ecosystem functioning have been varied. Many studies have found increased abundances with increased connectivity (Gonzalez et al. 1998; Kneitel and Miller 2003), however others have found lower abundances with increased connectivity (Forrest and Arnott 2006), and it seems clear that the effects of connectivity on abundance are often species specific (Holyoak and Lawler 1996; Holyoak 2000). Furthermore, many studies find no effect of dispersal on biomass (Shurin 2000; Shurin 2001; Forrest and Arnott 2006). Underscoring the fact that predictions about the relationship between connectivity and productivity rely on the relationship between con-

nectivity and richness, France and Duffy (2006) explicitly manipulated connectivity and richness and found that while richness often had marked effects on ecosystem functioning, dispersal did not. In fact, contrary to theoretical suggestions that connectivity should reduce temporal variation in productivity (Loreau et al. 2003), France and Duffy (2006) found that there was no effect of connectivity on spatial variation in ecosystem functions, and that connectivity significantly enhanced temporal variation in epiphytic chlorophyll.

Theoretical predictions about the relationship between connectivity and productivity rely on a variety of assumptions. For example, while much empirical research has found a positive relationship between biodiversity and ecosystem functioning (Loreau et al. 2001), there is disagreement as to whether this relationship is indicative of the effects of richness *per se*, of richer communities having higher functional diversity (Tilman et al. 1997), or of richer communities being more likely to include particularly productive species (Aarssen 1997). Furthermore, theoretical predictions about the role of connectivity in determining levels of ecosystem functioning also make assumptions about the levels of dispersal limitation and priority effects in the system, some of which may not be realistic. For example, in the model presented by Mouquet and Loreau (2003) the species best suited to a given community was initially present there, and as a result productivity could only decrease with increased dispersal. Conversely, had communities been initially dispersal limited (with poor correlation between local environmental conditions and species fitness optima) it is likely that dispersal would have led to increases in productivity. While much theoretical work is predicated on assumptions of regional heterogeneity that allows for spatial heterogeneity of fitness optima, and therefore productivity, I am aware

of no theoretical studies that investigate the effects of different levels of heterogeneity on ecosystem functioning.

Conclusion on Effects of Connectivity and Heterogeneity on Metacommunities

Dispersal between spatially discrete habitats has the potential to stabilize otherwise unstable community interactions such as competition and predation, however as dispersal rates increase to high levels these interactions often become unstable again, due to increasing patch synchrony and the loss of spatial structure. Heterogeneity generally stabilizes community interactions by supporting different fitness optima allowing for regional coexistence of species or alleles, and by increasing patch asynchrony. The effects of connectivity and heterogeneity on ecosystem functioning are not yet clear, and likely depend on the relationship between these factors and biodiversity or community composition. While there is good reason to believe that connectivity and heterogeneity would have interactive effects on ecological communities (for example, the stabilizing influence of regional heterogeneity is likely minimized at high levels of habitat connectivity) relatively little research has explicitly addressed such an interaction.

Freshwater Invertebrates as a Model System

Freshwater invertebrates possess many characteristics making them good study organisms for metacommunity ecology including: ecological importance, a wealth of background literature concerning most aspects of life history (including dispersal capability), and relatively discrete habitat boundaries.

This thesis focused on the effects of connectivity and regional heterogeneity on rotifers and microcrustaceans (including Cladocera, Copepoda, and Ostracoda). Rotifers

are a group of metazoans typically measuring between 0.1 and 1 mm in length. The phylum Rotifera is composed of roughly 2000 species that exist in the pelagic and littoral zones of freshwater bodies, moist soils, moss, and marine habitats (Wallace and Snell 2001). Rotifers have enormous potential for population growth and colonization of new habitats due to their short generation times (e.g. ~1-2 days at 22°C (King 1967)) and tendency to reproduce parthenogenetically (rotifers cycle between reproducing sexually and asexually with the majority of the life-cycle being asexual, a trait called cyclical parthenogenesis (Wallace and Snell 2001)). Cladocerans are a group of four microcrustacean orders containing roughly 400 species in total and ranging in size from 0.5 to 2 mm (Dodson and Frey 2001). Common to many freshwater habitats, cladocerans are similar to rotifers in that they also have relatively short generation times and have a life cycle involving cyclical parthenogenesis (Dodson and Frey 2001). Contrastingly, copepods, another group of microcrustaceans ranging in size from 0.5 to 2 mm in length, are distinguished from the cladocerans and rotifers by obligate sexual reproduction and relatively long life spans (Allan 1976; Williamson and Reid 2001). The majority of free-living species are included in three orders, the Calanoida which are primarily pelagic, the Cyclopoida which are primarily littoral, and the Harpacticoida which are benthic (Williamson and Reid 2001). Finally, the last group to be well represented in my thesis is the Ostracoda, a group of benthic microcrustaceans with roughly 420 freshwater species in North America (Delorme 2001).

Rotifers and cladocerans are typically described as filter-feeding herbivorous species, however there actually exists considerable diversity in food choice and feeding

method in both groups. While many rotifers and cladocerans are in fact filter-feeders their diets can be quite diverse, including algae, bacteria, and protists (Pace and Vaqué 1994; Wallace and Snell 2001). In addition, some cladocerans and rotifers are raptorial predators, preying primarily on rotifers and small crustaceans (e.g. copepod nauplii) (e.g. Pejler and Berzins 1993; Packard 2001). Still other cladoceran species scrape their food directly from the substrate without the aid of filtration currents (Fryer 1968), and some rotifers feed by piercing the contents of algal cells or rotifer eggs and sucking out the contained nutrients (Pourriot 1977). The three copepod orders each feed in different ways, with calanoids employing both filtration and raptorial feeding (Bundy and Vanderploeg 2002), cyclopoids relying completely on raptorial feeding (Williamson and Reid 2001), and harpacticoids scraping food in the benthos (Williamson and Reid 2001). Calanoid and cyclopoid copepods are considered to be largely omnivorous, with calanoids eating smaller items than cyclopoids (Williamson and Reid 2001). Harpacticoids are considered to be herbivorous, but similar to the “herbivorous” cladocerans their diets can include non-algal taxa, such as protozoans and fungi (Williamson and Reid 2001). Similar to harpacticoids, ostracods gather food directly from the substrate using their legs and consume mostly algae and detritus (Delorme 2001).

Many freshwater invertebrates have great potential for dispersal due to durable and drought resistant life history stages, and parthenogenetic life histories, though the extent to which this dispersal potential is realized is unclear (Bohonak and Jenkins 2003). While actual dispersal rates have proven hard to determine, a variety of vectors have been demonstrated to transfer freshwater invertebrates including wind and rain (Jenkins and

Underwood 1998), other animals (Allen 2007), and lotic pond connections (Michels et al. 2001; Van De Meutter et al. 2006; Van De Meutter et al. 2007).

Small size, high abundances, and short generation times make freshwater invertebrates well suited to experimental manipulation, and aquatic habitats offer relatively discrete habitat boundaries. As a result, freshwater invertebrates, particularly “zooplankton” have been extensively used as model systems in metacommunity ecology (Shurin 2000; Shurin et al. 2000; Shurin 2001; Forbes and Chase 2002; Cottenie and De Meester 2003; Cottenie et al. 2003; Cottenie and De Meester 2004).

Thesis Objectives

With this thesis I intended to investigate the effects of habitat connectivity and regional heterogeneity in ecologically relevant multitrophic biological communities. Specifically, I hoped to determine (1) whether the effects of habitat connectivity on species richness were dependent upon the extent of regional heterogeneity present; (2) whether species richness results would be robust to examination with other diversity indices; (3) whether community composition and its variation would be affected by connectivity, heterogeneity, or their interaction; (4) whether connectivity, heterogeneity, or their interaction would affect ecosystem functioning or its variability, and (5) which diversity indices were more strongly correlated to ecosystem functioning.

Chapter 2

**The effects of habitat connectivity and regional heterogeneity on biodiversity,
community composition, and ecosystem functioning of artificial pond
metacommunities**

In preparation for
Ecology

Abstract

Habitat connectivity and regional heterogeneity represent two important regional processes likely to affect biodiversity and ecosystem functioning across different spatial scales. I performed a 3 x 2 factorial design experiment to investigate the effects of both processes and their interaction on artificial pond communities of freshwater invertebrates at the local (α), among-community (β), and regional (γ) scales. Despite strong expectations that the effects of connectivity would depend on levels of regional heterogeneity, no significant interaction was found for species richness, Simpson diversity, or functional diversity (FD) at any spatial level. While connectivity had a significant effect on local richness, it had no effect on local Simpson or functional diversity, nor any of the investigated indices of ecosystem functioning (abundance, invertebrate biomass, and chlorophyll *a* concentration), raising questions about the ecological relevance of such an increase in local richness. Furthermore, connectivity significantly reduced among-community Simpson diversity, and nearly significantly reduced among-community richness. Conversely, heterogeneity significantly enhanced among-community species richness and Simpson diversity. Neither factor had significant effects on community composition or ecosystem functioning, though there was a significant effect of heterogeneity on variation of community composition. The major role of connectivity in ecological communities seems to be as a homogenizing force. Conversely, heterogeneity largely acts as a force maintaining diversity between communities. Despite strong expectations to the contrary, these two factors seem to exert their effects independently of one another.

Introduction

A central goal of community ecology is understanding the processes that control biodiversity. Such a goal is of considerable pure and applied value given the high present rates of biodiversity loss (Pimm et al. 1995, Thomas et al. 2004; Worm et al. 2006) and the important role of biodiversity in determining levels of ecosystem services, especially during times of disturbance (Loreau et al. 2001).

Ecologists are now very much aware that biological communities are subject to both local processes such as competition and predation, as well as regional processes such as dispersal and spatiotemporal heterogeneity. As a result biodiversity is now commonly partitioned into three components, local (α or within-community), among-community (β), and regional (γ or total) diversity (Whittaker 1972; Lande 1996).

The relationship between habitat connectivity and all three levels of biodiversity has recently received much attention both theoretically and empirically. Despite this attention few reliably general statements can be made about how regional processes affect biodiversity. While most studies find that dispersal increases local richness (Cadotte 2006b; but see Shurin 2000; Forbes and Chase 2002), the exact nature of this relationship is unclear, with some studies finding a monotonic positive response of richness to increasing connectivity (Gilbert et al. 1998; Warren 1996b) and others finding a unimodal response (Kneitel and Miller 2003; Mouquet and Loreau 2003; Cadotte 2006a). The relationship between among-community diversity and connectivity has proven more consistent, typically demonstrating a monotonic decrease with increasing connectivity (Warren 1996a; Mouquet and Loreau 2003), but even this is not invariable (Cadotte 2006a). Fi-

nally, the effects of connectivity on regional richness have proven to be quite variable, with a number of studies finding no effect (Warren 1996a; Warren 1996b; Cadotte et al. 2006a; Cadotte 2006b), increases with connectivity (Kneitel and Miller 2003), or decreases with connectivity (Forbes and Chase 2002; Mouquet and Loreau 2003; Cadotte and Fukami 2005; Cadotte 2006a).

Due to this ambiguity ecologists have increasingly turned to investigating interactions between dispersal and other factors in hopes of gleaning insight from a more holistic viewpoint (Östman et al. 2006). As a result, the effects of connectivity have been shown to depend on a variety of external factors such as disturbance (Warren 1996a; Östman et al. 2006), predation (Shurin 2001), and dispersal scale (Cadotte 2006a).

Surprisingly, despite the importance of regional heterogeneity to many spatial models of competitive coexistence and predation, relatively few empirical studies have attempted to explicitly investigate an interaction between habitat connectivity and regional heterogeneity (but see Cadotte 2006a). One of the primary differences between metacommunity perspectives is the amount of regional heterogeneity assumed (Leibold et al. 2004), and its presence or absence should determine which mechanisms contribute to determining biodiversity. For example, while one of the best studied mechanisms of competitive coexistence in metacommunities, the competition-colonization trade-off, does not require regional heterogeneity to operate (e.g. Hastings 1980), other mechanisms such as regional niche differentiation and mass effects, do (Mouquet et al. 2005). Accordingly then, it is likely that regional heterogeneity will play a large role in determining the response of biodiversity to connectivity, and it is possible that such an interaction has

contributed to previously observed differences in the relationship between connectivity and species richness (Forbes and Chase 2002).

Here I present the results of an artificial pond experiment designed to test an interaction between habitat connectivity and regional heterogeneity on communities of freshwater invertebrates. It was expected that in heterogeneous regions a unimodal response of local richness would be observed as at low connectivity mass effects would raise local richness, but that at higher levels of connectivity regionally dominant competitors would emerge, lowering local richness (Mouquet and Loreau 2003) (Figure 2.1). Conversely, it was expected that in homogeneous regions connectivity would have consistently positive effects on local richness, by allowing for competition-colonization trade-offs, rescue effects (Brown and Kodric-Brown 1977), and genetic rescue effects (Antonovics et al. 1997), and due to the assumption that the emergence of a distinct regionally determined community would not occur at high connectivity levels (as local and average regional environmental conditions should be identical). Among-community richness was expected to decline in both systems, but more so in heterogeneous regions which were expected to have generally higher levels of among-community richness. Regional richness was expected to decline at high connectivity levels in heterogeneous regions due to the simultaneous loss of local and among-community richness, but the nature of the response in homogeneous regions was expected to depend on the relative effects of connectivity on mean local and among-community richness, which was unknown *a priori* (Figure 2.1).

I extended my results to Simpson Diversity (Simpson 1949) and a measure of functional diversity (FD) (Petchey and Gaston 2002), in addition to the often used diversity index of species richness. While each measure has its benefits, the ecological relevance of metacommunity effects will be perhaps better evaluated with the former two as Simpson diversity takes relative species abundances into account, and there is some evidence that measures of functional diversity may correlate more strongly with ecosystem properties than measures of species richness (Tilman et al. 1997; Barnett and Beisner 2007).

To examine the effects of habitat connectivity and regional heterogeneity on ecosystem functioning I examined three indices of productivity (regional abundance, invertebrate biomass, and chlorophyll *a* concentration). Predictions about the nature of the relationship between connectivity and productivity have differed, with some authors arguing for a monotonic decrease in productivity with increasing connectivity (Mouquet and Loreau 2003), and others suggesting that the relationship is likely to be unimodal (Loreau et al. 2003). Empirical results have been ambiguous, finding that connectivity may have no effect on invertebrate biomass (Shurin 2000; Shurin 2001; Forrest and Arnott 2006), or algal biomass (France and Duffy 2006). Furthermore, whereas theory predicts that connectivity should decrease temporal variation in productivity (Loreau et al. 2003), there is some empirical indication that connectivity has little effect on spatial variation and actually may increase temporal variation in ecosystem functions (France and Duffy 2006). One possible reason for such discord between empirical and theoretical results is the strong assumption of regional heterogeneity often included in models (e.g. Mouquet

and Loreau 2003; Loreau et al. 2003) which may not be reflected in all empirical situations. In addition to evaluating this hypothesis, I also investigated the degree of correlation between indices of diversity and ecosystem functioning.

Finally, to broadly determine the effects of connectivity and heterogeneity on invertebrate communities I investigated total community composition by ordination.

Methods

Experimental Design

To test whether the effects of connectivity on species diversity, community composition, and ecosystem functioning depend on regional heterogeneity, I conducted an artificial pond mesocosm experiment at the Queen's University Biological Station (QUBS) in the summer of 2007. In total, seventy-two ponds were set up, grouped into eighteen regions of four ponds each. The experiment had a 3 x 2 factorial design with three levels of habitat connectivity (None, Low, and High), and two levels of regional heterogeneity (Homogeneous regions, Heterogeneous regions) (Appendix 1). Each cell of the design contained three replicate regions.

Experimental Set-Up

The ponds were created in 378 L cattle tanks filled with 350 L water from Opinicon Lake filtered through a 50 μ m mesh. Each pond was inoculated with a homogenized mixture of aquatic invertebrates gathered from 10 local lakes (Appendix 2). The invertebrates were collected from lakes by a total of 40 m of vertical hauls using 17.5 cm diameter nets, and timed littoral sweeps using a kick net. All nets had 50 μ m mesh. The use of invertebrates collected from distinctly different habitats creates a hyperdiverse inoculum

which ensures that the initial biota will be diverse enough to respond to the selection gradients imposed by treatments, and helps ensure that results are not simply idiosyncratic responses of a particular community to the treatments (DeClerck et al. 2007). Before seeding ponds the collected samples were inspected and macroinvertebrates (i.e. insects, water mites) were manually removed.

The ponds were inoculated on June 3, 2007 with 1L colonist aliquots dispensed from a constantly mixed tub. This volume was chosen to make the resulting concentration of aquatic invertebrates approximately equal to ambient levels (~107% ambient concentration). To minimize exogenous colonization during the experiment the ponds were covered with a 1 mm mesh, and were placed in a sheltered location at least 130 m from the closest water body. Despite these precautions, over the course of the experiment some ponds were colonized by water mites and *Chaborus*. The presence of these taxa did not affect the outcome of richness analyses, and so have been included in all results. The experiment ran twelve weeks, and ponds received nutrient additions based on nutrient levels in Opinicon Lake every two weeks until July 13th, and every three weeks after that (0.3914 g NaNO₃ and 0.01 g NaH₂PO₄).

Experimental Treatments

Connectivity levels were defined by transferring set volumes of water (and any included organisms) between ponds within a region on a weekly basis. In regions with no connectivity mock transfer events were performed, in regions with low connectivity 3 L of water was transferred from each pond to every other pond within the region (9 L total turnover per pond), and in regions of high connectivity 12 L of water was transferred (36

L total turnover per pond). Prior to transfer events the ponds were gently stirred using a paddle to homogenize the community. After stirring, the necessary volume of water was captured in 3 L tube samplers, and gently poured into buckets. To prevent back-dispersal, buckets containing water to be transferred were only added to destination ponds after all water for dispersal had been collected. My connectivity treatments are analogous to stream connections between ponds in that live zooplankton were transported along with materials and water from their pond of origin. While I chose relatively high levels of connectivity (2.6% tank volume and 10.2% tank volume turnover per week in low and high connectivity treatments, respectively), these levels are comparable to turnover rates in some natural systems (Michels et al. 2001).

Heterogeneity was created by modifying the substrate present in ponds. Homogeneous regions were composed of four ponds all with the same substrate (i.e. a bare tank), and heterogeneous regions were composed of four ponds each with a different substrate (i.e. bare tank, rocky bottom, short artificial macrophytes, and long artificial macrophytes). The same substrate combinations for each level of heterogeneity were present in each replicate. Previous work has shown that substrate can have significant impacts on community composition of planktonic and benthic invertebrates by altering physical structure of the water column and providing different habitats for epibiota (DeClerck et al. 2007).

Sampling Protocol

Temperature, dissolved oxygen (DO), conductivity, and pH were measured in ponds on a weekly basis starting June 20, and every six hours for twenty four hours on

three dates using a YSI 600 R multiparameter probe (YSI Inc., Yellow Springs, OH, USA). Aquatic invertebrates were sampled on June 04 to ensure that treatment cells did not significantly differ in terms of initial richness (Appendix 3), and on August 27 (85 days after inoculation) to generate final data (Results). Similar to dispersal events, during sampling the ponds were first gently homogenized with a paddle, and invertebrates were sampled by tube sampler. In addition, water samples were taken for chlorophyll *a* analysis. To sample invertebrates water was captured and then filtered through a 50 µm mesh. All captured animals were anaesthetized with club soda and preserved in 5.5% buffered sugar formalin. Known volumes of water for chlorophyll *a* analysis were passed through GF Whatman glass fibre filters, extracted in methanol for 24 hours, and analyzed using a TD 700 Fluorometer (Turner Designs, Sunnyvale, CA, USA).

Invertebrate Enumeration and Identification

For the enumeration and identification of all aquatic invertebrates a sample representing 0.9 L (0.257% of total pond volume) was counted in six successive subsamples. Each subsample was investigated at 40x magnification on a Leica MZ16 dissecting scope (Leica Microsystems (Canada) Inc., Richmond Hill, ON). When necessary, specimens were dissected, and identified under a Leica DM E compound microscope at 100x – 400x magnification (Leica Microsystems (Canada) Inc., Richmond Hill, ON). Sampling effort was initially determined by constructing sample-based species accumulation curves for four ponds (abundance range 985-1215 individuals) from the final sampling date and estimating which subsample marked the end of substantial richness increases (Appendix 4, Figure A4.1). Furthermore, I confirmed that species accumulation appears to approach an

asymptote at this sampling level in the pond with the greatest abundance (Pond 72), the pond with the greatest richness (Pond 58), and the pond with the lowest abundance and richness (Pond 35) (Appendix 4, Figure A4.1). As the use of raw richness data is acceptable where taxon-accumulation asymptotes have been reached (Gotelli and Colwell 2001), while my data are not rarefied, the accumulation curves suggest that my data represent actual trends in richness, and not simply variation in richness due to variation in abundance.

Monogonont rotifers were identified to genus using the taxonomy of Edmondson (1959). Bdelloid rotifers were simply identified to Bdelloidea. Unfortunately, there were some monogonont rotifers (n=13) that I was unable to satisfactorily identify to genus level. These unidentified rotifers are excluded from all analyses of biomass and diversity, but are included in ordinations and abundance analyses.

Cladocerans were identified to species using Flößner (2000), and Brooks (1959), however, due to taxonomic difficulties individuals of *Bosmina* and *Ceriodaphnia* were only identified to genus. Adult copepods were identified to species using Wilson and Yeatman (1959), Smith and Fernando (1978), and Dussart and Fernando (1990). Immature copepods were either identified to order (copepodids) or simply to class (nauplii), and as such were excluded from diversity analyses, but were included in all other analyses.

Other taxa were identified to varying taxonomic levels. Chaoborids, Cnidarians, Gastrotrichs, Hydracarina, and Turbellarians were identified to genus using James (1959), Hyman (1959), Brunson (1959), Smith et al. (2001), and Kolasa (2001), respectively. Os-

tracods and tardigrades were identified simply to Ostracoda and Tardigrada. While these last taxa were not given as rigorous taxonomic treatment as other groups, I felt that they made an important contribution to pond communities, and were included in all analyses. Identical enumeration rules were observed for final and initial sampling dates.

Community Diversity

I chose to analyze community diversity using three different indices, all of which address different aspects of diversity: species richness, Simpson diversity, and an index of functional diversity, FD. Richness reflects the number of taxa present in a community, and does not consider relative abundances of these taxa. Conversely, the Simpson Index ($1-\lambda$) gives a measure of diversity that considers both taxon presence and relative abundance, with $1-\lambda$ being the probability that two individuals come from different taxa (Lande 1996). Functional diversity attempts to describe the amount of functional space occupied by a given community. Richness, Simpson diversity, and FD were partitioned additively according to formulae given by Lande (1996) (Appendix 5):

Mean local diversity + Among-community diversity = Regional diversity.

My analysis of functional diversity (FD) follows that of Petchey and Gaston (2002). I analyzed FD based upon a trait matrix including: habitat, trophic level, method of feeding, and body size (Appendix 6). Barnett et al. (2007) used these traits to evaluate functional diversity of zooplankton due to their relatively greater reliability than life history-parameters, which can be strongly affected by temperature and feeding conditions, and due to the availability of published results for most taxa. The first three traits were assigned to species based on published literature or personal observation, though in

some cases it was necessary to generalize traits from closely related species or based on a particular trait (e.g. mastax type in rotifers). Body size was taken from the experiment-wide average of body lengths for each taxon (excepting the three taxa for which measurements were not available, where values were taken from the literature).

To generate the distance matrix from which the functional diversity dendrogram was created categorical traits were ranked (Habitat: pelagic = 0, littoral = 1; Feeding Method: foraging = 1, chydorid filtration = 2, filtration = 3, current-assisted grasping = 4, grasping = 5, sit-and-wait predation = 6; Trophic level: herbivore/bacteriovore/detritovore = 1, omnivore herbivore = 2, omnivore = 3, omnivore predator = 4, predator = 5), and the matrix of species traits (ranked categorical variables and body length) was converted to a standardized Euclidean distance matrix. Using this matrix a dendrogram was generated by unweighted pair-group average method (UPGMA). FD is the sum of branch lengths needed to join present species to the dendrogram root (Petchey and Gaston 2002). An important requirement for distance-based diversity indices is that adding species does not decrease diversity, a quality called set-monotonicity (Ricotta 2005). To ensure set-monotonicity I constructed a single FD dendrogram for the experiment-wide set of species (Petchey and Gaston 2002). Local and regional FD were calculated from this dendrogram based on present species. As with richness and Simpson diversity, among-community FD was defined as being the difference between regional FD and mean local FD.

Habitat Separated Analyses

In addition to my primary analyses investigating the ponds as a whole I also partitioned some of my data (richness data) into littoral and pelagic components based on habitat preferences for each species obtained from literature (Appendix 6). As one might expect littoral organisms to be more strongly affected by my substrate based heterogeneity treatment, my intent here was to gain insight on whether both communities responded similarly to my treatments.

Community Composition

I used statistical and visual analysis of ordinations produced by non-metric multidimensional scaling (NMDS) to examine differences in community composition between treatments. All counts were subjected to square-root and Wisconsin double standardization (standardization first of species by maxima and then sites by site totals) before analysis, which generally reduced ordination stress. Ordinations were based on Bray-Curtis distances, and dimensions were added to the NMDS analysis if they reduced stress by a minimum of 5 on a scale of 100. The best solution was found by a maximum of 500 iterations from multiple runs using random starts (maximum of 100 runs). Best solutions were accepted if their stress was lower than 95% of solutions using randomized data (McCune and Grace 2002). All ordinations were subjected to a principle components rotation. Ordinations were performed on both local and regional counts.

Biomass Calculations

The first 10 individuals of each taxon encountered in a pond were measured to the nearest 25 μm , and these data were used to estimate invertebrate dry biomass using pub-

lished length-weight regressions and volumetric formulae (Appendix 7). Where regressions or formulae did not exist for a given taxon I employed formulae developed for taxa of similar size and shape, published dry weights, or formulae for geometric shapes (Appendix 7). Where formulae for geometric shapes were employed the average relationship between height, length, and width was determined from 10 randomly selected individuals so that volume could be calculated solely as a function of length (Ruttner-Kolisko 1977).

To calculate dry mass from length-weight regressions I used published regressions in the form of $\ln W = \ln a + b(\ln L)$, where W = dry mass (μg), a = the regression intercept, b = the regression slope, and L = the length (mm). I employed the method suggested by Bird and Prairie (1985) in that I first calculated dry mass for each individual and then averaged dry mass within species and ponds, as opposed to using averages of log-transformed lengths to calculate dry mass (McCauley 1984) as the latter method underestimates biomass. For those species involving volumetric formulae a density of 1 mg/mm^3 was assumed, with a dry weight:wet weight ratio of 0.1:1.0 (Pace and Orcutt 1981). Unfortunately, due to a change in protocols, measurements for rotifers are only reliable for a subset of ponds (Ponds 25-72). As a result, average volumes for rotifer genera were found across all reliable ponds, instead of within individual ponds. Similarly, in ponds where measurements were unavailable for present taxa experiment-wide mean biomasses were substituted.

Data Analysis

The effects of treatments on abundance, invertebrate biomass, chlorophyll *a* concentration, and biodiversity indices were investigated by analysis of variance (ANOVA),

with Tukey's Highly Significant Difference (Tukey HSD) tests being used to determine which groups were responsible for significant differences when appropriate. The effects of treatments on community composition were investigated by performing multivariate analyses of variance (MANOVAs) on mean local or regional NMDS axis scores (three axes for the local ordination, two axes for the regional ordination). Among-community (within-replicate) variances of local biomass, abundance, and chlorophyll were investigated with ANOVAs of coefficients of variation (CVs) to compensate for differences in variance associated with differing means, whereas among-community variances of local NMDS scores were analyzed by MANOVAs of local variance. Spearman rank correlations were used to determine correlations between diversity and ecosystem functioning indices.

Assumptions of statistical tests were checked as follows. Heterogeneity of variances for each analysis was checked visually and with Brown-Forsythe tests. While normality of data was only evaluated visually, as ANOVAs are relatively robust to violations of normality and heteroskedasticity of variances when the design is fully balanced (Zar 1999) this should not have had any major effect on my results. Similarly for MANOVAs univariate normality and homogeneity of variances were evaluated visually and with Brown-Forsythe tests. While this does not necessarily guarantee that MANOVA assumptions of multivariate normality or equal covariance are met (though it makes this more likely (Quinn and Keough 2002)), Zar (1999) notes that MANOVAs are robust to departures from these assumptions, especially when designs are balanced and the Pillai trace is used. Transformations were performed on data where they clearly improved normality or

homogeneity of variances. All data analysis was performed in R (www.r-project.org) version 2.7.0 using the packages car (ver. 1.28), cluster (ver. 1.11.11), stats (ver. 2.70) and vegan (ver. 1.13-1).

Results

Environmental Variables

The values of conductivity, dissolved oxygen, pH, and temperature varied considerably over the course of the experiment (Appendix 8). There was no difference between treatment combinations in terms of average conductivity, DO, pH, or temperature (conductivity, $p = 0.08$; DO, $p = 0.86$; pH, $p = 0.82$; temperature, $p = 0.88$) (Table 2.1), though the difference in conductivity was close to significant. The marginally significant effect of treatment on conductivity was likely due to the presence of rock tanks in heterogeneous regions, which had significantly higher mean conductivities than all other substrate types when tanks from heterogeneous regions were considered (Tukey's HSD, $p < 0.01$) (Table 2.2) (Figure 2.2). Substrates did not differ in mean levels of any other physical variable (DO, $p = 0.97$; pH, $p = 0.73$; temperature, $p = 0.84$) (Table 2.2) (Figure 2.2).

Community Diversity

There was no significant interaction between connectivity and heterogeneity on mean local richness, among-community richness, or regional richness (mean local, $p = 0.29$; among-community, $p = 0.64$; regional, $p = 0.46$) (Table 2.3) (Figure 2.3). Connectivity had a significant effect on mean local richness, but not among-community or regional richness, though its effect on among-community richness was close to significant (mean local, $p = 0.04$; among-community, $p = 0.06$; regional, $p = 0.42$) (Table 2.3). Het-

erogeneity significantly enhanced among-community richness, but had no effect on mean local or regional richness (mean local, $p = 0.45$; among-community, $p = 0.02$; regional, $p = 0.10$) (Table 2.3). While there was greater among-community richness between tanks in heterogeneous regions this is likely due to the heterogeneity treatment, and not due to any one substrate being particularly speciose or depauperate, as substrate had no significant effect on local richness of ponds from heterogeneous regions (ANOVA, $F_{3,32} = 1.67$, $p = 0.19$).

Logarithmic transformations were applied to Simpson diversity data to improve normality for statistical tests. Similar to species richness there was no significant interaction between connectivity and heterogeneity on mean local diversity, among-community diversity, or regional diversity (mean local, $p = 0.91$; among-community, $p = 0.14$; regional, $p = 0.93$) (Table 2.4) (Figure 2.4). However, Simpson diversity differed from species richness in the effects of connectivity. There was no effect of connectivity on mean local diversity, or regional diversity, though there was a significant effect on among-community diversity (mean local, $p = 0.87$; among-community, $p < 0.01$; regional, $p = 0.35$) (Table 2.4) (Figure 2.4). Heterogeneity had a significant positive effect on among-community diversity, but no effect on mean local or regional diversity (mean local, $p = 0.28$; among-community, $p = 0.02$; regional, $p = 0.89$) (Table 2.4) (Figure 2.4).

The FD dendrogram produced largely followed taxonomic categories, though some branches show grouping by ecological characteristics and not taxonomy (Figure 2.5). There were no significant interactions between connectivity and heterogeneity at any spatial scale (mean local, $p = 0.55$; among-community, $p = 0.37$; regional, $p = 0.57$)

(Table 2.5) (Figure 2.6). Furthermore, neither factor had significant main factor effects on FD at any spatial scale (Connectivity: mean local, $p = 0.13$; among-community, $p = 0.56$; regional, $p = 0.42$; Heterogeneity: mean local, $p = 0.95$; among-community, $p = 0.07$; regional, $p = 0.25$) (Table 2.5) (Figure 2.6).

Habitat Separated Analyses

The pelagic and littoral communities differed in their responses to connectivity and heterogeneity (Appendix 9). Littoral richness followed a pattern similar to the total community data, with a significant effect of connectivity on mean local richness ($p = 0.04$), and of heterogeneity on among-community richness ($p = 0.03$) (Appendix 9, Table A9.1), however the pelagic community responded differently. Pelagic mean local richness was unaffected by connectivity, and among-community richness was unaffected by heterogeneity, though among-community richness was significantly decreased by connectivity ($p = 0.01$) (Appendix 9, Table A9.2).

Community Composition

The ordination of the local communities was optimized at three dimensions with a stress of roughly 16.90 (Appendix 10, Figure A10.1). The ordination of regional communities was optimized at two dimensions, with a stress of roughly 17.32 (Appendix 10, Figure A10.2). There was no significant effect of either treatment, nor their interaction on mean local community composition (NMDS scores) (connectivity, $p = 0.52$; heterogeneity, $p = 0.65$; interaction, $p = 0.53$) (Table 2.6), nor on regional community composition (NMDS scores) (connectivity, $p = 0.89$; heterogeneity, $p = 0.41$; interaction, $p = 0.69$) (Table 2.6). After logarithmic transformation to improve normality there was a significant

effect of heterogeneity on variance of community composition (variance of NMDS scores) and a nearly significant interaction (connectivity, $p = 0.24$; heterogeneity, $p = 0.04$; interaction, $p = 0.06$) (Table 2.6). Interestingly, despite the significant effect of heterogeneity on among-community richness and Simpson diversity, there was no effect of substrate on community composition of heterogeneous regions (MANOVA, Pillai's $\text{trace}_{9,96} = 0.15$, approximate $F = 0.57$, $p = 0.82$).

Abundance, Biomass, and Chlorophyll a

Regional abundances were normally distributed with a mean of ~980 animals sampled per pond (Appendix 4, Table A4.1), giving an average density of ~1089 animals/L in the ponds. Regional abundances of total communities did not differ by either treatment, nor their interaction (connectivity, $p = 0.76$; heterogeneity, $p = 0.35$; interaction $p = 0.12$) (Table 2.7) (Figure 2.7). Logarithmic transformations were applied to chlorophyll and invertebrate biomass data to improve normality. Similar to abundance data, invertebrate biomasses did not significantly differ by any treatment (connectivity, $p = 0.61$; heterogeneity, $p = 0.09$; interaction, $p = 0.08$) (Table 2.7) (Figure 2.7), nor did chlorophyll concentrations (connectivity, $p = 0.97$; heterogeneity, $p = 0.71$; interaction, $p = 0.88$) (Table 2.7) (Figure 2.7). Similarly, there was no effect of either treatment, nor their interaction on regional CVs of abundance (connectivity, $p = 0.07$; heterogeneity, $p = 0.27$; interaction, $p = 0.90$) (Table 2.8) (Figure 2.8), invertebrate biomass (connectivity, $p = 0.93$; heterogeneity, $p = 0.47$; interaction, $p = 0.11$) (Table 2.8) (Figure 2.8), or chlorophyll concentrations (connectivity, $p = 0.67$; heterogeneity, $p = 0.59$; interaction, $p = 0.56$) (Table 2.8) (Figure 2.8).

Relationship between Diversity and Ecosystem Functioning

While there was a significant correlation between species richness and functional diversity ($p > 0.01$) (Table 2.9), and between invertebrate biomass and chlorophyll *a* concentration ($p = 0.03$) (Table 2.9), none of the correlations between regional diversity indices and regional indices of productivity were significant (Table 2.9).

Discussion

Both connectivity and regional heterogeneity had significant effects on species richness. I found an increase in mean local richness at low levels of connectivity (on average ~ 4.6 more species than in no connectivity treatments), though it was impossible to determine whether the relationship of local richness to connectivity was unimodal or monotonic positive (i.e. whether high levels of dispersal resulted in losses of local richness relative to low levels of connectivity). Positive effects of habitat connectivity or dispersal on local richness have been observed in many experiments (Cadotte 2006b), including studies with zooplankton (Shurin 2001; Forrest and Arnott 2006), though some evidence has suggested that dispersal may play a limited role in structuring undisturbed zooplankton communities relative to the influence of local environmental conditions (Shurin 2000, 2001; Cottenie and De Meester 2003, 2004). As expected, among-community richness was significantly enhanced by heterogeneity, and there was a marginally significant negative effect of connectivity on among-community richness. Declines of among-community richness with increasing connectivity have been well established in both theoretical and empirical studies (e.g. Warren 1996b; Mouquet and Loreau 2003), however the only similar result I am aware of regarding increases in among-

community richness with increased heterogeneity is Cadotte (2006a) who actually manipulated among-community richness as a form of biotic heterogeneity. Finally, neither factor had significant effects on regional richness, a finding that is unsurprising given the ambiguous nature of other results concerning the relationship between connectivity and regional richness (e.g. Cadotte 2006b).

Despite strong expectations that the responses of species richness to habitat connectivity would be dependent upon regional heterogeneity, no significant interactions were found at any spatial level of species richness. Forbes and Chase (2002) originally hypothesized that different degrees of regional heterogeneity might cause different results concerning the effects of connectivity on species richness, a hypothesis that seemed quite likely given the different processes expected to affect species richness in homogeneous and heterogeneous regions. While there are some results supporting the existence of such an interaction (Cadotte 2006a), my results do not. There are a variety of reasons why theoretical predictions may not have matched my results. For example, many theoretical studies have focused on strictly competitive metacommunities (e.g. Mouquet and Loreau 2003). Conversely, my study involved a relatively large number of species and likely involved at least three trophic levels due to the inclusion of multiple predatory and omnivorous species. As the inclusion of predation into models of competitive metacommunities has been shown to dramatically alter the conditions for competitive coexistence (e.g. Shurin and Allen 2001) it seems likely that models designed for strictly competitive assemblages may not accurately describe the multitrophic communities that are more akin to natural systems. Furthermore, many models involving both heterogeneity and

competition-colonization trade-offs involve strict competitive hierarchies that may not exist in actual biological communities (Hubbell 2001; Laird and Schamp 2008), and considering intransitive competitive systems or non-antagonistic species interactions may yield different predictions (Laird and Schamp 2008; Gross 2008).

Theoretical models often investigate communities at equilibrium conditions, which can not be identified using my sampling approach (representing a “snap-shot” in time). The existence of such community equilibria in natural systems is unclear, especially in invertebrate communities where seasonality has a large effect on community composition (Wallace and Snell 2001), however, there is definite merit to demonstrating that observed results are not transient. Indeed, experiments have found effects of time [from treatment initiation] upon local richness (e.g. Starzomski et al. 2008), and significant time x treatment interactions (e.g. Cadotte 2006a; Cadotte et al. 2006a). Given the rapid life histories of most species in my communities, and the relatively long duration of the experiment, it is likely that my results were as representative of long term community dynamics as could be hoped from an experimental investigation.

Finally, though heterogeneity has an important role in maintaining diversity between communities, it is not unreasonable that homogeneous and heterogeneous regions could respond similarly to connectivity, especially in complex ecological communities such as my system. For example, increased connectivity was predicted to decrease among-community richness in both homogeneous and heterogeneous regions, albeit more strongly in heterogeneous regions. Similarly, while regional heterogeneity determines whether regional competitive coexistence is mediated solely by life-history trade-offs

(such as the competition-colonization trade-off), or also includes regional niche differentiation, the ultimate result of high connectivity may be a lack of coexistence in both cases (at high levels of connectivity the demands posed by trade-offs on the colonization ability of the weaker competitor may become unreasonable, and at high levels of connectivity regional heterogeneity can be overwhelmed by dispersal (Mouquet and Loreau 2003)).

Why Cadotte (2006a) should have found evidence for an interaction between connectivity and heterogeneity, while I did not, is unclear. It is possible that subtle differences in the ways I defined my treatments caused different effects. For example, while Cadotte's definition of connectivity was based on relative opportunity for dispersal, I imposed connectivity treatments by forced mixing (a process thought to be more appropriate for passively dispersing taxa such as most rotifers and microcrustaceans). While the argument could be made that Cadotte's design allowed for stronger life-history trade-offs (due to the inclusion of dispersal ability, a factor minimized by the forced nature of my treatments), there is every reason to believe that life-history trade-offs would still operate in my ponds, as the metric considered by most trade-off models is not dispersal *per se*, but rather colonization ability (Cadotte et al. 2006b). Furthermore, whereas Cadotte's design involved biotic heterogeneity created by explicitly altering initial among-community richness, I present the first study experimentally manipulating permanent regional heterogeneity by explicitly altering the physical environment by substrate, a factor known to alter zooplankton community composition (Declerck et al. 2007). As a result, it was impossible for me to quantify *a priori* the amount of heterogeneity that would be experienced in each region, however it seems clear from the significant effect of heterogeneity

on among-community richness and Simpson diversity that my heterogeneity treatments were effective. It is worth noting that as I replicated identical regions (one with heterogeneity and one without heterogeneity) as opposed to heterogeneity *per se*, it is technically impossible to distinguish the effects of heterogeneity and regional identity from my design. Consequently it is possible that the lack of an interaction is particular to my two heterogeneity treatments. However, given that there was an effect of heterogeneity on among-community richness, but not on local richness, it appears that the major difference between my heterogeneity treatments was in fact biotic heterogeneity and not regional identity. The design of Cadotte (2006a) is similar in that the same community compositions (one with no among-community richness and one with among-community richness = 6) were employed in all of his replicates.

Another important consideration in studies of connectivity appears to be the identity of the focal system. Cadotte (2006b) found that the response of biodiversity to dispersal depends on the taxonomic group investigated, and Cottenie (2005) has shown that dispersal mode, habitat type, and the spatial scale of the system explain a large amount of variation in relative importance of space and environment to metacommunities. The importance of the identity of the focal system is further supported by my finding that littoral and pelagic communities did not respond similarly to my treatments.

The effects of habitat connectivity and regional heterogeneity differed across different indices of community diversity. While patterns of Simpson diversity and species richness were similar at the among-community level, neither Simpson diversity nor FD was affected by connectivity at the local level. Furthermore, among-community FD was

not significantly affected by heterogeneity. This may partially be due to the relatively high levels of local FD compared to regional FD, which may limit the ability of connectivity and heterogeneity to affect FD levels across space.

While species richness is of particular relevance to metacommunity theory, and the mass-effects perspective in particular, metacommunity ecologists would do well to also consider presenting other diversity indices. Species richness is a notoriously difficult index to accurately measure if sampling has not been exhaustive and requires sample sizes many times larger than Simpson diversity to rank community diversity with confidence (Lande et al. 2000). While many authors employ rarefaction to standardize their richness data sets to a given number of individuals, this does not negate the need for extensive sampling as rarefaction curves converge at small sample sizes and can intersect multiple times when compared between communities with differing evenness (Gotelli and Colwell 2001). Furthermore, where sampling has not been exhaustive it is impossible to accurately measure among-community richness unless proportionately more effort has been spent on more speciose communities (Magurran 2004). Given these problems, the obvious value of a diversity measure that considers both richness and relative abundance, and the relative robustness of Simpson diversity to small sample sizes, or samples that vary in size, Lande et al. (2000) argued that where ecologists present richness data Simpson data should also be presented. Metacommunity ecologists have thus far largely ignored this advice, even though formulae for spatially partitioning Simpson diversity have been available for over a decade (Lande 1996).

Despite the significant effects of both connectivity and heterogeneity upon species richness, there were no effects of either treatment, nor any interaction between them, on any index of ecosystem functioning or overall community composition as represented by NMDS scores. Other studies have found positive effects of habitat connectivity on abundance (Gonzalez et al. 1998; Holyoak 2000; Kneitel and Miller 2003), but connectivity has also been found to decrease community or species abundances (Holyoak 2000; Forrest and Arnott 2006), and many empirical studies with zooplankton have found no relationship between connectivity and productivity (Shurin 2000; Shurin 2001; Forrest and Arnott 2006). While I did not test for effects of my treatments on the abundances of individual species, there was no effect of either treatment on regional abundance or biomass. This insensitivity of variation in productivity to connectivity is surprising, given theoretical predictions that connectivity should reduce variation in productivity, although some studies have found that dispersal can actually increase variability of some ecosystem traits (Loreau et al. 2003; France and Duffy 2006). While theoretical research suggests that connectivity strongly affects community composition (Mouquet and Loreau 2003) my results found no effect of either treatment on mean local or regional community composition. This may indicate that as opposed to Mouquet and Loreau (2003) no species in my communities were particularly dominant at the regional level. Despite the absence of treatment effects on mean community composition, there was a significant effect of heterogeneity upon the variance of local community composition, and a nearly significant interaction between both treatments on variance, indicating that heterogeneity likely increased variance in community composition.

The ecological relevance of species richness is coming under increasing scrutiny, with many authors suggesting that the putative effects of species richness on ecosystem functions may be more due to functional diversity, or the specific identity of species in a community (Aarssen 1997; Tilman et al. 1997; Downing and Leibold 2002). This is further underscored by my finding that while connectivity had a significant effect upon local richness, it had no effects upon any other local community characteristic investigated, including diversity and productivity indices. Surprisingly, at the regional level no diversity index was significantly correlated to any index of ecosystem functioning.

Connectivity and heterogeneity both have important and marked effects on community composition of aquatic invertebrates. Connectivity plays a clear role in decreasing differences between the different communities in a region by decreasing among-community diversity, though this homogenizing effect may not be as widespread as originally thought, given the lack of significant effects on variation of ecosystem functioning. Conversely, heterogeneity seems to increase spatial variance in community composition and among-community diversity. Given the absence of any interaction between connectivity and heterogeneity on species richness, and the significant effects of both connectivity and regional heterogeneity in isolation, it appears unlikely that an interaction between these factors is a primary driver of differences in richness - connectivity relationships observed in earlier research. Instead other factors, such as dispersal mode, habitat type, and taxonomic identity may be responsible for these differences.

Table 2.1: ANOVAs on average conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C , dissolved oxygen (mg/L), pH, and temperature ($^\circ\text{C}$) of artificial ponds by treatment cell of the factorial design (averaged over all dates and within regions). Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Conductivity	Treatment	5	2.61	<i>0.08</i>
	Error	12		
Dissolved Oxygen	Treatment	5	0.38	0.86
	Error	12		
pH	Treatment	5	0.43	0.82
	Error	12		
Temperature	Treatment	5	0.34	0.88
	Error	12		

Table 2.2: ANOVAs on average conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C, dissolved oxygen (mg/L), pH, and temperature (°C) of artificial ponds by pond substrate (averaged over all dates). Data from heterogeneous regions only. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Conductivity	Substrate	3	15.31	< 0.01
	Error	32		
Dissolved Oxygen	Substrate	3	0.08	0.97
	Error	32		
pH	Substrate	3	0.44	0.73
	Error	32		
Temperature	Substrate	3	0.27	0.84
	Error	32		

Table 2.3: ANOVAs on mean local richness, among-community richness, and regional richness by connectivity, heterogeneity, and their interaction. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Mean Local Richness	Connectivity	2	4.36	0.04
	Heterogeneity	1	0.61	0.45
	Connectivity x Heterogeneity	2	1.38	0.29
	Error	12		
Among-community Richness	Connectivity	2	3.57	<i>0.06</i>
	Heterogeneity	1	7.01	0.02
	Connectivity x Heterogeneity	2	0.47	0.64
	Error	12		
Regional Richness	Connectivity	2	0.93	0.42
	Heterogeneity	1	3.21	<i>0.10</i>
	Connectivity x Heterogeneity	2	0.83	0.46
	Error	12		

Table 2.4: ANOVAs on log-transformed mean local Simpson diversity, among-community Simpson diversity, and regional Simpson diversity by connectivity, heterogeneity, and their interaction. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Mean Local Simpson Diversity	Connectivity	2	0.15	0.87
	Heterogeneity	1	1.30	0.28
	Connectivity x Heterogeneity	2	0.09	0.91
	Error	12		
Among-community Simpson Diversity	Connectivity	2	7.85	< 0.01
	Heterogeneity	1	6.95	0.02
	Connectivity x Heterogeneity	2	2.37	0.14
	Error	12		
Regional Simpson Diversity	Connectivity	2	1.16	0.35
	Heterogeneity	1	0.02	0.89
	Connectivity x Heterogeneity	2	0.07	0.93
	Error	12		

Table 2.5: ANOVAs on mean local FD, among-community FD, and regional FD by connectivity, heterogeneity, and their interaction. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Mean Local FD	Connectivity	2	2.38	0.13
	Heterogeneity	1	0.00	0.95
	Connectivity x Heterogeneity	2	0.62	0.55
	Error	12		
Among-community FD	Connectivity	2	0.62	0.56
	Heterogeneity	1	4.12	<i>0.07</i>
	Connectivity x Heterogeneity	2	1.08	0.37
	Error	12		
Regional FD	Connectivity	2	0.95	0.42
	Heterogeneity	1	1.47	0.25
	Connectivity x Heterogeneity	2	0.58	0.57
	Error	12		

Table 2.6: MANOVAs on mean local NMDS scores (axes 1-3), regional NMDS scores (axes 1-2), and log-transformed variance of local NMDS scores by connectivity, heterogeneity, and their interaction. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	Pillai's Trace	approx. F	p
Local NMDS Scores	Connectivity	6,22	0.39	0.90	0.52
	Heterogeneity	3,10	0.14	0.56	0.65
	Connectivity x Heterogeneity	6,22	0.38	0.87	0.53
Regional NMDS Scores	Connectivity	4,24	0.09	0.28	0.89
	Heterogeneity	2,11	0.15	0.97	0.41
	Connectivity x Heterogeneity	4,24	0.17	0.56	0.69
Variance of Local NMDS Scores	Connectivity	6,22	0.57	1.44	0.24
	Heterogeneity	3,10	0.55	4.05	0.04
	Connectivity x Heterogeneity	6,22	0.80	2.47	<i>0.06</i>

Table 2.7: ANOVAs on regional abundance, log-transformed average invertebrate dry-biomass (μg), and log-transformed average chlorophyll *a* ($\mu\text{g/L}$) by connectivity, heterogeneity, and their interaction. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Regional abundance	Connectivity	2	0.28	0.76
	Heterogeneity	1	0.94	0.35
	Connectivity x Heterogeneity	2	2.60	0.12
	Error	12		
Invertebrate Biomass	Connectivity	2	0.51	0.61
	Heterogeneity	1	3.42	<i>0.09</i>
	Connectivity x Heterogeneity	2	3.19	<i>0.08</i>
	Error	12		
Chlorophyll <i>a</i>	Connectivity	2	0.03	0.97
	Heterogeneity	1	0.15	0.71
	Connectivity x Heterogeneity	2	0.13	0.88
	Error	12		

Table 2.8: ANOVAs on coefficients of variation (CV) of local abundance, local invertebrate biomass (μg), and local chlorophyll *a* ($\mu\text{g/L}$) by connectivity, heterogeneity, and their interaction. Bold p-values indicate $p < 0.05$. Italics indicate $0.05 < p < 0.10$.

		DF	F	p
Local Abundance CV	Connectivity	2	3.34	<i>0.07</i>
	Heterogeneity	1	1.35	0.27
	Connectivity x Heterogeneity	2	0.10	0.90
	Error	12		
Local Invertebrate Biomass CV	Connectivity	2	0.07	0.93
	Heterogeneity	1	0.56	0.47
	Connectivity x Heterogeneity	2	2.63	0.11
	Error	12		
Local Chlorophyll <i>a</i> CV	Connectivity	2	0.42	0.67
	Heterogeneity	1	0.30	0.59
	Connectivity x Heterogeneity	2	0.60	0.56
	Error	12		

Table 2.9: Spearman rank correlation coefficients between diversity and productivity indices (regional richness, regional Simpson diversity, regional FD, regional abundance, average invertebrate biomass (μg), average chlorophyll *a* ($\mu\text{g/L}$)). Bold p-values indicate $p < 0.05$ based on $H_0: r_s = 0$, $H_A: r_s \neq 0$. Italics indicate $0.05 < p < 0.10$.

	Regional Richness	Regional Simpson Diversity	Regional FD	Regional Abundance	Average Invertebrate Biomass	Average Chloro- phyll <i>a</i>
Regional Richness	0.00	0.35	0.75	-0.02	-0.04	0.27
Regional Simpson Diversity		0.00	0.19	-0.32	-0.12	0.01
Regional FD			0.00	0.02	-0.19	0.06
Regional Abundance				0.00	0.38	0.28
Average Invertebrate Biomass					0.00	0.50
Average Chlorophyll <i>a</i>						0.00

Figure 2.1: Predicted responses of local richness, among-community richness, and regional richness to connectivity and heterogeneity. The dashed lines in the regional plot indicate that regional predictions are contingent upon the relative changes in mean local and among-community richness. Open symbols = homogeneous regions, closed symbols = heterogeneous regions.

Figure 2.2: Boxplots of environmental variables by pond substrate, averaged over all dates. A) conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C , B) dissolved oxygen (mg/L), C) pH, and, D) temperature ($^{\circ}\text{C}$). Lower case letters above plots indicate $p < 0.05$ by Tukey HSD tests. Data from heterogeneous regions only. Blank = no added substrate, Long = long artificial macrophyte substrate, Rock = rock substrate, Short = short artificial macrophyte substrate. Boxes represent interquartile range, and whiskers extend to the most extreme data point within a distance of 1.5 interquartile ranges from the box margins.

Figure 2.3: Barplots of mean local richness, among-community richness, and regional richness by connectivity and heterogeneity. Lower case letters above plots indicate significant differences ($p < 0.05$) between connectivity levels by Tukey HSD tests. White bars = homogeneous regions, black bars = heterogeneous regions. Error bars represent ± 1 standard error.

Figure 2.4: Barplots of mean local Simpson diversity, among-community Simpson diversity, and regional Simpson diversity by connectivity and heterogeneity. Lower case letters above plots indicate significant differences ($p < 0.05$) between connectivity levels by Tukey HSD tests. White bars = homogeneous regions, black bars = heterogeneous regions. Error bars represent ± 1 standard error.

Figure 2.5: UPGMA dendrogram produced from species distance matrix based upon species traits.

Figure 2.6: Barplots of mean local FD, among-community FD, and regional FD by connectivity and heterogeneity. White bars = homogeneous regions, black bars = heterogeneous regions. Error bars represent ± 1 standard error.

Figure 2.7: Barplots of regional abundances, average invertebrate biomass (μg), and average chlorophyll *a* concentrations ($\mu\text{g/L}$) by connectivity and heterogeneity. White bars = homogeneous regions, black bars = heterogeneous regions. Error bars represent ± 1 standard error.

Figure 2.8: Barplots of coefficients of variation (CV) of local abundances, local invertebrate biomass (μg), and local chlorophyll *a* concentrations ($\mu\text{g/L}$) by connectivity and heterogeneity. White bars = homogeneous regions, black bars = heterogeneous regions. Error bars represent ± 1 standard error.

Chapter 3

General Discussion and Future Directions

Using a combination of diversity and productivity indices I investigated the relationship between habitat connectivity and regional heterogeneity in experimental communities of freshwater invertebrates. Despite predictions to the contrary, no interactions were found for any diversity index at any spatial scale. In accordance with predictions and previous research mean local richness was enhanced by connectivity at low levels. However, connectivity did not have a significant effect on mean local Simpson diversity, mean local functional diversity or mean levels of any productivity index, which raises questions as to the ecological significance of the observed increase in species richness. As expected, among-community diversity was generally enhanced by regional heterogeneity, and reduced by increasing habitat connectivity. All indices of regional diversity were unaffected by either treatment. Neither treatment factor affected invertebrate community composition nor any index of ecosystem functioning, though regional heterogeneity increased the variation of community composition.

Generally, my results support the role of habitat connectivity as a homogenizing force. Furthermore, my results support the role of regional heterogeneity as a diversifying force maintaining differences among communities.

My results argue against the hypothesis that community responses to connectivity depend heavily on regional heterogeneity (Forbes and Chase 2002). Instead, it may be that differences in responses to connectivity between theoretical and empirical work result from the increased ecological complexity (e.g. trophic structure, intransitive competition) of empirical communities. Differing responses in empirical communities may result from a variety of factors, such as the extent of trophic interactions, or the use of different

focal communities (Cadotte 2006b), the latter being supported by my finding that responses of diversity to connectivity and heterogeneity treatments differed between littoral and pelagic assemblages.

Future Directions

There are a variety of logical extensions to my research, including:

Effects of Connectivity and Heterogeneity on Intra-specific Diversity

Community ecologists are becoming increasingly aware that intra-specific diversity is a natural parallel to the inter-specific diversity, and that it can have important effects on community characteristics (Vellend 2006; Urban and Skelly 2006). Given that a number of population level responses to connectivity are explicitly dependent on regional heterogeneity (e.g. the genetic storage effect (Gandon et al. 1996; Urban and Skelly 2006), and the genetic rescue effect (Antonovics et al. 1997; Urban and Skelly 2006)), a logical extension to my work here would be to consider the effects of habitat connectivity and regional heterogeneity on intra-specific diversity. Furthermore, such research would clarify the roles of connectivity and regional heterogeneity in evolutionary processes.

Effects of Focal Community

While I feel strongly that my experimental system was ecologically relevant, there are limits to the generalizability of any biological system. Previous research has demonstrated that patterns of biodiversity responses to connectivity are not necessarily identical across taxonomic boundaries (Cadotte 2006b), and it may well be that further studies of connectivity x heterogeneity interactions (particularly in plants) will yield different results. Furthermore, while my intent was to provide an ecologically relevant examination

of metacommunity theory, it would be interesting to examine the problem of a connectivity x heterogeneity interaction in the context of a strictly competitive zooplankton metacommunity (e.g. a community of different species of *Daphnia*) to further evaluate theoretical predictions and to confirm whether my results were in fact likely to have differed from theoretical predictions due to the influence of trophic interactions.

Classical Island Metacommunities vs. Mainland-Island Metacommunities

Finally, while the vast majority of empirical research has focused on the effects of connectivity in “classical” or “Levins” type metacommunities, where each patch is assumed to have roughly equal probabilities of species extinction, there is some evidence that natural metacommunities more often resemble mainland-island metacommunities (Harrison 1991). In these metacommunities it is assumed that the probability of species extinction in the island communities is relatively high, and that in the mainland is approximately zero. Theoretical predictions for the two metacommunity types can substantially differ (Tanneyhill 2000), and it would be interesting to follow up my research questions in such an environment.

Summary

- 1) Connectivity appears to largely exert its effects on communities of freshwater invertebrates by homogenizing local communities, as evidenced by its significantly negative effect on among-community Simpson diversity, and its marginally significantly negative effect on among-community species richness.
- 2) Heterogeneity appears to largely exert its effects on communities of freshwater invertebrates by maintaining differences between habitats, as evidenced by its significantly positive effect on among-community richness and among-community Simpson diversity, as well as its significant effect on variance of community composition.
- 3) Despite predictions to the contrary, there was no significant interaction between habitat connectivity and regional heterogeneity on species richness at any spatial scale.
- 4) Different diversity indices respond differently to connectivity and heterogeneity treatments.
- 5) Neither treatment, nor their interaction, had significant effects on community composition, nor on any investigated index of ecosystem functioning.
- 6) No index of species diversity was significantly correlated to any investigated index of ecosystem functioning.

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Appendices

Appendix 1: Schematic of experimental design.

Figure A1.1: Schematic of experimental design. Three levels of habitat connectivity were employed (here represented by arrow width): None, Low, and High; and two levels of heterogeneity: Homogeneous regions, and Heterogeneous regions. Heterogeneity was created by altering habitat substrate, here represented by colour, such that all ponds in homogeneous regions contained the same substrate (bare tank), and each pond in heterogeneous substrate had a different substrate (one bare tank substrate, one rock substrate, one long artificial macrophyte substrate, one short artificial macrophyte substrate). Identical substrate combinations were used in all replicates. Regions consisted of four ponds each, here figured in a square group for ease of display but which were actually arranged in a line.

Appendix 2: Lakes sampled to form invertebrate inocula.

Lake	Location of lake's approximate centre
Buck	44°32'29"N, 76°25'57"W
Devil	44°34'46"N, 76°26'52"W
Indian	44°35'34"N, 76°19'40"W
Lindsay	44°32'14"N, 76°23'25"W
Long	44°31'39"N, 76°24'11"W
Lower Rock	44°31'00"N, 76°22'15"W
Opinicon	44°33'28"N, 76°19'50"W
Round	44°32'16"N, 76°24'00"W
Upper Rock	44°29'50"N, 76°24'40"W
Warner	44°31'43"N, 76°22'55"W

Appendix 3: Initial richness analyses.

Table A3.1: ANOVAs on initial local, among-community, and regional richnesses by cell of the factorial design based on June 04, 2007 samples.

		DF	F	p
Mean Local Richness	Cell	5	0.58	0.72
	Error	12		
Among-community Richness	Cell	5	2.88	0.06
	Error	12		
Regional Richness	Cell	5	1.64	0.22
	Error	12		

Appendix 4: Descriptive statistics of final pond counts, and species accumulation curves for Ponds 3-6, 35, 58, 72 (the first four ponds used to determine sampling effort, the least abundant and speciose pond, the most speciose pond, and the most abundant pond).

Table A4.1: Means, medians, and range of counts from pond samples. August 27, 2007 data only.

	Local Abundance	Regional Abundance	Local counts for diversity data	Regional counts for diversity data
Minimum Value	55	1558	47	1075
Median	896.5	4068	624	2922
Mean	979.9	3919.7	727.6	2910.3
Maximum Value	4065	6724	3795	5771
Total Across All Ponds		70555		52385

Figure A4.1: Cumulative richness of identified groups (morphospecies and immature stages) by subsample in August 27 samples. A) Curves for the first four ponds counted: Pond 3 (empty circles), Pond 4 (empty triangles), Pond 5 (filled circles), Pond 6 (filled triangles). B) Curves for the least abundant and speciose pond, Pond 35 (empty circles); the most speciose pond, Pond 58 (filled circles); and the most abundant pond, Pond 58 (empty triangles).

Appendix 5: Formulae used to generate diversity data (Lande 1996).

Regional diversity = Mean local diversity + Among-community diversity

Species Richness

Regional richness = Mean local richness + Among-community richness,

where Regional richness = the total number of species in a region, and Mean local richness = the average number of species in a community averaged over all communities included in a region.

Simpson Diversity

Regional Simpson diversity = Mean local Simpson diversity + Among-community Simpson diversity,

where Regional Simpson diversity = $1 - \sum \bar{p}_i^2$, Local Simpson diversity = $1 - \sum p_i^2 = 1 - \lambda$, Mean local Simpson diversity = $1 - \bar{\lambda}$, Among-community Simpson diversity = $\bar{\lambda} - \sum \bar{p}_i^2$, p_i = the proportion of a given community contributed by species i , $\bar{p}_i$ = the mean proportion of communities contributed by species i (averaged over all communities in a region), and $\bar{\lambda}$ = the mean value of $\sum p_i^2$ averaged over all communities in the region.

Functional Diversity

To calculate FD, a histogram was constructed from a standardized Euclidean distance matrix of pairwise species distances for all species recorded during the experiment. Both local and regional FD were calculated as the sum of branch lengths needed to connect the histogram root to the tips of branches for all species present, either at the local or regional level. As with other diversity indices, Regional FD = Mean local FD - Among-community FD, where Mean local FD = the average of local FD across all ponds in a region.

Appendix 6, Table A6.1: Ecological traits used to generate the FD dissimilarity matrix and to split taxa for habitat separated analyses. Superscript numerals indicate references for each trait where applicable. Brackets indicate a trait generalized from other taxa.

Taxon	Habitat	Trophic Level	Feeding Type	Mean Length (mm)
Cladocera				
<i>Acroperus harpae</i>	Littoral ¹	Herbivore ¹	Chydorid Filtration ¹	0.49
<i>Alona costata</i>	Littoral ¹	Herbivore ¹	Chydorid Filtration ⁽¹⁾	0.28
<i>Alona guttata</i>	Littoral ¹	Herbivore ⁽¹⁾	Chydorid Filtration ⁽¹⁾	0.27
<i>Alona quadrangularis</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ⁽¹⁾	0.50
<i>Alona</i> sp. near <i>rustica</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ⁽¹⁾	0.43
<i>Alonella excisa</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ¹	0.28
<i>Alonella exigua</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ¹	0.27
<i>Alonella nana</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ¹	0.21
<i>Bosmina</i>	Pelagic ³	Herbivore ³	Filtration ³	0.31
<i>Ceriodaphnia</i>	Pelagic ³	Herbivore ³	Filtration ³	0.52
<i>Chydorus sphaericus</i>	Littoral ³	Herbivore ³	Chydorid Filtration ³	0.29
<i>Daphnia galeata mendotae</i>	Pelagic ⁴	Herbivore ⁽³⁾	Filtration ⁽³⁾	1.34
<i>Daphnia pulex</i>	Pelagic ³	Herbivore ³	Filtration ⁽³⁾	1.38
<i>Diaphanosoma brachyurum</i>	Littoral ³	Herbivore ³	Filtration ⁽³⁾	0.77

Table A6.1 (cont.)

Taxon	Habitat	Trophic Level	Feeding Type	Mean Length (mm)
<i>Eurycercus lamellatus</i>	Littoral ²	Herbivore ⁵	Chydorid Filtration ⁶	1.17
<i>Graptolebris kingi</i>	Littoral ²	Herbivore ²	Foraging ²	0.42
<i>Kurzia latissima</i>	Littoral ²	Herbivore ⁽³⁾	Chydorid Filtration ⁽³⁾	0.45
<i>Lathonura rectirostris</i>	Littoral ²	Herbivore ⁷	Foraging ⁷	0.51
<i>Pleuroxus denticulatus</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ¹	0.44
<i>Pleuroxus procurvus</i>	Littoral ²	Herbivore ¹	Chydorid Filtration ¹	0.43
<i>Polyphemus pediculus</i>	Pelagic ³	Predator ⁸	Grasping ⁸	0.52
<i>Scapholebris kingi</i>	Littoral ²	Herbivore ⁶	Filtration ⁶	0.46
<i>Simocephalus serrulatus</i>	Littoral ²	Herbivore ⁶	Filtration ⁶	1.07
Copepoda				
Calanoida				
<i>Skistodiaptomus oregonensis</i>	Pelagic ³	Omnivore ³	Current assisted grasping ⁹	1.24
Cyclopoida				
<i>Acanthocyclops robustus</i>	Pelagic ³	Omnivore ³	Grasping ⁽¹⁰⁾	0.95
<i>Diacyclops bicuspidatus thomasi</i>	Pelagic ³	Omnivore Carnivore ³	Grasping ⁽¹⁰⁾	0.90
<i>Diacyclops navus</i>	Littoral ¹¹	Omnivore Carnivore ¹²	Grasping ⁽¹⁰⁾	1.08

Table A6.1: (cont.)

Taxon	Habitat	Trophic Level	Feeding Type	Mean Length (mm)
<i>Eucyclops serrulatus</i>	Littoral ¹¹	Omnivore Herbivore ³	Grasping ⁽¹⁰⁾	0.83
<i>Macrocyclops albidus</i>	Littoral ¹¹	Omnivore Carnivore ¹³	Grasping ⁽¹⁰⁾	1.18
<i>Mesocyclops edax</i>	Pelagic ¹¹	Omnivore Carnivore ³	Grasping ⁽¹⁰⁾	1.05
<i>Microcyclops rubellus</i>	Littoral ¹¹	Omnivore Herbivore ¹³	Grasping ⁽¹⁰⁾	0.49
<i>Tropocyclops extensus</i>	Pelagic ¹¹	Omnivore Herbivore ¹⁴	Grasping ⁽¹⁰⁾	0.49
Harpacticoida				
<i>Attheyella americana</i>	Littoral ²	Herbivore ¹⁰	Foraging ⁽¹⁰⁾	0.58
Rotifera				
Bdelloidea				
Bdelloidea	Littoral ¹⁵	Herbivore ¹⁶	Filtration ¹⁶	0.5 ⁽¹⁵⁾
Monogononta				
<i>Anuraeopsis</i>	Pelagic ¹⁵	Herbivore ¹⁶	Filtration ¹⁶	0.08
<i>Beauchampiella</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.15
<i>Conochilus</i>	Pelagic ¹⁵	Herbivore ¹⁶	Filtration ¹⁶	0.13
<i>Dicranophorus</i>	Littoral ¹⁵	Predator ¹⁷	Grasping ¹⁷	0.3 ¹⁸
<i>Euchlanis</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.24
<i>Kellicottia</i>	Pelagic ¹⁵	Herbivore ¹⁶	Filtration ¹⁶	0.38
<i>Keratella</i>	Pelagic ¹⁸	Herbivore ¹⁶	Filtration ¹⁶	0.14
<i>Lecane</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.14

Table A6.1: (cont.)

Taxon	Habitat	Trophic Level	Feeding Type	Mean Length (mm)
<i>Lepadella</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.08
<i>Monostyla</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.09
<i>Mytilina</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.19
<i>Platytas</i>	Littoral ¹⁸	Herbivore ¹⁸	Filtration ⁽¹⁶⁾	0.19
<i>Ploesma</i>	Pelagic ¹⁵	Omnivore ⁽¹⁸⁾	Grasping ¹⁶	0.21
<i>Polyarthra</i>	Pelagic ¹⁵	Herbivore ¹⁶	Grasping ¹⁶	0.11
<i>Squatinella</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.10
<i>Synchaeta</i>	Pelagic ¹⁵	Herbivore ¹⁶	Grasping ¹⁶	0.20
<i>Testudinella</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.16
<i>Trichocerca</i>	Pelagic ¹⁶	Herbivore ¹⁶	Foraging ¹⁶	0.17
<i>Trichotria</i>	Littoral ¹⁵	Herbivore ⁽¹⁶⁾	Filtration ⁽¹⁶⁾	0.15
Other Taxa				
Chaoboridae				
<i>Chaoborus</i>	Pelagic ¹⁹	Predator ²⁰	Sit-and-wait ²⁰	2.50
Gastrotichia				
<i>Chaetonus</i>	Littoral ²¹	Herbivore ²¹	Foraging ²¹	0.75
Hydracarina				
<i>Piona</i>	Pelagic ²²	Predator ²²	Grasping ²³	0.59
Hydrozoa				
<i>Hydra</i>	Littoral ²⁴	Predator ²⁴	Sit-and-wait ²⁴	4.24 ²⁴
Ostracoda				
Ostracoda	Littoral ²⁵	Herbivore ²⁶	Foraging ²⁵	0.22

Table A6.1: (cont.)

Taxon	Habitat	Trophic Level	Feeding Type	Mean Length (mm)
Tardigrada				
Tardigrada	Littoral ²⁶	Herbivore ²⁶	Foraging ²⁶	0.10
Turbellaria				
<i>Mesostoma</i>	Littoral ²⁷	Predator ²⁷	Sit-and-wait ²⁷	2.35

¹ Fryer (1968)² Brooks (1959)³ Barnett et al. (2007)⁴ Dodson and Frey (2001)⁵ Smirnov (1962)⁶ Fryer (1987)⁷ Fryer (1974)⁸ Packard (2001)⁹ Bundy and Vanderploeg (2002)¹⁰ Williamson and Reid (2001)¹¹ Smith and Fernando (1978)¹² Reid et al. (1989)¹³ Fryer (1957)¹⁴ Adrian and Frost (1992)¹⁵ Edmondson (1959)¹⁶ Pourriot (1977)¹⁷ Pejler and Berzins (1993)¹⁸ Stemberger (1979)¹⁹ Wood (1956)²⁰ Swift and Fedorenko (1975)²¹ Strayer and Hummon (2001)²² Riessen (1982)²³ Personal observation²⁴ Slobodkin and Bossert (2001)²⁵ Delorme (2001)²⁶ Clifford (2001)²⁷ Kolasa (2001)

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Appendix 7, Table A7.1: Formulae and references used to estimate invertebrate biomass. W = (dry weight (μg)); L = length (mm); V = volume (mm³). Superscript numerals indicate generalized formulae and taxa for which formulae were originally intended.

Taxon	Formula used	Reference
<i>Acanthocyclops robustus</i>	$\ln W = 2.2266 + 3.2 * \ln L$	Rosen (1981)
<i>Acroperus harpae</i>	$\ln W = 1.16666 + 0.85 * \ln L$	Dumont et al. (1975)
<i>Alona costata</i>	$\ln W = 2.2367 + 2.742 * \ln L$	Malley et al. (1989) ¹
<i>Alona guttata</i>	$\ln W = 2.2367 + 2.742 * \ln L$	Malley et al. (1989) ¹
<i>Alona quadrangularis</i>	$\ln W = 2.7676 + 3.84 * \ln L$	Dumont et al. (1975) ²
<i>Alona</i> sp. near <i>rustica</i>	$\ln W = 2.7676 + 3.84 * \ln L$	Dumont et al. (1975) ²
<i>Alonella excisa</i>	$\ln W = 0.922 + 1.39 * \ln L$	Dumont et al. (1975)
<i>Alonella exigua</i>	$\ln W = 0.922 + 1.39 * \ln L$	Dumont et al. (1975)
<i>Alonella nana</i>	$\ln W = 4.49 + 3.93 * \ln L$	Dumont et al. (1975) ³
<i>Anuraeopsis</i>	$V = 0.03L^3$	Ruttner-Kolisko (1977)
<i>Attheyella americana</i>	$\ln W = 2.5265 + 4.4 * \ln L$	Dumont et al. (1975) ⁴
Bdelloidea	0.25 μg	Dumont et al. (1975)
<i>Beauchampiella</i>	$V = 0.03L^3$	Ruttner-Kolisko (1977) ⁵
<i>Bosmina</i>	$\ln W = 4.9344 + 4.849 * \ln L$	Rosen (1981)
Calanoid copepodids	$\ln W = 0.9227 + 2.4235 * \ln L$	Malley et al. (1989) ⁶
<i>Ceriodaphnia</i>	$\ln W = 1.915 + 2.02 * \ln L$	Dumont et al. (1975)
<i>Chaetonus</i>	0.00769 μg	Strayer (1985)
<i>Chaoborus</i>	$\ln W = -2.183 + 3.2345 * \ln L$	Dumont and Balvay (1979)
<i>Chydorus sphaericus</i>	$\ln W = 4.49 + 3.93 * \ln L$	Dumont et al. (1975)
<i>Conochilus</i>	0.05 μg	Cajander (1983)
Cyclopoid copepodids	$\ln W = 1.3135 + 2.9005 * \ln L$	Malley et al. (1989) ⁷
<i>Daphnia galeata mendotae</i>	$\ln W = 2.64 + 2.54 * \ln L$	Bottrell et al. (1976)
<i>Daphnia pulex</i>	$\ln W = 1.4663 + 3.1932 * \ln L$	Bottrell et al. (1976)

Table A7.1: (cont.)

Taxon	Formula Used	Reference
<i>Diacyclops bicuspidatus thomasi</i>	$\ln W = 0.7606 + 3.9145 * \ln L$	Lawrence et al. (1987)
<i>Diacyclops navus</i>	$\ln W = 0.7606 + 3.9145 * \ln L$	Lawrence et al. (1987) ⁸
<i>Diaphanosoma brachyurum</i>	$\ln W = 1.6242 + 3.0468 * \ln L$	Bottrell et al. (1976)
<i>Dicranophous</i>	0.45 µg	Dumont et al. (1975)
<i>Euchlanis</i>	$V = 0.1L^3$	Ruttner-Kolisko (1977)
<i>Eucyclops serrulatus</i>	$\ln W = 0.7606 + 3.9145 * \ln L$	Lawrence et al. (1987) ⁸
<i>Eurycercus lamellatus</i>	$\ln W = 2.54 + 2.62 * \ln L$	Lemke and Benke (2004) ⁹
<i>Graptolebris testudinaria</i>	$\ln W = 3.39 + 3.48 * \ln L$	Dumont et al. (1975) ²
Harpacticoid copepodid	$\ln W = 2.5265 + 4.4 * \ln L$	Dumont et al. (1975) ⁴
<i>Hydra</i>	21.16 µg	Slobodkin (1964)
Hydracarina adult	$V = 2.5413L^3$	Spheroid
Hydracarina larvae	0.33 µg	Lanciani (1975)
<i>Kellicottia</i>	0.05 µg	Cajander (1983)
<i>Keratella</i>	$V = 0.02L^3$	Ruttner-Kolisko (1977)
<i>Kurzia latissima</i>	$\ln W = 2.7676 + 3.84 * \ln L$	Dumont et al. (1975) ²
<i>Lathonura rectirostris</i>	$\ln W = 1.915 + 2.02 * \ln L$	Dumont et al. (1975) ¹⁰
<i>Lecane</i>	$V = 0.1L^3$	Andersson et al. (2003)
<i>Lepadella</i>	$V = 0.1L^3$	Andersson et al. (2003)
<i>Macrocyclops albidus</i>	$\ln W = 1.3472 + 3.0087 * \ln L$	Lawrence et al. (1987) ¹¹
<i>Mesocyclops edax</i>	$\ln W = 1.3472 + 3.0087 * \ln L$	Lawrence et al. (1987)
<i>Mesostoma</i>	$V = 0.0472L^3$	Triangular prism
<i>Microcyclops rubellus</i>	$\ln W = 1.7116 + 3.6663 * \ln L$	Lawrence et al. (1987) ¹²
<i>Monostyla</i>	0.12 µg	Dickerson and Robinson (1984)

Table A7.1: (cont.)

Taxon	Formula Used	Reference
<i>Mytilina</i>	0.5 µg	Dumont et al. (1975)
nauplii	$\ln W = 0.6977 + 0.569 * \ln L$	Rosen (1981)
Ostracoda	$V = 2.122L^3$	Spheroid
<i>Platyias</i>	$V = 0.08L^3$	Ruttner-Kolisko (1977) ¹⁴
<i>Pleuroxus denticulatus</i>	$\ln W = 3.5723 + 4.03 * \ln L$	Dumont et al. (1975) ¹⁴
<i>Pleuroxus procurvus</i>	$\ln W = 3.5723 + 4.03 * \ln L$	Dumont et al. (1975) ¹⁴
<i>Ploesma</i>	$V = 0.23L^3$	Ruttner-Kolisko (1977)
<i>Polyarthra</i>	$V = 0.28L^3$	Ruttner-Kolisko (1977)
<i>Polyphemus pediculus</i>	$\ln W = 2.7792 + 2.152 * \ln L$	Rosen (1981)
<i>Scapholebris kingi</i>	$\ln W = 2.8713 + 3.079 * \ln L$	Rosen (1981)
<i>Simocephalus serrulatus</i>	$\ln W = 1.3863 + 3.81 * \ln L$	Dumont et al. (1975) ¹⁵
<i>Skistodiaptomus oregonensis</i>	$\ln W = 0.9717 + 2.7323 * \ln L$	Malley et al. (1989)
<i>Squatinella</i>	$V = 0.03L^3$	Ruttner-Kolisko (1977) ¹⁶
<i>Synchaeta</i>	$V = 0.1L^3$	Ruttner-Kolisko (1977)
Tardigrada	0.3 µg	Nalepa and Quigley (1980)
<i>Testudinella</i>	$V = 0.08L^3$	Ruttner-Kolisko (1977)
<i>Trichocerca</i>	0.1 µg	Dumont et al. (1975)
<i>Trichotria</i>	$V = 0.13L^3$	Andersson et al. (2003)
<i>Tropocyclops extensus</i>	$\ln W = 1.7116 + 3.6663 * \ln L$	Lawrence et al. (1987)

Taxon of original intent:¹ *Alona rectangula*² *Alona affinis*³ *Chydorus sphaericus*

- ⁴ General Harpacticoid equation
- ⁵ *Kellicottia*
- ⁶ *Skistodiaptomus oregonensis* copepodids
- ⁷ Mixed *Diacyclops bicuspidatus thomasi* and *Mesocyclops edax* copepodids
- ⁸ *Diacyclops bicuspidatus thomasi*
- ⁹ *Eurycercus vernalis*
- ¹⁰ *Ceriodaphnia*
- ¹¹ *Mesocyclops edax*
- ¹² *Tropocyclops extensus*
- ¹³ *Testudinella*
- ¹⁴ *Pleuroxus aduncus*
- ¹⁵ *Simocephalus vetulus*
- ¹⁶ *Anaeuropsis*

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Appendix 8: Ranges, amplitudes, and means of observed conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C , dissolved oxygen (mg/L), pH, and temperature ($^\circ\text{C}$) from weekly and sub-daily measurements.

Table A8.1: Range and means of observed conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C , dissolved oxygen (mg/L), pH, and temperature ($^\circ\text{C}$) from weekly data (taken at $\sim 13\text{h}00$).

Environmental Variable	Mean recorded value	Minimum recorded value	Maximum recorded value
Conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C	184.2	144	266
Dissolved Oxygen (mg/L)	6.7	0.29	14
pH	7.9	6.6	10.5
Temperature ($^\circ\text{C}$)	21.2	15.8	28.1

Table A8.2: Amplitudes of changes in observed conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C , dissolved oxygen (mg/L), pH, and temperature ($^{\circ}\text{C}$) from measurements taken every 6 hours for 24 hours on 3 days (July 17-18, 2007; July 24-25, 2007; and July 31 - August 01, 2007). Measurements taken in one tank per region.

Environmental Variable	Mean amplitude	Minimum amplitude	Maximum amplitude
Conductivity ($\mu\text{S}/\text{cm}$) standardized to 25°C	4.52	1	21
Dissolved Oxygen (mg/L)	0.66	0.1	2.09
pH	0.15	0.05	0.5
Temperature ($^{\circ}\text{C}$)	1.88	0.92	3.81

Appendix 9: Results of habitat separated richness analyses.

Table A9.1: ANOVAs on local, among-community, and regional richness of littoral communities.

		DF	F	p
Local Richness	Connectivity	2	4.20	0.04
	Heterogeneity	1	1.47	0.25
	Connectivity x Heterogeneity	2	1.70	0.22
	Error	12		
		DF	F	p
Among-community Richness	Connectivity	2	0.36	0.70
	Heterogeneity	1	6.36	0.03
	Connectivity x Heterogeneity	2	1.47	0.27
	Error	12		
		DF	F	p
Regional Richness	Connectivity	2	2.03	0.18
	Heterogeneity	1	4.27	<i>0.06</i>
	Connectivity x Heterogeneity	2	1.74	0.22
	Error	12		

Table A9.2: ANOVAs on local, among-community, and regional richness of pelagic communities.

		DF	F	p
Local Richness	Connectivity	2	1.92	0.19
	Heterogeneity	1	0.16	0.70
	Connectivity x Heterogeneity	2	1.17	0.35
	Error	12		
		DF	F	p
Among-community Richness	Connectivity	2	6.39	0.01
	Heterogeneity	1	0.52	0.48
	Connectivity x Heterogeneity	2	0.27	0.77
	Error	12		
		DF	F	p
Regional Richness	Connectivity	2	0.19	0.83
	Heterogeneity	1	0.01	0.92
	Connectivity x Heterogeneity	2	0.89	0.44
	Error	12		

Appendix 10: Site-plots from NMDS ordinations of local and regional communities.

Figure A10.1: NMDS ordination site-plot of local pond counts. Number indicates pond identity (regions being multiples of four starting at Pond 1), colour indicates treatment: no connectivity, homogeneous (grey); no connectivity, heterogeneous (black); low connectivity, homogeneous (orange-red); low connectivity, heterogeneous (dark red); high connectivity, homogeneous (light blue); high connectivity, heterogeneous (dark blue).

Figure A10.2 NMDS ordination site-plot of regional counts. Symbol form indicates treatment: homogeneous regions (empty symbols), heterogeneous regions (filled symbols), no connectivity (circles), low connectivity (triangles), high connectivity (squares).