

**REGIONAL PLANKTON DIVERSITY AS A BUFFER AGAINST
ENVIRONMENTAL CHANGE IN FRESHWATER ECOSYSTEMS**

by

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ABSTRACT

Many experiments show that species diversity at small, local scales affects ecosystems; however, conservation is concerned with extinctions of species across broad landscapes. The relevance of global or regional diversity to ecosystems therefore remains in question. I asked whether regional biodiversity in freshwater zooplankton affects the resilience and resistance of local ecosystems to the multiple stressors of warming and salinization. I hypothesised that dispersal of species from the regional community should buffer ecosystems against environmental change by providing species with traits adapted to the novel conditions. I subjected freshwater zooplankton communities in mesocosms that were either connected to or isolated from the larger regional species pool to a factorial manipulation of experimental warming and increased salinity. Dispersal introduced heat-tolerant regional taxa that were able to compensate for reductions in local taxa under warmed conditions. Dispersal also dampened the effects of warming on net primary productivity, suggesting that regional diversity can provide stability against some aspects of climate change. However, other measures of ecosystem performance like decomposition and sedimentation were affected by warming and salinity but not dispersal. The results indicate that regional biodiversity provides important insurance that can stabilize ecosystems in a dynamic environment. However, compensation by the regional biota could not buffer all ecosystem rates against all sources of stress. My results show that the connectivity of habitats to regional biodiversity introduces species with broad ranges of traits that can maintain some local ecosystem function in the face of environmental changes.

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CO-AUTHORSHIP STATEMENT

The manuscript chapter of this thesis was written in collaboration with Dr. Jonathan Shurin, UBC. I was primarily responsible for all aspects of the research including the design and implementation of the experiment, as well as data analysis and writing. Dr. Shurin provided guidance and supervision throughout this process and worked closely with me to prepare the manuscript.

1 INTRODUCTION

1.1 Globally Changing Environmental Conditions

Anthropogenic ecological stressors are currently causing environmental change at local and global scales (Vitousek et al. 1997). Ecological stressors are any abiotic or biotic variable exceeding its normal range of variation as a result of human activity (Vinebrooke et al. 2004). These include, but are not restricted to, climate warming, acid deposition, eutrophication, salinization, heavy metals, and invasive species. It has been suggested that current rates of extinction in freshwater fauna in North America is roughly five times that in terrestrial ecosystems and comparable to that in tropical forests (Ricciardi and Rasmussen 1999, Sala et al. 2000). Multiple ecological stressors impact aquatic ecosystems both directly and in concert through their interactions among physical and biological processes. The nature of these interactions determines the net impact on an ecosystem (Tilman and Lehman 2001, Vinebrooke et al. 2004). Furthermore, these interactions are often synergistic or antagonistic, making them complex and unpredictable (Christensen et al. 2006), emphasizing the need to incorporate multiple stressors when studying how they impact ecosystems.

1.2 Climate Warming and Freshwater

Current decreases in biodiversity of freshwater fauna have been largely attributed to changing climate (Ricciardi and Rasmussen 1999), one aspect of which is increasing surface water temperatures. Magnuson et al. (1997) predict an increase of 1-7°C in surface water temperatures in Northern Hemisphere lakes under a forecasted doubling

of atmospheric carbon dioxide concentrations in the twenty first century. Higher surface water temperatures are expected to extend the ice-free season, causing a positive feedback loop by allowing for more sunlight to be absorbed into the lake as a result of reduced albedo, further increasing temperatures (Magnuson et al. 1997). Earlier ice-free seasons also lead to seasonal shifts in the phenology of lakes and can disrupt predator-prey interactions if the timing of population blooms of both species are not affected similarly (Winder and Schindler 2004a, b). In larger waterbodies, warming can also cause increased surface water stability, thereby decreasing mixing and upwelling of nutrients, which can result in reduced primary productivity (O'Reilly et al. 2003). This is not generally the case in pond ecosystems, which are usually too shallow to stratify. Rather, ponds are at risk of drying out if temperature or precipitation patterns change (Riordan et al. 2006).

Warmer conditions are expected to disproportionately impact organisms at higher trophic levels, as they are often more sensitive to warmer conditions (Petchey et al. 1999, Strecker et al. 2004). This may be because warming often disproportionately impacts larger organisms because of their higher metabolic requirements, and so zooplankton are more sensitive than phytoplankton to increases in temperature (Daufresne et al. 2009). This increase in metabolic requirements has been shown to destabilizing populations of zooplankton because they deplete their food sources faster (Beisner et al. 1997, Petchey et al. 1999). Zooplankton can also die from thermal stress if temperatures exceed a critical threshold (Lahdes 1995). In comparison, effects of elevated temperature on phytoplankton are often seen as changes in community composition rather than changes in overall biomass (Strecker et al. 2004, Thompson et

al. 2008). Additionally, warming has been shown to cause larger phytoplankton taxa to be replaced by smaller taxa (Sommer and Lengfellner 2008). Overall, the community level responses to climate warming will be a combination of the direct influence of warmer temperatures and altered precipitation patterns as well as the way in which they interact with other ecological stressors (Keller 2007).

1.3 Increasing Salinity in Freshwater

Increases in salinity concentrations in lakes and ponds are a secondary effect of climate change due to increased evaporation; warmer temperatures and decreased precipitation concentrate salts present in the water (Evans and Prepas 1996). In low-lying coastal regions climate change induced rises in sea level can cause intrusions of sea water into previously freshwater lakes (Schallenberg et al. 2003). While increased salinity is often a result of climate change, the biological stress produced differs from that of thermal stress and so can be considered a separate type of ecological stress. Furthermore, increased salinity can also be the result of other factors that are unrelated to climate change, such as run-off of salt from roads (Kaushal et al. 2005) and agricultural irrigation (Isidoro et al. 2006).

Chronic exposure to salinity concentrations greater than 250 mg/L has been shown to be toxic to freshwater life (Environment Canada 2001). Concentrations of salt in many urban and suburban areas already exceed this amount, while in rural streams there is an increasing trend in salinity over the past four decades that will soon exceed this threshold in parts of the United States (Kaushal et al. 2005). Even small increases in

salinity result in decreases in zooplankton diversity, survival, and growth rates, although zooplankton show marked differences in tolerance, even within species (Schallenberg et al. 2003, Grzesiuk and Mikulski 2006, Goncalves et al. 2007). Physiological tolerance to salinity in freshwater zooplankton depends on water temperature; salinity sensitivity in cladocerans increases with temperature (Hall and Burns 2002, Grzesiuk and Mikulski 2006). Phytoplankton show a varied range of salinity tolerance (Goncalves et al. 2006) and increases in salinity coincide with lower frequencies of phytoplankton blooms and reduced prevalence of cyanobacteria in Canadian prairie lakes (Evans and Prepas 1996). However, it seems that phytoplankton communities are more resilient than zooplankton communities to increased salinity, as Hall and Burns (2003) found no change in chlorophyll a as a result of salinity increases up to 4.8 g L⁻¹.

1.4 Ecosystem Function

Ecosystem functioning is reliant on the ability of its component biota to perform basic processes such as primary productivity, grazing, decomposition, and nutrient cycling (Chapin et al. 1997). Ecological stressors are generally expected to disrupt the way organisms provide these services and function. Some ecosystem function rates are expected to increase (primary production under eutrophication) while others will decrease (grazing rates with acidification). However, rates of ecosystem function are expected to change as organisms struggle to adjust to the new environmental conditions (Chapin et al. 1997). Evidence for how specific ecological stressors affect ecosystem function rates is scarce. However, under stressful conditions, organisms

must exert more energy in order to maintain the same levels of function, thus decreasing the efficiency of resource use (Odum 1985).

1.5 Ecosystem Connectivity

The direct and interactive effects of ecological stressors on freshwater ecosystems are often studied (eg. Petchey et al. 1999, Schallenberg et al. 2003, Christensen et al. 2006), yet most studies deal only with one local ecosystem and its resident community. In reality, these patches are intrinsically linked through dispersal of organisms from patches in the surrounding regional metacommunity (Leibold et al. 2004). Climate warming also causes species to shift their ranges to higher latitudes and elevations (Parmesan 1996). This results in differences between the current community and that which may be present in the future under warmer environmental conditions. By incorporating dispersal of organisms from the regional metacommunity, we can include the idea of range shifts into our studies, making them more realistic.

Dispersal of freshwater plankton among lakes within regions is sufficiently rapid that community composition at a given lake should not be limited by dispersal (Havel and Shurin 2004) but rather by interspecific interactions in the resident community, which prevent successful colonization by new species (Shurin 2000). However, environmental perturbations that result in loss of biodiversity or biomass weaken interspecific interactions and thereby make successful colonization more likely. Dispersal is therefore expected to allow for species sorting along environmental gradients. This provides a mechanism by which compensatory dynamics could occur, where colonizing species

compensate for losses of local species within a given functional group (Klug et al. 2000). In this way, dispersal could potentially buffer ecosystems against changes in environmental conditions brought on by ecological stressors (Loreau et al. 2003).

1.6 Compensatory Dynamics

From the perspective of ecosystem function, it does not matter which taxa support specific ecosystem processes, but rather just that they are provided. In changing environmental conditions, compensatory dynamics (when a reduction of one species is offset by increases in another functionally similar species) can help to stabilize overall ecosystem function (Klug et al. 2000). In the few studies that have investigated how compensatory dynamics maintain ecological function in communities affected by ecological stressors (Klug et al. 2000, Fischer et al. 2001), none have examined the role of dispersal. Vinebrooke *et al.* (2003) report detecting compensatory dynamics in experimentally acidified Lake 302S, whereby acid-tolerant phytoplankton and rotifer species replaced lost species, resulting in maintenance of ecosystem function. Holzapfel and Vinebrooke (2005) showed compensatory dynamics when alpine zooplankton were experimentally exposed to warmer conditions and dispersal of montane zooplankton was facilitated. Alpine zooplankton communities have low diversity and are often dispersal limited because of their remote locations due to high altitude, but these results suggest that compensatory dynamics might also occur in communities with higher diversity and dispersal.

As stressors occur simultaneously, the potential for compensatory dynamics to occur should be reduced since any compensatory species must be co-tolerant for each stressor involved (Tilman and Lehman 2001, Vinebrooke et al. 2004). More diverse, fast growing, and rapidly dispersing lower trophic levels should show higher incidence of co-tolerance causing disproportionately negative impacts on higher trophic levels.

My thesis combines ecological stressor experimentation with dispersal theory to ask how ecosystem connectivity affects the resilience and resistance of local pond communities to environmental change. Applying a metacommunity approach to traditional ecological stressor research allows me to ask how biodiversity on larger scales than a single habitat patch affects the way that local communities respond to stress. This is important because we normally think about conservation on these large scales rather than the small, isolated communities that are generally studied in ecological stressor experiments.

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2 Regional Zooplankton Biodiversity Buffers Pond Ecosystems Against Climate Change¹

2.1 Introduction

Anthropogenic ecological stressors such as climate change, eutrophication, chemical pollution, habitat destruction, and the introduction of invasive species change environmental conditions globally and locally (Vitousek et al. 1997, Schindler 2001). Communities faced with increasingly stressful conditions may either be buffered by changes that maintain their structure and function (Vinebrooke *et al.* 2004), or experience losses of biodiversity or declines in their performance as ecosystems (Chapin *et al.* 1997). Losses of biodiversity and changes in the environment are presently occurring at unprecedented rates (Ricciardi and Rasmussen 1999, Sala et al. 2000, Pounds et al. 2006), altering the functioning of virtually all ecosystems (Chapin et al. 1997, Loreau et al. 2001, Ptacnik et al. 2008). Predicting future changes is complicated by the fact that multiple ecological stressors often interactively affect ecological communities in complex ways (Tilman and Lehman 2001, Christensen et al. 2006, Darling and Cote 2008). Understanding the properties that allow ecosystems to maintain their resilience in the face of change, rather than collapse under multiple ecological stressors, is vital to minimizing the impacts of global environmental change on natural ecosystems and the services they provide to humanity.

¹ A version of this chapter has been submitted for publication. Thompson, P.L., and J.B. Shurin. Regional Zooplankton Biodiversity Provides Limited Buffering of Pond Ecosystems Against Climate Change.

The impact of environmental change on an ecological community is determined by the response of its resident species, as well as the changes in composition due to dispersal and colonization from the regional species pool (Cottenie et al. 2003, Leibold et al. 2004). Many species with high dispersal rates may fail to colonize new habitats as a result of filters imposed by interactions with species that are already present (Shurin 2000). However, ecological stressors that disrupt community stability may permit colonization of stress tolerant species from the regional species pool (Shurin 2001). Additionally, climate change is driving range shifts by many species as the conditions that include their environmental niches move upward in elevation and latitude (Parmesan 1996). Species of virtually every taxonomic group are colonizing new habitats and becoming novel members of local ecological communities and ecosystems (Parmesan 2006). Loreau et al. (2003) and Leibold and Norberg (2004) predict that within a heterogeneous landscape, dispersal and colonization should provide spatial insurance against locally changing environments. Species that are maladapted to new conditions would be replaced by new species from the region with traits that are favoured. These compensatory dynamics could allow community function to be maintained if the new species perform similar roles to those they replace (Klug et al. 2000, Fischer et al. 2001). This theory predicts that dispersal by species in the region or beyond should increase local community resistance and resilience to environmental stress.

Current ideas of how regional biodiversity affects the stability of communities under environmental change are based on theoretical models that have yet to be experimentally tested (Yachi and Loreau 1999, Loreau et al. 2003, Leibold and Norberg

2004). Here I employed a large mesocosm design to test how the dispersal of freshwater zooplankton from a regional metacommunity affects the response of local communities to environmental changes resulting from multiple ecological stressors. I applied factorial stressors of climate warming (increase of ~ 2.5 °C) and increased salinity (increase of 0.3 psu) to a naturally assembled local plankton community in 1000L field mesocosms. The diversity and composition of plankton communities in the experiment were comparable to those found in natural assemblages in the region. The warming treatment followed the diurnal temperature fluctuations experienced by the ambient mesocosms (Fig. 1). This increase in temperature corresponds to the conservative range of predicted scenarios for northern hemisphere freshwater lakes and ponds under a forecasted doubling of atmospheric carbon dioxide (Magnuson *et al.* 1997). The salinity treatment is approximately half of the concentration that has been shown to be chronically toxic to freshwater life (Kaushal *et al.* 2005). Such increases in salinity are often caused by run off of road de-icing salt (Kaushal *et al.* 2005) as well as higher evaporation rates that accompany climate warming (Evans and Prepas 1996). The salinity and temperature stress treatments were crossed with two levels of dispersal; communities were either isolated (no dispersal facilitated) or connected to the regional species pool (assisted dispersal of plankton from 40 waterbodies in the region of Southwestern BC). A number of ecosystem processes were measured in the mesocosms, including primary productivity, zooplankton grazing, leaf litter decomposition, sedimentation, and periphyton growth. I also measured the standing stocks of zooplankton and phytoplankton biomass (as chlorophyll-*a*). This design allowed me to determine the potential of regional species to impart resilience and

maintain ecosystem functioning in the face of significant and relevant levels of environmental change.

I predicted that reductions in biodiversity and biomass in response to the ecological stressors would be mitigated when dispersal of regional organisms is facilitated. That is, I expected to see interactive effects of the dispersal and stress treatments on rates of ecosystem processes. Additionally, I expected that stress-induced changes in ecosystem function measurements, such as zooplankton grazing and primary productivity, would be reduced by dispersal as a result of stress tolerant regional species compensating for losses in local species abundance and function. I did not expect to see any effects of dispersal on processes such as leaf litter decomposition, periphyton colonization, and sedimentation since they are removed from the direct influence of zooplankton. However, I measured these rates to compare their responses to stress with those of processes related to zooplankton, and to test for potential indirect effects of zooplankton colonization. I also examined the association between species responses to the salinity and warming treatments to ask whether traits that confer tolerance to the two forms of stress are related.

2.2 Methods

2.2.1 Experimental Design

The experiment was conducted during the summer of 2008 at the Experimental Pond Facility on the University of British Columbia Campus, Vancouver, BC. Forty – 1000 L plastic cylindrical livestock watering tanks (Rubbermaid®, Sandy Springs, USA) were used as experimental mesocosms. Tanks were filled with Vancouver, BC city water on

April 23 and the bottoms were covered with rinsed, coarse sand as a benthic substrate. One litre of peat moss was added to each mesocosm on May 2 to increase the organic content of the water. Mesocosms were inoculated with plankton and nutrients from a nearby pond on May 8 by adding sediment and live plankton collected using a 64 μ m conical tow net. Three mesocosms used to measure natural dispersal were established in similar fashion but received no peat moss, plankton, or sediment. These mesocosms were fertilized with 10 μ g/L phosphorous as KH_2PO_4 and 160 μ g/L nitrogen as NaNO_3 on May 28 to simulate natural nutrient concentrations. Experimental communities were allowed to establish and stabilize for five weeks before treatments were applied.

2.2.2 Application of Treatments

The treatments of environmental warming, increased salinity, and artificial dispersal of plankton were applied factorially and replicated 5 times. The warming and salinity treatments were applied on June 17. The dispersal treatment was first applied on June 30 as described below to allow the original community time to adjust to the new environmental conditions before new species were added. The dispersal treatment was repeated on July 15 and August 12 to allow multiple opportunities for colonization.

Tanks were warmed by 300W submersible aquarium heaters (Hagen®, Montreal, Canada) running constantly so that warmed mesocosms were $\sim 2.5^\circ\text{C}$ (mean standard deviation – 0.429°C) warmer than ambient (mean standard deviation – 0.293°C) mesocosms at all times. The heating treatment allowed the warmed mesocosms to follow the natural pattern of diurnal temperature fluctuations that occurred in the ambient mesocosms, but at a higher temperature (Fig. 1). Artificial heaters, made of

clear plastic tubing filled with sand sealed off from the water with rubber stoppers, were added to all ambient temperature mesocosms to control for the physical presence of the heaters.

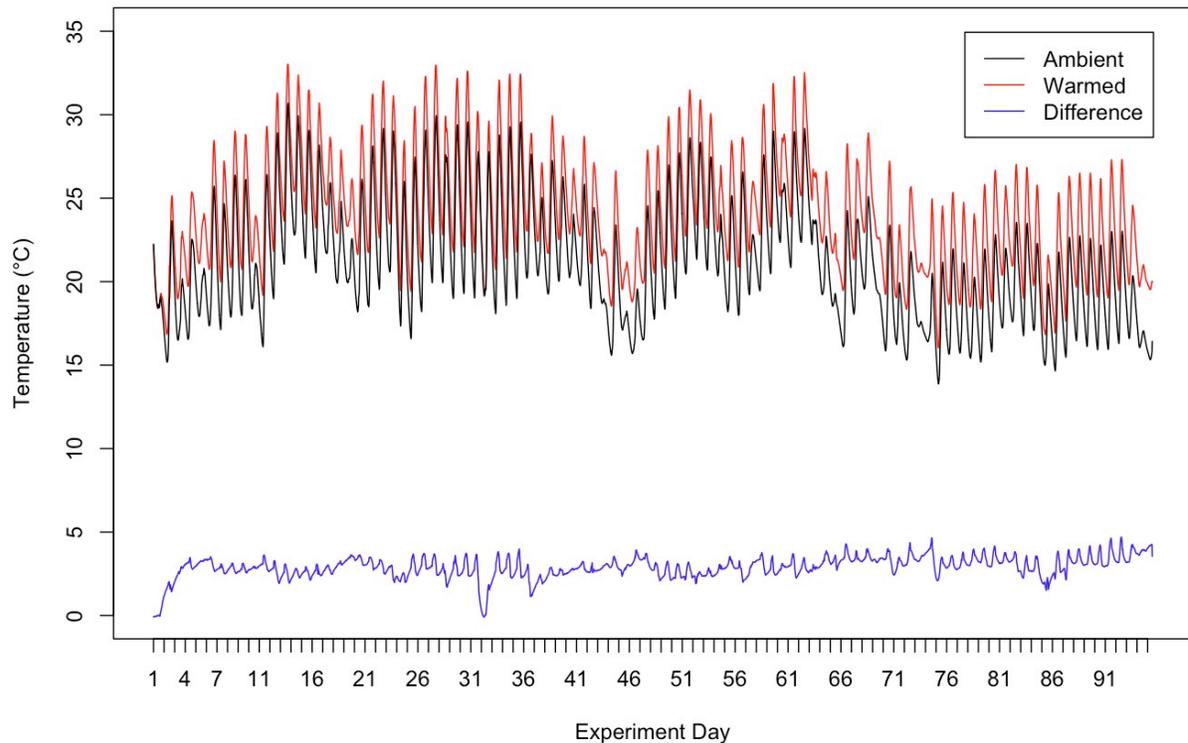


Figure 1. Ambient and warmed mesocosm water temperatures. The difference in temperature between the two treatments is shown in blue. N=20 for both treatments.

Lab grade NaCl was added to increase the salinity to 0.3 psu from an ambient concentration of <0.1 psu. This concentration of salt was chosen because it is approximately half of the level that is acutely toxic to freshwater organisms (Kaushal *et al.* 2005) and thus can be considered a non-lethal stress. Evaporation caused salinity levels to reach a maximum of 0.6 psu in the warming with increased salinity treatment and 0.5 psu in the salinity without warming treatment in late July. 400 L of water from a nearby pond with similar chemical composition was pumped into each tank on July 22

to offset the high levels of evaporation. All added water was sieved through a 64 μm mesh to prevent introduction of new zooplankton into the mesocosms. The same volume of water was added to tanks in all the treatments.

Concentrated 60 mL aliquots of live plankton were added to each dispersal treatment mesocosm during each of the three dispersal treatments. The plankton were collected from 40 lakes and ponds in south western British Columbia spanning a salinity gradient of 0.0-2.8 psu and a temperature gradient of 17.0- 23.6 °C at the time of collection. Plankton were mixed together in a bucket prior to dispersing. Zooplankton were dispersed from the bucket within 15 minutes of being mixed together to minimize the stress of being in such high densities. An average of 755 individuals (range among dates: 226-1410) with an average SE of 63.6 (range among dates: 12.8-156.8) were added to the tanks in each dispersal event. In total, 16 identified taxa were added in the dispersal treatments. This represented an addition of about 1.5 % of the total estimated density of zooplankton individuals already present in the mesocosms. Dispersing individuals included copepods, cladocerans, and rotifers, some of which were already present in the local community. Identical aliquots of plankton were heat killed and added to each non-dispersal treatment mesocosm to control for added nutrients and water. Dispersal treatments were always applied at least two weeks prior to the next sampling date to ensure that plankton sampled were viable members of the plankton community rather than declining sink populations. Communities of regional plankton were maintained in additional livestock watering tanks in between dispersal treatments so that regional plankton only needed to be collected once. Sediment from each regional lake was added, in addition to live plankton, to the holding tanks. This was done to

provide a seed bank of plankton so that those taxa not present in the water column at the time of sampling could still potentially emerge in the holding tanks and be present in the dispersal treatment. The composition of the regional species pool changed over time in the tanks. However, maintaining the species pool in this way was necessary because of the logistical challenge of sampling 40 widely-dispersed waterbodies multiple times over the course of the experiment.

The average of 755 individuals added in each of the dispersal treatments represents a high but not unnatural rate of dispersal. Vanschoenwinkel *et al.* (2008) collected over 850 viable zooplankton propagules from 17 different taxa in 28 days in 9 wind socks placed nearby to mountain ponds that were subject to drying out. While this study was conducted in a windy environment and only a small number of these propagules would have landed in waterbodies, it demonstrates the potential intensity of zooplankton dispersal. Additionally, the 16 taxa introduced in the dispersal treatment is comparable to the numbers found by Cohen and Shurin (2003), Cáceres and Soluk (2002) and Louette *et al.* (2008) in studies of natural colonization of mesocosms and newly formed ponds. At the end of the experiment I found that three taxa (*Daphnia*, *Ceriodaphnia*, *Calanoid* copepods), that were common in both the regional and local species pools, had colonized the three mesocosms that had not been initially seeded with plankton. Therefore, natural levels of dispersal into the mesocosms was not as high as those found by the above studies, and the 16 taxa that were introduced was around 5x the level of background dispersal.

2.2.3 Sampling and Analysis

Chlorophyll and salinity were sampled bi-monthly starting June 16, the day before the initial application of treatments. Chlorophyll *a* concentrations were measured using the in-vivo fluorescence method on a Trilogy fluorometer (Turner Designs, Sunnyvale USA). Salinity, pH, and conductivity were measured using a handheld probe (YSI®, Yellow Springs, USA). Zooplankton were sampled on June 16, the day before the initial application of treatments, and twelve weeks later on September 9. Zooplankton samples were taken by collecting 10 L of water, using a depth integrated sampler constructed from PVC pipe, and filtering it through a 64 µm sieve. Samples were preserved in 70 % ethanol. A separate integrated sampler was used for each mesocosm and the 64 µm sieve was rinsed thoroughly between samples to prevent unintentional dispersal of organisms between tanks.

Zooplankton samples were counted using a dissecting microscope at 10x magnification and at 60x magnification for identification and for taking length measurements. Whole samples were analysed and taxa with less than 500 individuals were counted. Samples with more than 500 individuals of any taxa were sub-sampled so that at least 500 animals were counted. Biomass of each taxa was estimated by measuring length of 10 haphazardly selected individuals per sample and using length mass regressions for crustaceans and length volume regressions for rotifers (Dumont and Balvay 1979, McCauley 1984, Johnston and Cunjak 1999).

2.2.4 Ecosystem Function Measurements

Daily cycles in dissolved oxygen concentrations were measured using a handheld probe (YSI®, Yellow Springs, USA) at dawn, dusk, and dawn on August 6 and 7 and again on September 10 and 11 to estimate primary production and respiration. Net productivity was calculated as the increase of oxygen over 24 hrs (Downing and Leibold 2002).

Pre-weighed 60 mL centrifuge tubes were fixed, uncapped, to the bottom of the mesocosms in an upright position between June 30 and September 8 to measure sedimentation rates. Tubes were capped during sampling and when water levels were topped up to avoid accidental deposition of sediment. Following the experiment, tubes were placed uncapped in a drying oven and left to evaporate prior to weighing. The sedimentation rate was calculated as dry weight of sediment deposited per day that the tubes were in the mesocosms.

Two 4 L plastic cubitainers were placed in each mesocosm to measure zooplankton grazing rates. One contained mesocosm water, with ambient densities of zooplankton and the other containing mesocosm water sieved through a 64 µm mesh to remove zooplankton. In vivo chlorophyll a concentrations in the cubitainers were measured after two days and the daily grazing rate was calculated as the difference in chlorophyll-a concentration between the two containers, divided by the length of the trial in days.

Pre weighed oven dried *Alnus rubra* leaves in mosquito netting bags (0.5 mm mesh) were deployed on August 18 and left anchored in the centre of the mesocosms for four weeks. The litterbags were then removed, dried at 40 °C for two days and reweighed.

Decomposition was calculated as the percent difference in mass over time (Bärlocher 2005).

Unglazed 25 cm² clay tiles were deployed on July 18 and left until September 10 to measure periphyton growth rates. Tiles were then removed from the mesocosms and scrubbed with a toothbrush to brush off periphyton onto a pre-weighed Whatman GF/C filter paper. Filter papers were analysed for chlorophyll after cold extraction in acetone using the non-acidification method on a Turner Trilogy fluorometer (Turner Designs, Sunnyvale, USA)(Welschmeyer 1994). Periphyton colonization was calculated as the total concentration of chlorophyll divided by the number of days the tiles were in the mesocosms.

2.2.5 Statistical Analysis

The effect of the three treatments on zooplankton community composition was analysed using redundancy analysis (RDA). Zooplankton community data was transformed using a Hellinger transformation to reduce the influence of outliers (Legendre and Gallagher 2001). Significance of each treatment combination was determined using Monte Carlo permutation tests on the results of the RDA. The effect of the treatments on the ecosystem function rates and standing stocks were tested using three-way factorial ANOVA. Ecosystem function rates were standardized to standard deviation units so the effect size of the treatment combinations could be compared. Other variables that were non-normally distributed were log transformed prior to analysis. Chlorophyll concentrations were averaged over all sample dates prior to analysis. All analyses were

performed using R (R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria).

2.3 Results

2.3.1 Zooplankton Community Composition

The warming, salinity, and zooplankton dispersal treatments had independent and interactive effects on zooplankton community composition, as shown in the redundancy analysis ordination plot (Fig. 2, Table 1). Taxa plotted in the direction of the treatment arrows in Figure 1 increased in abundance with that treatment or combination of treatments, while taxa plotted in the opposite direction declined in abundance. The results of the corresponding univariate tests can be found in the Supporting Information. Here I describe the trends shown in the redundancy analysis because we are interested in the effects of treatments on overall community composition rather than the abundance of individual taxa. *Daphnia pulex* abundance was negatively associated with the warming and salinity regardless of the dispersal treatment. The genera *Scapholoberis*, *Ceriodaphnia*, *Bosmina*, *Diaphanosoma*, *Polyphemus*, and *Chydorus* were all positively associated with the warming, dispersal and warming with dispersal treatments. The dominant local calanoid copepod, *Skistodiaptomus oregonensis* declined in the salinity treatment while cyclopoid copepod abundance increased. *Chaoborus spp.* abundance decreased with the warming treatment. Rotifers showed no association with the dispersal treatment and their contribution to zooplankton community biomass was negligible. The warming X dispersal interaction explained 5 %

of the total variation in zooplankton composition and 20 % of the explained variation (Table 1).

Table 1. Redundancy analysis of the Hellinger transformed biomass ($\mu\text{g/L}$) of the zooplankton community composition (17 taxa).

Treatment	λ	F	P
Warming (Warm)	0.07	3.21	0.02
Salinity (Salt)	0.08	3.83	0.01
Dispersal (Disp.)	0.05	2.51	0.04
Warm x Salt	0.04	1.63	0.11
Warm x Disp.	0.05	2.15	0.04
Salt x Disp.	0.01	0.70	0.64
Warm x Salt x Disp	0.01	0.68	0.74

Notes: λ indicates zooplankton community variance explained by treatment combination. P- values based on permutation tests. Statistical significance ($P < 0.05$) indicated in bold.

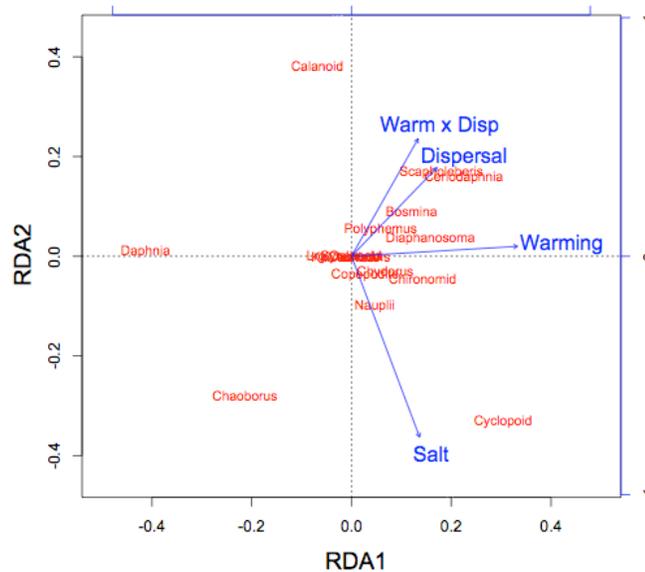


Figure 2. Redundancy analysis ordination representing the response of the zooplankton community composition. All 8 treatment combinations ($n=5$) were included in the analysis but treatment combinations that were not significant ($p > 0.05$) are not shown on the figure.

2.3.2 Ecosystem Function Rates

Warming and salinity both independently and interactively altered ecosystem function rates. Figure 3 compares the magnitude of these responses to warming and salinity with and without dispersal. Ecosystem rates that responded differently to a stress with and

without zooplankton dispersal are plotted off the 1:1 line of Figure 3. My hypothesis predicts that rates should fall in the lower right on Figure 3, where stress impacts on function are greater in the isolated tanks than those connected to the regional pool by dispersal. This was the case for August net primary productivity where dispersal negated the positive effect of warming (W , $P=0.005$, $W*D$, $P=0.003$). All other rates were unaffected by dispersal and so fall on or near to the 1:1 line. Periphyton growth increased with both warming (W , $P=0.001$) and salinity (S , $P=0.037$). Leaf litter decomposition declined when warming and salinity were combined ($W*S$, $P=0.028$) but not with either single stressor. Sedimentation rates were greater with high salinity (S , $P=0.039$). Zooplankton grazing rates were largely unaffected by any of the treatments. Warming caused net productivity to decrease in September (W , $P=0.009$).

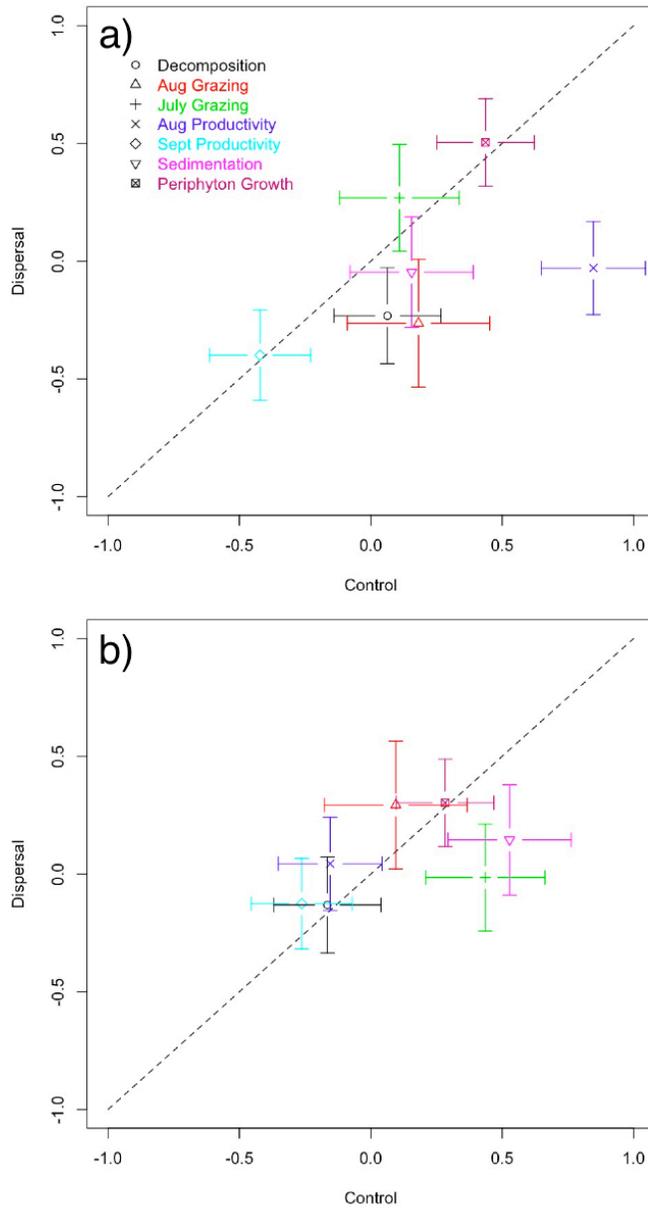


Figure 3. Effect size of warming (a) and increased salinity (b) treatments on the measured ecosystem function rates with and without facilitated dispersal of plankton. N=5 for all treatment combinations. Error bars represent 1 standard error.

2.3.3 Total Zooplankton Biomass

Increased salinity reduced zooplankton community biomass (S, $P=0.036$), and this effect was synergistically greater when combined with warming ($W*S$, $P=0.009$, Fig. 4a).

The dispersal treatment had no significant effect on zooplankton community biomass

but there was a trend towards higher biomass in any treatment combination when dispersal was facilitated.

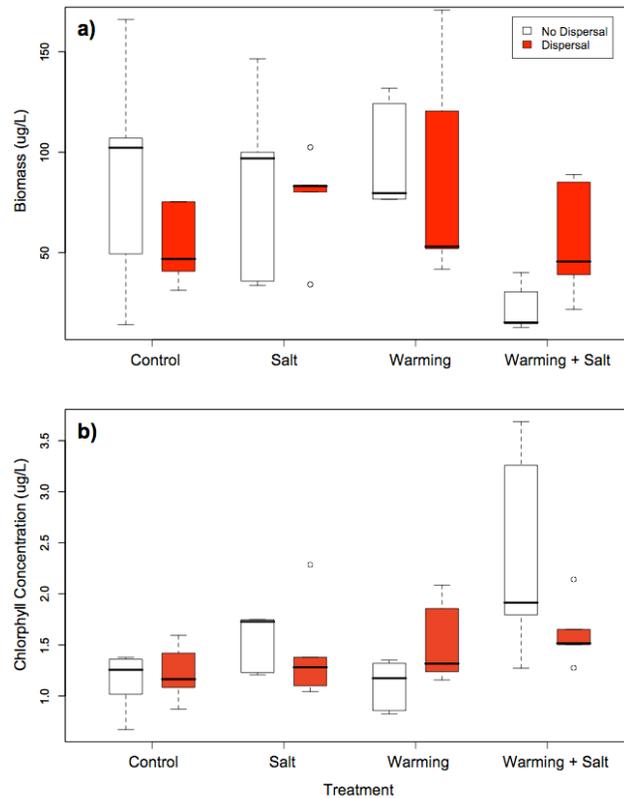


Figure 4. Total zooplankton community biomass (a) and chlorophyll concentrations (b). Chlorophyll concentrations are averaged over 5 dates spanning from July until September. N=5 for all treatment combinations.

2.3.4 Phytoplankton

Chlorophyll-*a* concentrations increased in the high salinity treatment (S, $p=0.002$) but not when dispersal was facilitated (S*D, $p=0.025$, Fig. 4b). Warming also caused higher phytoplankton biomass (W, $p=0.047$). Means of chlorophyll-*a* concentration and total zooplankton community biomass for each treatment combination were strongly negatively correlated ($n=8$, Pearson's $R= -0.887$, $p=0.003$).

2.3.5 Zooplankton species co-tolerance to stress

The 17 taxa found in the experiment exhibited a wide range of tolerances to climate warming and salinization (Fig. 5). The local taxa (those commonly found only in the no-dispersal treatment) generally showed lower tolerances to warming but a wider range of responses to salinity compared to the regional taxa (those that responded most strongly to the dispersal treatment). The regional taxa showed mostly neutral responses to increased salinity but higher tolerances to warming compared to the local taxa.

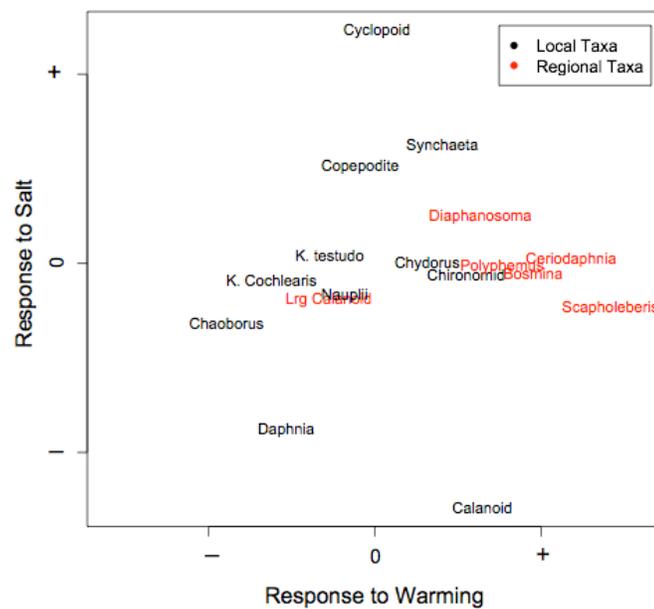


Figure 5. Response of local and regional taxa to each individual stressor. Response was determined by the loadings of each taxa on the RDA axis that had the highest correlation with each stress treatment. Regional species are those that showed a positive association with the dispersal treatment.

2.4 Discussion

These findings indicate a role for regional biodiversity and habitat connectivity in increasing the resistance and resilience of ecosystems against changing environments. Most experimental studies of biodiversity effects on ecosystem function deal with small spatial scales and single trophic levels (Hooper et al. 2005, Srivastava and Vellend

2005, Duffy et al. 2007). The discrepancy between the scope of these experiments and the broad geographic scales of extinction limit our understanding of how biodiversity loss may impair ecosystems. In this study, the climate warming treatment caused compositional changes in the local community that were mediated by the presence of regional species introduced through dispersal that could tolerate heat stress. Ecological stressors cause changes in ecosystem function both through direct influences on resident taxa and by changing community composition through range shifts (Parmesan 2006). Dispersal can indirectly affect ecosystem function through the second mechanism by facilitating community compositional changes resulting from ecological stressors. These results indicate that large-scale biodiversity can provide insurance that allows ecosystems to maintain their function in a variable environment.

The experiment also shows that the potential buffering capacity of regional biodiversity is limited, and depends on the ecosystem process and the source of stress. As expected, ecosystem function measurements that are not heavily influenced by zooplankton (decomposition, periphyton colonization, and sedimentation) were affected mainly by the direct impacts of the ecological stressors with no compensation by the regional biota. Dispersal of organisms such as benthic macroinvertebrates that play larger roles in these processes may have shown similar stabilizing effects. In addition, the interactive effects of stress and zooplankton colonization depended on the season and the source of stress. No compensation was evident for the salinity treatment, and the interactive effect with warming was apparent in August but not September. Taken together, these results indicate that maintaining high regional diversity and habitat

connectivity may help manage for ecosystem resilience, but does not provide general protection under all climate change scenarios.

The stabilizing effect of dispersal in the response of August net productivity to warming likely reflects the grazing impacts of heat tolerant zooplankton species that invaded and reduced phytoplankton biomass. Phytoplankton biomass appeared to be top-down controlled by zooplankton grazing as chlorophyll-*a* (a proxy for phytoplankton biomass) is inversely related to zooplankton community biomass (Fig. 3). I found no effects of the treatments on rates of chlorophyll removal in the grazing trials. This may have been because the zooplankton had already reduced phytoplankton biomass at the time of the grazing trials, so I am hesitant to place too much importance in this lack of apparent congruency. Additionally, I did not witness the same stabilizing effect of dispersal on net primary production in September. This is not surprising since, warming caused net productivity to decrease in September rather than increase as it did in August. Yet, the finding that dispersal can buffer against the effects of climate warming on primary productivity suggests that similar stabilizing effects might occur for other measurements of ecosystem function that are closely related to the function of the dispersing organisms.

The various measurements of ecosystem function responded idiosyncratically to environmental stress, suggesting that environmental impacts are felt differently by various processes, just as they are for different species. Hector and Bagchi (2007) show that as more ecosystem rates are measured, the importance of biodiversity to their maintenance becomes more apparent since those species responsible for maintaining

one function may not be the same as those that maintain another. While the dispersal treatment only affected one aspect of ecosystem function (net primary productivity in August), it may still have complex indirect effects on others that arise as a consequence of stabilization of productivity. Measuring ecosystem rates over longer time periods could illuminate the potential for such effects.

An ecological community's resilience and resistance to ecological stressors depends on the presence of stress tolerant species in the local or regional species pool (Vinebrooke *et al.* 2004). In order to maintain community biomass, diversity, and ecosystem function in the face of multiple ecological stressors there must be species adapted to the full range of conditions encountered. I found that the local zooplankton species pool at the site contained cyclopoid copepods that were tolerant to increases in salinity, but many species that showed declining populations with even a few degrees of warming. This suggests that the local community had some adaptive capacity to resist increases in salinity but not environmental warming. This was surprising because the sampling of the regional pool included naturally saline ponds (max salinity: 2.8 psu compared to max experimental salinity: 0.6 psu) in the interior of British Columbia. The regional zooplankton community contained small cladocerans such as *Ceriodaphnia*, *Scapholeberis*, and *Bosmina* that were tolerant to warming, but few taxa that were tolerant to high salinity (Fig. 5). Colonization by regional zooplankton therefore stabilized some ecosystem function under climate warming but not salinization.

Warming and salinity had synergistic effects on ecosystem rates and zooplankton biomass. This suggests that neither the local nor regional species pools contained

enough taxa that could withstand both stressors to maintain performance, limiting the resistance of the ecosystem to the combined stress. The ability of regional diversity and dispersal to maintain community resilience and resistance to environmental change breaks down in the face of multiple combined sources of stress. The lack of species with co-tolerance to both stressors allows for little buffering capacity by regional biodiversity and resulted in synergistic losses in zooplankton community biomass. Since many environmental changes often occur simultaneously, including warming and salinization (Schindler 2001, Christensen et al. 2006), this lack of ecosystem resilience is likely to factor in the response of lentic systems to ongoing global changes.

The potential for regional diversity to buffer local communities may be weaker at higher trophic levels as there are fewer species and they are more dispersal limited in freshwater communities (Vinebrooke et al. 2003, Shurin et al. 2009). I found this to be the case for the top predator, *Chaoborus spp.* since no other comparable invertebrate predator successfully colonized in the dispersal treatment. Predators may be at high risk of extinction due to small population sizes, and may have disproportionate influences on ecosystems through cascading trophic interactions (Duffy *et al.* 2003). Additionally, I found no evidence of regional omnivorous copepods that were able to colonize successfully, but multiple regional cladoceran (herbivorous) species were able to form viable members of the local community. This agrees with Vinebrooke et al. (2003) who suggested that dispersal of regional species as a buffer against environmental change is greater at lower trophic levels. I found little evidence for successful colonization of rotifers, perhaps as a result of low local and regional rotifer diversity. These results

agree with others showing that large crustacean zooplankton are more sensitive to elevated temperatures than smaller taxa (Moore et al. 1996, Sommer et al. 2007).

Several other studies have shown the importance of colonization in influencing the long-term dynamics of ecosystems in changing environments. Schindler et al. (Schindler *et al.* 2008) argue that nitrogen limitation in boreal lakes following a phosphorous addition is only possible in short-term, before colonization by nitrogen fixing cyanobacteria. Leibold et al. (1997) suggest that the results of short-term predator and resource manipulation experiments do not correspond to correlational studies that compare systems because short time spans do not allow for compositional changes to occur within the community. By facilitating dispersal of regional biota, I was able to allow for such compositional changes in a short-term experiment, highlighting their importance as communities adjust to changing environmental conditions.

2.5 Manuscript Conclusions

This study provides evidence for the importance of regional biodiversity for maintaining the performance of ecosystems experiencing environmental change. Although ecosystem function often declines with the loss of biodiversity, several studies have shown that very few species are able to maintain ecosystem function under stable conditions (Downing 2005, Hooper et al. 2005, Cardinale et al. 2006). However, in a dynamic and changing environment, higher biodiversity may be necessary to provide insurance and maintain function under novel conditions. Regional species represent the pool of potential functional biodiversity at local scales. Their dispersal increases the

potential for compensation when changing conditions impair the performance of the local community. Fragmentation that isolates habitats by reducing dispersal and the loss of regional biodiversity may therefore decrease ecosystem resilience in the face of environmental changes.

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3 THESIS CONCLUSIONS

3.1 Contributions to The Field

This research has integrated a metacommunity approach into testing how ecological stressors impact communities. Previous studies have generally applied ecological stressors to communities in meso- or micro-cosms that were isolated from their regional metacommunities (Rae and Vincent 1998, Petchey et al. 1999, Strecker et al. 2004). This approach provides important insight into how communities respond to changing environmental conditions on short temporal scales. However, ecologists are more often concerned with how global change affects ecosystems on large spatial and temporal scales. Incorporating a dispersal treatment in my study allowed me to ask how regional community composition affects the response of local communities to change. As a result, these findings should provide more realistic insight into how natural communities will respond to ecological stressors.

My findings also illustrate the complexity of the effect of regional biodiversity on local resilience to ecological stressors. I showed that regional biota had high tolerance for warming but not for increased salinity. The potential buffering effect of dispersal therefore depends upon the nature of the ecological stress, and the range of traits conferring tolerance to that stress among regional taxa. The theoretical models that originally proposed the idea that dispersal could buffer communities against environmental change (Yachi and Loreau 1999, Loreau et al. 2003, Leibold and Norberg 2004) did not address the fact that different types of stress impact communities differently, and thus the tolerance of regional taxa should also differ. This finding is

especially important when considering the way that ecosystems respond to multiple stressors.

3.2 Strengths and Limitations of Research

Only one ecosystem function measurement (August net primary productivity) showed a response to the dispersal treatment. This could be superficially interpreted as evidence against the buffering ability of dispersal and regional biodiversity. However, most of the ecosystem function processes that were measured are very loosely connected to zooplankton and therefore were not expected to show a large response to dispersal. Rather, these ecosystem functions were measured to test for any unanticipated indirect effects of zooplankton community composition, and to estimate the direct impacts of warming and salinity. The finding that dispersal buffered August net productivity against the effects of warming was strong evidence that dispersal could buffer some ecosystem processes from certain types of stress. While September net productivity showed no effect from dispersal, this is not in conflict with the positive result seen in August as productivity in September decreased with warming rather than increase as it did in August. Therefore, there was no potential for the zooplankton community to stabilize productivity through grazing. Coupled with the compensatory dynamics observed in zooplankton community composition, these results provide evidence that regional biodiversity and dispersal can increase local community resilience and resistance to environmental change.

Finding a realistic and feasible method for applying an experimental warming treatment was one of the biggest challenges I faced in designing this experiment. Other studies that have used warming treatments in aquatic environments have controlled both the ambient and warmed conditions at steady but different temperatures (Petchey et al. 1999, Holzapfel and Vinebrooke 2005, Thompson et al. 2008). However, pond temperatures show large daily and seasonal fluctuations (Strecker et al. 2004). To address this issue, Baulch et al. (2003) designed a system that allowed them to control the warming of mesocosms so that the warmed treatments matched the ambient treatments but at a few degrees higher. This treatment involved complex computer software and control systems and proved to be too expensive to use on the scale of replication (twenty) employed in my experiment. Instead, I used heaters designed for 300L aquaria to heat my 1000L mesocosms. Because of their limited heating capacity, the heaters were able to raise the water temperature by only ~ 2.5 °C over ambient. Once this difference was achieved, the amount of heat lost to the atmosphere was equal to the output from the heaters so they did not warm further. The mesocosms followed air temperature fluctuations, maintaining their ~ 2.5 °C difference from the ambient tanks. There was very little deviation in the output from the heaters and so the replicates all received very similar heating treatments. This method allowed me to have twenty heated mesocosms at a low cost with very little maintenance.

Unfortunately it was impossible to manipulate natural dispersal for my dispersal treatment because it was logistically unfeasible to exclude colonists from half of my mesocosms without also altering light (shading) and gas exchange with the atmosphere. Additionally, I was concerned that the effects of natural dispersal would not

be detected over the 12-week time span in which I ran my experiment. As a result, I chose to use the less realistic method of manually dispersing plankton at higher levels than would be seen naturally, as has been used in other experiments testing for the importance of dispersal of plankton (Shurin 2000, 2001). This method represented very high levels of dispersal from a broad region, such as might be found in lakes connected on river networks (Cottenie et al. 2003). However, using facilitated dispersal may have reduced the realism of my results so that the effect of dispersal that was detected for zooplankton community composition and primary productivity would most likely not have been as strong in most natural communities over a similar time scale. Yet, the mesocosms represented much smaller targets for natural dispersal so the experimental dispersal rates may be comparable to those seen in larger lakes and ponds.

Additionally, I would argue that these results apply to longer time scales as regional species gradually colonize and buffer local community composition and ecosystem function. These results apply more to systems with high interconnectivity, such as surface water connections, and systems with high regional biodiversity.

The regional species pool was collected from forty water bodies around south western British Columbia that were chosen because they varied both in temperature and salinity. The fact that no salinity tolerant taxa colonized the salt treatment was unexpected since the regional pool included species collected from naturally saline ponds. It is possible that the plankton from the saline lakes did not survive transport back from the field since they were collected from further away (Kamloops, BC) and had to endure a five hour ride back to Vancouver in the back of a hot car, despite my efforts to keep them cool. Also, the plankton were placed in holding tanks between dispersal treatments so only

the taxa that survived in those holding tanks were added in the later applications of the dispersal treatment.

I originally proposed to examine bacterial diversity in addition to zooplankton and chlorophyll concentrations. This would have been done in collaboration with a microbial ecology research group at UBC (the Suttle lab). Unfortunately, this collaboration fell through because no one had the time to analyse my samples. As a consequence, my results are based on zooplankton diversity and chlorophyll a concentrations rather than the whole food web as originally planned.

3.3 Future Research

This research suggests that regional biodiversity can provide some buffering capacity for community composition and for some aspects of ecosystem function against changing environmental conditions. It has been suggested that species diversity and genetic diversity are functionally similar in that both provide individuals with varying tolerances to environmental conditions (Hughes et al. 2008). It would be interesting to test if dispersal of individuals from genetically isolated populations of the same species offer a similar buffering capacity as dispersing members of different species did in this experiment.

It would also be useful to ask whether dispersal and regional biodiversity affect ecosystem resilience against a larger variety of ecosystem stressors. This experiment showed that there was some buffering capacity against the effects of warming but not of

increased salinity. Understanding how ecosystem connectivity affects the ability to adapt to various types and combinations of stress would be extremely useful for predicting how ecosystems will respond to future changes in environmental conditions. In addition, I only applied two levels of each stress treatment (ambient and elevated). The effects of stress on communities may be non-linear and involve sudden and catastrophic shifts in ecosystem state (Scheffer et al. 2001). Testing for such effects would require imposing stress treatments over a range of values, and could reveal a richer variety of ecosystem responses.

This experiment tested its hypothesis in freshwater plankton communities. It would be worthwhile to see how these results compare to other communities in terrestrial and marine ecosystems since these ecosystems have very different levels of dispersal, and are affected differently by environmental changes. Furthermore, I was unable to incorporate vertebrates in my study, but their inclusion, as well as organisms at higher trophic levels, would be very interesting in future studies.

3.4 Broader Implications

This research demonstrates that ecosystem connectivity and regional biodiversity can contribute to local scale ecological resilience and resistance to environmental change. This highlights the importance of limiting ecosystem fragmentation so that organisms are able to freely move between habitat patches. Furthermore, this research also suggests that maintaining high regional biodiversity will allow local ecosystems to best maintain their function in the face of environmental changes. This may be useful when

planning conservation areas since it suggests that large areas of interconnected habitat with high biodiversity may be better able to maintain function when faced with changing climate and ecological stressors.

3.5 References

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4 APPENDIX

Table 2. Results of ANOVA tests for all measured variables.

Variable	Treatment	Estimate	Std. Error	T-value	Sig.
<i>Bosmina</i> ($\mu\text{g/L}$)	Control	0.256	0.107	2.40	0.022
	Warming (Warm)	0.168	0.107	1.58	0.124
	Salinity (Salt)	-0.086	0.107	-0.80	0.428
	Dispersal (Disp)	0.198	0.107	1.86	0.072
	Warm x Salt	-0.035	0.107	-0.33	0.744
	Warm x Disp	0.157	0.107	1.48	0.150
	Salt x Disp	-0.098	0.107	-0.92	0.364
	Warm x Salt x Disp	-0.020	0.107	-0.19	0.852
<i>Calanoid</i> ($\mu\text{g/L}$)	Control	1.695	0.122	13.89	<0.001
	Warming (Warm)	0.346	0.122	0.28	0.779
	Salinity (Salt)	-0.775	0.122	-6.35	<0.001
	Dispersal (Disp)	0.162	0.122	1.33	0.194
	Warm x Salt	0.108	0.122	-0.88	0.383
	Warm x Disp	0.103	0.122	0.85	0.403
	Salt x Disp	0.237	0.122	1.94	0.061
	Warm x Salt x Disp	0.119	0.122	0.97	0.338
<i>Ceriodaphnia</i> ($\mu\text{g/L}$)	Control	0.544	0.113	4.80	<0.001
	Warming (Warm)	0.216	0.113	1.91	0.065
	Salinity (Salt)	-0.250	0.113	-0.22	0.827
	Dispersal (Disp)	0.265	0.113	2.34	0.026
	Warm x Salt	-0.118	0.113	-1.04	0.306
	Warm x Disp	0.411	0.113	3.63	<0.001
	Salt x Disp	-0.783	0.113	-0.69	0.494
	Warm x Salt x Disp	-0.098	0.113	-0.87	0.392
<i>Chaoborus</i> ($\mu\text{g/L}$)	Control	1.642	0.174	9.45	<0.001
	Warming (Warm)	-0.355	0.174	-2.04	0.050
	Salinity (Salt)	0.081	0.174	0.47	0.643
	Dispersal (Disp)	-0.259	0.174	-1.49	0.146
	Warm x Salt	-0.264	0.174	-1.52	0.139
	Warm x Disp	-0.285	0.174	-1.64	0.111
	Salt x Disp	0.020	0.174	0.12	0.909
	Warm x Salt x Disp	0.309	0.174	1.78	0.085
<i>Chironomid</i>	Control	0.847	0.089	9.48	<0.001
	Warming (Warm)	0.313	0.089	3.50	0.001
	Salinity (Salt)	-0.088	0.089	-0.99	0.331
	Dispersal (Disp)	-0.089	0.089	-0.99	0.329
	Warm x Salt	-0.136	0.089	-1.53	0.136
	Warm x Disp	-0.006	0.089	-0.07	0.943
	Salt x Disp	0.040	0.089	0.45	0.659
	Warm x Salt x Disp	-0.015	0.089	-0.17	0.866
<i>Chydorus</i> ($\mu\text{g/L}$)	Control	0.727	0.103	7.09	<0.001
	Warming (Warm)	0.215	0.103	2.10	0.044
	Salinity (Salt)	0.018	0.103	0.17	0.863
	Dispersal (Disp)	-0.096	0.103	-0.93	0.358

	Warm x Salt	-0.160	0.103	-1.56	0.128
	Warm x Disp	0.096	0.103	0.94	0.356
	Salt x Disp	0.133	0.103	1.30	0.204
	Warm x Salt x Disp	0.053	0.103	0.52	0.606
<i>Copepodite</i> ($\mu\text{g/L}$)	Control	0.119	0.040	2.96	0.006
	Warming (Warm)	0.036	0.040	0.89	0.379
	Salinity (Salt)	0.050	0.040	1.25	0.220
	Dispersal (Disp)	0.000	0.040	-0.01	0.996
	Warm x Salt	0.024	0.040	0.60	0.555
	Warm x Disp	-0.037	0.040	-0.91	0.369
	Salt x Disp	0.019	0.040	0.47	0.642
	Warm x Salt x Disp	-0.016	0.040	-0.39	0.699
<i>Cyclopoid</i> ($\mu\text{g/L}$)	Control	1.100	0.104	10.54	<0.001
	Warming (Warm)	0.182	0.104	1.75	0.090
	Salinity (Salt)	0.386	0.104	3.70	<0.001
	Dispersal (Disp)	0.035	0.104	0.33	0.741
	Warm x Salt	0.227	0.104	2.17	0.037
	Warm x Disp	-0.035	0.104	-0.37	0.715
	Salt x Disp	0.020	0.104	0.19	0.849
	Warm x Salt x Disp	0.003	0.104	0.03	0.981
<i>Daphnia pulex</i> ($\mu\text{g/L}$)	Control	2.826	0.219	12.92	<0.001
	Warming (Warm)	-0.491	0.219	-2.24	0.032
	Salinity (Salt)	-0.299	0.219	-1.36	0.182
	Dispersal (Disp)	-0.158	0.219	-0.72	0.476
	Warm x Salt	-0.441	0.219	-2.02	0.052
	Warm x Disp	-0.102	0.219	-0.47	0.644
	Salt x Disp	0.244	0.219	1.11	0.274
	Warm x Salt x Disp	0.114	0.219	0.52	0.607
<i>Diaphanosoma</i> ($\mu\text{g/L}$)	Control	0.317	0.116	2.72	0.011
	Warming (Warm)	0.111	0.116	0.96	0.346
	Salinity (Salt)	0.035	0.116	0.30	0.764
	Dispersal (Disp)	0.234	0.116	2.01	0.053
	Warm x Salt	0.087	0.116	0.74	0.463
	Warm x Disp	0.098	0.116	0.84	0.407
	Salt x Disp	-0.007	0.116	-0.06	0.950
	Warm x Salt x Disp	0.113	0.116	0.97	0.341
<i>K. cochlearis</i> ($\mu\text{g/L}$)	Control	1.08E-04	4.51E-05	2.40	0.022
	Warming (Warm)	-1.02E-04	4.51E-05	-2.26	0.031
	Salinity (Salt)	9.08E-05	4.51E-05	2.01	0.053
	Dispersal (Disp)	6.52E-05	4.51E-05	1.45	0.158
	Warm x Salt	-8.72E-05	4.51E-05	-1.93	0.062
	Warm x Disp	-6.40E-05	4.51E-05	-1.42	0.166
	Salt x Disp	7.53E-05	4.51E-05	1.67	0.105
	Warm x Salt x Disp	-7.23E-05	4.51E-05	-1.60	0.119
<i>K. testudo</i> ($\mu\text{g/L}$)	Control	1.27E-04	1.15E-04	1.11	0.278
	Warming (Warm)	-1.27E-04	1.15E-04	-1.10	0.278
	Salinity (Salt)	1.27E-04	1.15E-04	1.11	0.277
	Dispersal (Disp)	-1.04E-04	1.15E-04	-0.91	0.372
	Warm x Salt	-1.27E-04	1.15E-04	-1.10	0.278
	Warm x Disp	1.04E-03	1.15E-04	0.91	0.371

	Salt x Disp	-1.04E-04	1.15E-04	-0.91	0.372
	Warm x Salt x Disp	1.04E-04	1.15E-04	0.91	0.371
<i>Lrg. Calanoid</i> ($\mu\text{g/L}$)	Control	0.327	0.082	3.98	<0.001
	Warming (Warm)	-0.173	0.082	-2.11	0.043
	Salinity (Salt)	0.122	0.082	1.48	0.148
	Dispersal (Disp)	0.327	0.082	3.98	<0.001
	Warm x Salt	-0.161	0.082	-1.96	0.059
	Warm x Disp	-0.173	0.082	-2.11	0.043
	Salt x Disp	0.122	0.082	1.48	0.148
	Warm x Salt x Disp	-0.161	0.082	-1.96	0.059
<i>Nauplii</i> ($\mu\text{g/L}$)	Control	0.966	0.123	7.86	<0.001
	Warming (Warm)	-0.056	0.123	-0.46	0.650
	Salinity (Salt)	-0.020	0.123	-0.17	0.869
	Dispersal (Disp)	0.155	0.123	1.26	0.217
	Warm x Salt	-0.019	0.123	-0.15	0.881
	Warm x Disp	-0.197	0.123	-1.60	0.118
	Salt x Disp	0.124	0.123	1.01	0.320
	Warm x Salt x Disp	-0.113	0.123	-0.92	0.365
<i>Polyphemus</i> ($\mu\text{g/L}$)	Control	0.147	0.095	1.54	0.132
	Warming (Warm)	0.109	0.095	1.15	0.261
	Salinity (Salt)	-0.040	0.095	-0.42	0.680
	Dispersal (Disp)	0.131	0.095	1.37	0.180
	Warm x Salt	-0.346	0.095	-0.36	0.719
	Warm x Disp	0.126	0.095	1.32	0.197
	Salt x Disp	-0.056	0.095	-0.59	0.560
	Warm x Salt x Disp	-0.018	0.095	-0.19	0.851
<i>Scapholeberis</i> ($\mu\text{g/L}$)	Control	0.407	0.062	6.59	<0.001
	Warming (Warm)	0.182	0.062	2.95	0.006
	Salinity (Salt)	-0.157	0.062	-2.55	0.016
	Dispersal (Disp)	0.354	0.062	5.74	<0.001
	Warm x Salt	-0.031	0.062	-0.50	0.622
	Warm x Disp	0.180	0.062	2.92	0.006
	Salt x Disp	-0.125	0.062	-2.03	0.051
	Warm x Salt x Disp	-0.050	0.062	-0.80	0.427
<i>Sychaeta</i> ($\mu\text{g/L}$)	Control	8.34E-06	5.26E-06	1.59	0.123
	Warming (Warm)	8.34E-06	5.26E-06	1.59	0.123
	Salinity (Salt)	5.83E-06	5.26E-06	1.11	0.275
	Dispersal (Disp)	2.69E-06	5.26E-06	0.51	0.612
	Warm x Salt	5.83E-06	5.26E-06	1.11	0.275
	Warm x Disp	2.69E-06	5.26E-06	0.51	0.612
	Salt x Disp	7.40E-07	5.26E-06	0.14	0.889
	Warm x Salt x Disp	7.40E-07	5.26E-06	0.14	0.889
Total Zooplankton Community	Control	4.077	0.099	41.35	<0.001
	Warming (Warm)	-0.132	0.099	-1.34	0.191
	Salinity (Salt)	-0.216	0.099	-2.20	0.036
	Dispersal (Disp)	0.075	0.099	0.76	0.455
	Warm x Salt	-0.273	0.099	-2.76	0.009
	Warm x Disp	0.088	0.099	0.89	0.379
	Salt x Disp	0.153	0.099	1.55	0.131
	Warm x Salt x Disp	0.127	0.099	1.29	0.208

Chlorophyll a ($\mu\text{g/L}$)	Control	0.341	0.045	7.65	<0.001
	Warming (Warm)	0.092	0.045	2.07	0.047
	Salinity (Salt)	0.153	0.045	3.42	0.002
	Dispersal (Disp)	-0.003	0.045	-0.07	0.944
	Warm x Salt	0.042	0.045	0.95	0.348
	Warm x Disp	0.001	0.045	0.03	0.975
	Salt x Disp	-0.105	0.045	-2.34	0.025
	Warm x Salt x Disp	-0.057	0.045	-1.27	0.214
Decomposition	Control	0.016	4.02E-04	39.19	<0.001
	Warming (Warm)	-2.19E-04	4.02E-04	-0.55	0.590
	Salinity (Salt)	-3.81E-04	4.02E-04	-0.95	0.350
	Dispersal (Disp)	2.56E-04	4.02E-04	0.64	0.529
	Warm x Salt	-9.22E-04	4.02E-04	-2.30	0.028
	Warm x Disp	-3.79E-04	4.02E-04	-0.94	0.352
	Salt x Disp	4.24E-05	4.02E-04	0.11	0.917
	Warm x Salt x Disp	-1.59E-04	4.02E-04	-0.40	0.694
Sedimentation	Control	2.93E-03	1.69E-04	17.36	<0.001
	Warming (Warm)	5.85E-05	1.69E-04	0.35	0.731
	Salinity (Salt)	3.64E-04	1.69E-04	2.15	0.039
	Dispersal (Disp)	-3.62E-05	1.69E-04	-0.21	0.832
	Warm x Salt	5.89E-05	1.69E-04	0.35	0.729
	Warm x Disp	-1.09E-04	1.69E-04	-0.65	0.522
	Salt x Disp	-2.07E-04	1.69E-04	-1.23	0.229
	Warm x Salt x Disp	-1.76E-04	1.69E-04	-1.05	0.304
July Grazing	Control	0.108	0.031	3.53	0.001
	Warming (Warm)	0.037	0.031	1.21	0.235
	Salinity (Salt)	0.041	0.031	1.35	0.187
	Dispersal (Disp)	-0.021	0.031	-673.00	0.506
	Warm x Salt	-0.044	0.031	-1.43	0.162
	Warm x Disp	0.016	0.031	0.51	0.612
	Salt x Disp	-0.044	0.031	-1.44	0.159
	Warm x Salt x Disp	0.001	0.031	0.04	0.966
August Grazing	Control	0.046	0.026	1.77	0.086
	Warming (Warm)	-0.006	0.026	-0.24	0.815
	Salinity (Salt)	0.030	0.026	1.14	0.262
	Dispersal (Disp)	-0.002	0.026	-0.10	0.925
	Warm x Salt	0.034	0.026	1.30	0.203
	Warm x Disp	-0.039	0.026	-1.51	0.141
	Salt x Disp	0.016	0.026	0.61	0.547
	Warm x Salt x Disp	-0.057	0.026	-2.19	0.036
August Net Productivity	Control	-3.28E-02	1.61E-03	-20.37	<0.001
	Warming (Warm)	4.90E-03	1.61E-03	3.05	0.005
	Salinity (Salt)	-6.67E-04	1.61E-03	-0.42	0.681
	Dispersal (Disp)	-2.08E-05	1.61E-03	-0.13	0.990
	Warm x Salt	-1.94E-03	1.61E-03	-1.20	0.237
	Warm x Disp	-5.25E-03	1.61E-03	-3.27	0.003
	Salt x Disp	1.19E-03	1.61E-03	0.74	0.466
	Warm x Salt x Disp	-2.08E-04	1.61E-03	-0.13	0.898
September Net	Control	-1.17E-03	2.35E-03	-0.50	0.620
	Warming (Warm)	-6.57E-03	2.35E-03	-2.80	0.009

Productivity	Salinity (Salt)	-3.11E-03	2.35E-03	-1.33	0.194
	Dispersal (Disp)	9.06E-04	2.35E-03	0.39	0.702
	Warm x Salt	-2.01E-03	2.35E-03	-0.86	0.398
	Warm x Disp	1.77E-04	2.35E-03	0.08	0.940
	Salt x Disp	1.09E-03	2.35E-03	0.47	0.645
	Warm x Salt x Disp	3.78E-03	2.35E-03	1.61	0.117
Periphyton	Control	2.84E-02	3.72E-03	7.63	<0.001
Colonization	Warming (Warm)	1.32E-02	3.72E-03	3.56	0.001
	Salinity (Salt)	8.12E-03	3.72E-03	2.18	0.037
	Dispersal (Disp)	-1.14E-03	3.72E-03	-0.31	0.761
	Warm x Salt	8.19E-03	3.72E-03	2.20	0.035
	Warm x Disp	9.86E-04	3.72E-03	0.27	0.793
	Salt x Disp	2.94E-04	3.72E-03	0.08	0.938
	Warm x Salt x Disp	1.24E-03	3.72E-03	0.33	0.741

