University of Alberta

The potential adaptability of alpine zooplankton communities to environmental warming

by

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ABSTRACT

Climate change forces species to respond to changes in their environment. Mountain zooplankton are expectedly vulnerable to environmental change due to topographical dispersal barriers. I examined the dispersal potential of zooplankton in the Canadian Rocky Mountains using data from 379 sites. Dispersal limitation was evident among alpine communities; however, I could not discount the potential confounding effect of predation by introduced sportfish. Therefore, I conducted an experiment consisting of three dispersal levels (alpine only, alpine+montane, montane only) and two warming levels (13°C versus 20°C) to test if dispersal potential affected invasion success by montane species in warmed alpine lakes. Invasion success depended on the introduction of montane species and was enhanced by warming, which significantly suppressed the resident alpine copepod species (*Hesperodiaptomus arcticus*). I conclude that zooplankton are most vulnerable to climate warming at high elevations because colonization of sensitive alpine communities by montane species appears to be dispersal-limited.

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CHAPTER 1: GENERAL INTRODUCTION

Climate warming affects the abiotic environment in lakes (Schindler et al. 1990; Hauer et al. 1997; Sommaruga-Wögrath et al. 1997), thereby potentially influencing ecological processes that control zooplankton communities (Moore et al. 1996; Scheffer et al. 2001). The ability of zooplankton species to persist despite environmental change is expected to depend on their dispersal ability, especially among insular alpine lakes and ponds (Strecker et al. 2004). However, little is known about the regional and local processes that control mountain zooplankton richness, including the dispersal potential of species in extreme terrains. The objective of my thesis research was to predict the potential adaptability of mountain zooplankton communities to environmental change, such as climate warming.

Effects of climate change on aquatic systems

Global change is having a major impact on ecosystems around the world, requiring organisms to migrate in response to the loss of their habitat (Sala et al. 2000). The temperature of many northern lakes in North America have already warmed by 2°C over the past 20 years (Findlay et al. 2001) and are expected to warm by as much as 7°C by the year 2100 (Magnusson et al. 1997). It is expected that alpine and arctic systems will be most sensitive to climate warming (Intergovernmental Panel on Climate Change 2001) due to reduced snowpack and ice cover which results in even more warming, expansion of tree line, and increased productivity (Fyfe and Flato 1999; Vinebrooke and Leavitt 2005). The effect of warming on coldwater ecosystems is of concern, especially warming at high elevations (Bradley et al. 2004), since aquatic alpine ecology is not well-studied. Many of the predicted climate effects on alpine lakes and ponds are speculative, being extrapolations of findings from studies conducted at lower elevations (Hauer et al. 1997; Schindler 1997).

Climate warming has already been documented at high elevation sites in the European Alps (Beniston et al. 1994). Temperature change is expected to increase with elevation and is predicted to be especially large in the 35 to 50°N latitude range in the North American Rocky Mountains (Bradley et al. 2004). Climate warming may result in the loss of many coldwater habitats at higher elevations, which would require organisms to migrate upward by approximately 100 m for every 0.6°C increase in temperature (Körner 1999).

Dispersal by Zooplankton

The ability of organisms to migrate in response to climate warming and habitat loss is dependent on their dispersal potential as affected by regional (climate, landscape, biogeographical events) and local factors (chemical, physical, biological), which operate at various geographic scales (Maly and van Leeuwen 1988, Shurin et al. 2000, Shurin 2001). Many zooplankton species can disperse over short, flat distances (Jenkins and Buikema 1998; Lukaszewski et al. 1999; Shurin et al. 2000; Cáceres and Soluk 2002), and are presumed to be dispersal-limited only over very large geographic scales or short time scales (Pinel-Alloul et al. 1995; Stemberger 1995; Shurin et al. 2000). Dispersal limitation over short distances may be more evident in the presence of large topographical barriers, such as mountain ranges, and low connectivity (Donald et al. 2001; Knapp et al. 2001). Ecologists generally assume that all zooplankton disperse rapidly, though some recent studies suggest that dispersal and colonization ability vary among zooplankton species due to differences in body and egg size as well as reproductive strategies and generation time (Jenkins and Buikema 1998; Cáceres and Soluk 2002; Cohen and Shurin 2003).

Zooplankton species exhibit several modes of dispersal. Most zooplankton species can produce resistant resting stages, in the form of resting eggs or through diapause, which may enhance dispersal ability (Maly and van Leeuwen 1988). Resting stages and adult organisms can be transported by waterfowl, aquatic mammals, and wind or rain (Maguire 1963; Proctor 1964; Peck 1975; Daborn 1976; Cáceres and Soluk 2002). The rates and frequency of dispersal due to these vectors is difficult to study and thus remains largely untested, especially in mountain regions; however Cáceres and Soluk (2002) found that wind and rain were the most important dispersal vectors in low elevation experimental ponds.

Regional and Local Controls of Zooplankton Species Richness

In addition to dispersal, other regional processes, such as climate and biogeography have been shown to affect the species richness patterns of local environments. Extreme climatic environments support fewer species than do less severe environments because there are fewer ecological niches and shorter periods of tolerable physical conditions (Anderson 1971; Patalas 1971). Geographic events, such as glaciation history, influence the number of available species in the regional pool that can colonize a given community. Glacial retreat patterns determine long-term migratory routes available to zooplankton (Ricklefs 1987; Stemberger 1995).

Local processes also influence species richness. Numerous potential local controls can be divided into abiotic and biotic factors. Some of the abiotic factors for freshwater systems include lake morphometry (Patalas 1971; Dodson 1992; Pinel-Alloul et al. 1995), productivity (Dodson et al. 2000) and ion concentration (Pinel-Alloul et al. 1995; McNaught et al. 2000). Studies relating lake morphometry to species richness have shown that larger lakes support more species because there are more ecological niches available (Dodson 1992; Pinel-Alloul et al. 1995). Dodson et al. (2000) found that lakes with very high productivity support fewer species, and maximum species richness occurs in oligotrophic and mesotrophic lakes. Species richness also increases with increasing ion concentration in mountain lakes (McNaught et al. 2000).

Local biotic factors that influence species richness include predation and competition (Cornell and Karison 1997; Shurin 2000; Donald et al. 2001; Dzialowski and O'Brien 2004). Size selective predation by fish causes a shift towards smaller zooplankton species and prevents habitat domination by a few large zooplankton species (Donald et al. 2001), while predation by large invertebrates cause a shift to larger zooplankton species (Dzialowski and O'Brien 2004). Shurin (2000) found that new species were more successful in invading habitats when the habitat was experimentally perturbed by filtration, suggesting that competition is an important regulator of species richness.

Aquatic alpine ecosystems are extreme environments having low water temperatures, short growing seasons, high ultraviolet radiation, and dilute chemical concentrations (Anderson 1971, Vinebrooke and Leavitt 2005). As a result, many fishless alpine lakes and ponds contain only one or two dominant zooplankton species (Knapp et al. 2001). The way that species richness is controlled in a habitat can indicate how resiliant the assemblage will be to environmental changes. The relative importance of local and regional factors in determining community composition has been assessed using local-regional richness relationships (Cornell 1985) and the additive partitioning of alpha and beta richness (Loreau 2000; Gering and Crist 2002).

Local-Regional Richness Relationships

Local-regional richness plots compare local richness (average number of species in individual sampling sites) with regional richness (total number of species found in a defined area) (Fig. 1-1). This plot results in either a linear relationship or a curvilinear relationship. Linear relationships indicate that the number of species in a local habitat depends directly on the number of species in the surrounding region, suggesting that the species richness is controlled by regional processes.

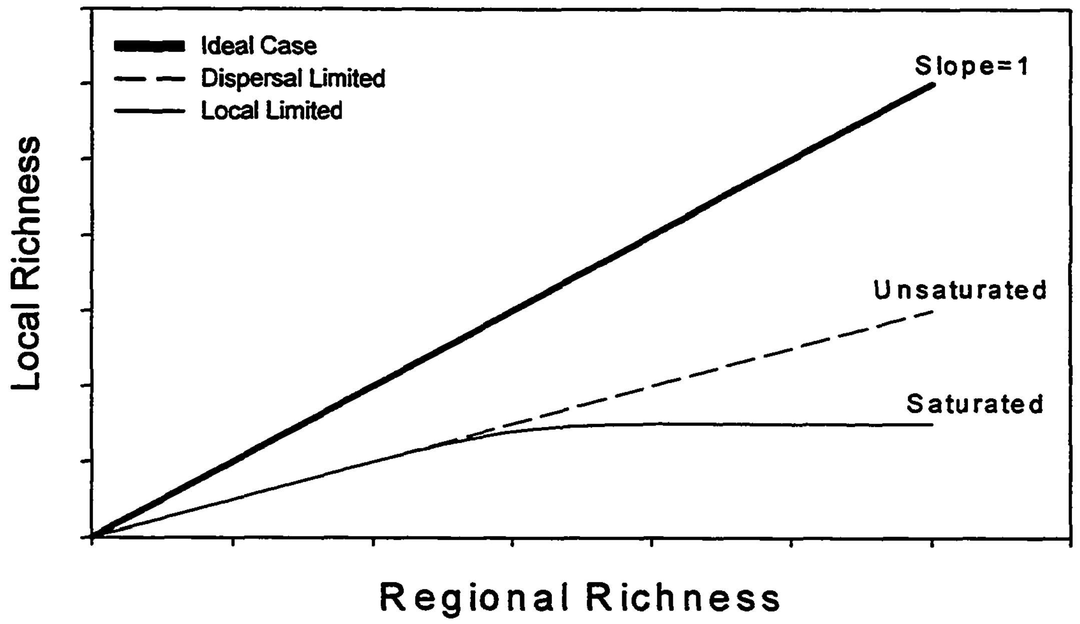

Figure 1-1 Local versus regional richness plot. The relationship between local and regional richness can be either linear or curvilinear. Linear relationships suggest unsaturated communities that are under regional control, with dispersal-limitation indicated by slopes less than 1. Curvilinear relationships suggest saturated communities that are under local control.

A one-to-one linear relationship represents the ideal unsaturated pattern with no dispersal limitation, where local richness is equal to regional richness. The degree of dispersal limitation may be inferred by the degree of departure of the observed local-regional relationship from the one-to-one line (Fig. 1-1). A curvilinear relationship indicates that species richness in a local habitat becomes independent of the number of species in the regional species pool, suggesting that assemblages are saturated and that local processes such as competition or predation are controlling species richness (Fig.1-1: Ricklefs 1987; Cornell and Karlson 1997; Shurin 2000; Gering et al. 2003). More recently, biologists are finding that numerous natural communities exhibit linear unsaturated patterns, implying that regional processes have a strong influence on local richness within these assemblages (Shurin et al. 2000; Loreau 2000; Cornell and Karlson 1997). These findings challenge the view that communities are saturated and are thus controlled solely by local processes.

Alpha-Beta Richness Partitioning

A more recent approach to the local versus regional debate is to use alpha-beta partitioning of regional richness. Alpha richness is the within-site richness and is equivalent to local richness, thus it can be determined by the average number of species in sites within a region. Beta richness is the among-site richness, the species turnover between sites, and is easily determined by the difference between regional richness and alpha (local) richness (Loreau 2000; Gering et al. 2003). Regional richness is the total richness in a region, and is thus defined as the total number of species found in the region. In this approach, alpha and beta richness are additive with their sum equal to regional richness (Loreau 2000; Gering and Crist 2002).

Alpha-beta partitioning can be used to interpret the influence of local and regional processes. When the relationship is graphed, it can be determined if alpha (within-site) or beta (among-site) richness contribute more significantly to regional richness by comparing the proportion of the total richness each factor explains (Fig. 1-2). If alpha richness contributes a greater amount than beta, it suggests that local processes may have a greater influence on species richness and that dispersal limitation is not a significant factor, because the habitats in the region have very similar species compositions. However, Jenkins and Buikema (1998) suggest that local abiotic conditions alone cannot determine community composition but that colonization history, generally a regional process involving dispersion, determines the community composition in environmentally similar habitats.

Large beta richness indicates that the habitats in the region differ greatly in their species composition, suggesting that regional processes may have more control over species richness (Loreau 2000; Gering et al. 2003), or that the region contains high habitat heterogeneity. If the habitats are heterogeneous, local conditions may not be appropriate for supporting similar species communities, and therefore local processes can be identified as influencing species richness. However, if the habitats are homogeneous, dispersal limitation can be identified as being the dominant control of species richness.

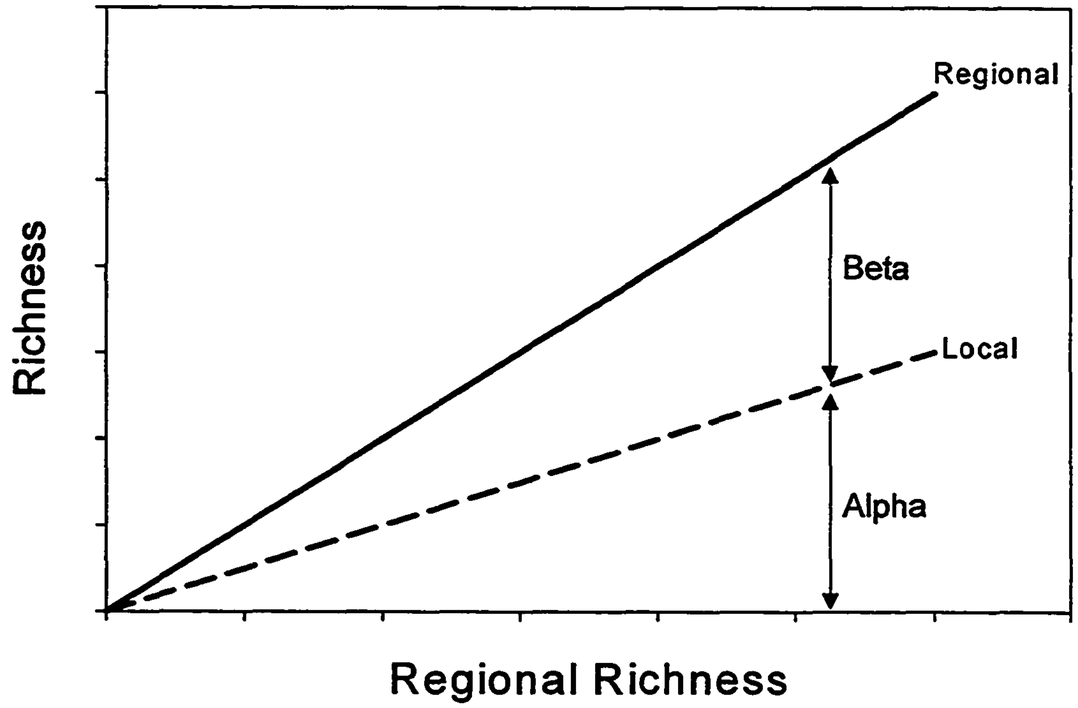

Figure 1-2 Alpha-beta richness partitioning. Regional richness is the sum of alpha and beta richness. The area under the local richness line represents the portion of regional richness explained by alpha (within-site) richness. The area between the regional and local richness lines is the portion of regional richness explained by beta (among-site) richness.

OBJECTIVES AND METHODS

The main goals of my thesis research were to:

1. Investigate the major factors that are influencing zooplankton species richness in mountain lakes and determine if zooplankton communities in alpine lakes are unsaturated and dispersal limited (Chapter 2).
2. Determine if environmental warming and increased dispersal will allow montane zooplankton species to invade alpine lakes and ponds (Chapter 3).

To achieve the first objective (Chapter 2), I statistically analysed a database of limnological and zooplankton data for 379 lakes, arranged into 13 regions, in the Canadian Rocky Mountains. The data was examined by combining 3 approaches:

1. Local-regional richness relationships
2. Alpha-beta richness partitioning
3. Direct gradient analyses to examine environmental heterogeneity

To achieve the second objective (Chapter 3), I empirically examined an alpine zooplankton community using experimental mesocosms in growth chambers. The specific objectives of this chapter were to:

1. Determine the effect of warming and increased dispersal on the ability of montane species to invade alpine communities.
2. Determine the effect of warming and increased dispersal by montane species on alpine zooplankton specialist species.

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CHAPTER 2: REGIONAL VERSUS LOCAL FACTORS OF MOUNTAIN ZOOPLANKTON DIVERSITY

INTRODUCTION

Global climate change increasingly tests the ability of organisms to migrate in response to loss of their habitat (Sala et al. 2000). Therefore, dispersal-limitation holds important ramifications for species and their potential adaptability to future environmental change. If dispersal-limitation can be demonstrated for a group of organisms in a specific region, then this would highlight the need for continued conservation and restoration efforts in that area (e.g., McNaught et al. 1999; Knapp et al. 2001).

Dispersal by zooplankton is affected by regional (among-lakes) and local (within-lake) factors that operate at different geographic scales (Shurin et al. 2000). Various modes of overland transport (Maguire 1963; Proctor 1964; Bohonak and Jenkins 2003) and resting eggs that can remain viable for decades (Hairston 1996; Arnott and Yan 2002) likely enhance dispersal ability of zooplankton. Dispersal limitation may be more evident over very long distances or short timescales (Pinel-Alloul et al. 1995; Stemberger 1995; Shurin et al. 2000). However, large topographic barriers (e.g., mountain ranges) and low connectivity may limit dispersal over short distances as zooplankton often require decades to reappear in insular mountain lakes following the removal of stocked fish (Donald et al. 2001; Knapp et al. 2001). In contrast, many zooplankton can disperse readily across short, flat distances (~100 km), resulting in local factors having greater relative impacts on community structure in well-connected systems along smaller spatial scales at lower elevations (Jenkins and Buikema 1998; Lukaszewski et al. 1999; Shurin 2000; Cáceres and Soluk 2002).

Local-regional richness relationships have been used to identify the relative importance of local and regional factors regulating species richness in an ecosystem (Cornell 1985). Local richness is defined as the average number of species found in an individual sampling site and regional richness is the total number of species found in all of the sampled sites in a defined area. A linear relationship may reflect unsaturated communities, open to new species, and controlled by regional processes. Regional factors of species richness include history and biogeography, such as postglacial colonization and dispersal routes (Stemberger 1995; Shurin et al. 2000). Alternatively, if local richness becomes independent of regional richness at high levels of regional richness (e.g., an asymptotic curvilinear relationship), the community may be saturated and closed to new species. Controls of local richness can involve species tolerance to abiotic conditions and biotic factors, such as competitive exclusion (Winder et al. 2003) and predation (Donald and Anderson 2003). Regional and local processes may also interact at various levels to determine local species richness, as the dispersing species must be able to tolerate the local environment to establish a viable population (Bohonak and Jenkins 2003).

Several factors confound interpretations of local-regional richness relationships (Caley and Schluter 1997; Srivastava 1999; Shurin et al. 2000). Environmental heterogeneity and local disturbance may produce a linear relationship that may be incorrectly interpreted as evidence of dispersal limitation and regional control. Also, larger areas support more species, known as the species-area hypothesis, thus large variations in area size between the regions can result in pseudosaturation. In addition, the number of species found in a region increases to a maximum richness with increasing the number of sites sampled within each region. Thus, a local-regional richness relationship provides only a basis for developing hypotheses for the relative importance of regional and local factors in determining local species richness. To gain a better understanding of factors affecting zooplankton assemblages, I must also consider the environmental heterogeneity (Gering and Crist 2002) and ecological history of the region (Fischer et al. 2001; Chase 2003).

The potential importance of environmental heterogeneity to community assembly can be assessed through the examination of the alpha and beta components of regional richness (Loreau 2000; Gering and Crist 2002). Alpha richness is defined as the average number of species inhabiting each site, and beta richness as the average difference in species composition between sites (i.e. species turnover) in a region. If regional richness is primarily attributable to alpha richness, then species are expected to easily disperse across relatively homogeneous habitats. Alternatively, greater beta richness suggests the existence of distinct communities owing to dispersal-limitation (e.g., low connectivity; Forbes and Chase 2002), high environmental heterogeneity, or both. If environmental variables can explain high beta richness using direct gradient analysis, then this provides evidence that environmental heterogeneity rather than dispersal limitation is the primary factor controlling local richness.

My main objective was to assess the potential adaptability of mountain zooplankton communities to environmental change by examining the relative importance of regional versus local factors on zooplankton richness using local-regional relationships, alpha-beta richness partitioning and direct gradient analyses. The influence of environmental heterogeneity on local-regional richness relationships and species assemblages was assessed to provide additional insight into the controls of local species richness. These zooplankton communities were expected to be unsaturated because of the insular nature of most mountain lakes and predation by introduced sportfish (Donald et al. 2001; Vinebrooke and Leavitt 2005). As a result, I hypothesized that mountain zooplankton communities should show greater beta than alpha richness.

METHODS

Study area and data collection

I used presence-absence data for zooplankton species and limnological data that were generated from field surveys of national mountain parks conducted by the Canadian Wildlife Service between 1966 and 1983. Over 500 lakes and ponds located in the Canadian Rocky Mountains were each sampled one to three times during the ice-free season. The database contained both published (Anderson 1968; Anderson 1970; Anderson 1971; Anderson 1972; Anderson 1974; Donald et al. 2001) and unpublished data.

Zooplankton were collected from the deepest point in each lake by conducting several vertical hauls at a rate of 0.5 $m \cdot s^{-1}$ using a Wisconsin-style plankton net (aperture size 65 - 76 cm^2, diameter 25 cm, length 100cm, #20 mesh size) (Anderson 1971, Anderson 1974; Donald et al. 2001). Shallow ponds were sampled horizontally from shore when the plankton net could be thrown more than 15 m (Anderson 1974). Detailed collection methods for water chemistry analysis can be found in Anderson (1970), and all zooplankton identifications were performed by R.S. Anderson and followed the procedures outlined by Anderson (1974).

I assigned 379 lakes and ponds, from the database of over 500 lakes and ponds, to one of 13 regions based on geographic location and shared drainage basins. Lakes and ponds were excluded from the study if they could not be placed in a common catchment, or if the zooplankton data were incomplete. Regions were constructed to include a minimum of 10 lakes and ponds located within a single drainage basin. Only single drainage basins and mountain ranges were contained in each region to minimize heterogeneity of geologic and glacial history. The landscape area for each region was estimated using 1:250 000 scale digital topographic maps in ArcView version 3.3 (ESRI 2002). I drew a freeform shape to encompass all of the lakes in the region, allowing ArcView to calculate the area contained within that freeform shape. The use of freeform shapes, instead of rectangles or circles, allowed the area calculation to contain only the mountain range and drainage basin used to define the region. Table 2-1 summarizes the regions used in the study and Figure 2-1 shows the location of each region.

Local richness and regional richness were calculated for each region in the study (Table 2-1). Local richness was defined as the average number of species collected from a site based on one or more sampling events. Therefore, local species richness was a conservative approximation of total zooplankton richness because single-year samples can underestimate the actual number of species inhabiting a lake (Arnott et al. 1998). Mean local richness was calculated by averaging values for all sampling sites in a region. Regional richness was defined as the total number of species found in all of the lakes in the region. Rotifers were excluded from the analysis because data were lacking for many lakes.

Statistical analyses

Linear regression was used to test the relationship between local and regional richness using SYSTAT version 10.0 (SPSS 2000). Exploratory data analysis using visual inspection of the local-regional richness plot, and insertion of a quadratic term in the regression model, were used to test the relationship for curvilinearity. Use of a quadratic term provided a simple statistical test for a declining slope in the local-regional relationship, although it would not accurately capture an asymptotic saturation relationship (Caley and Schluter 1997; Shurin et al. 2000).

Table 2-1 Summary of the 13 regions used in the study. Local and regional richness values are for adult crustacean zooplankton, consisting primarily of copepod, cladoceran, and anostracan species.

Region name	No. lakes	Region area (km2)	Mean elevation (m)	Mean lake surface area (km2X10-2)	Local richness	Regional richness
1 Victoria Cross	24	708.16	1949.58 (2180-1006)	9.98 (58.00-0.40)	3.33	19
2 Jasper	46	165.77	1385.00 (2430-1024)	10.95 (127.40-0.20)	7.78	46
3 Maligne	29	707.15	1993.93 (2310-1442)	96.56 (2066.00-0.20)	3.86	26
4 Southesk	12	177.14	2172.42 (2325-1830)	33.38 (150.00-1.50)	3.42	11
5 Sunwapta	29	753.80	1633.45 (2225-1174)	16.67 (80.00-0.60)	4.83	28
6 Hidden Lakes	26	250.71	2330.42 (2621-1857)	8.64 (4.50-0.27)	1.58	8
7 Cascade	21	219.06	2296.84 (2438-1996)	5.84 (29.37-0.10)	3.24	19
8 Bow	61	1248.27	1957.30 (2423-1384)	43.83 (1663.00-0.20)	3.97	37
9 Yoho	37	481.34	1995.54 (2455-1300)	11.53 (116.00-0.01)	2.76	26
10 Kootenay	16	673.96	1473.63 (2241-1183)	8.55 (57.50-0.50)	5.88	32
11 Kananaskis	11	710.42	1936.36 (2225-1234)	12.15 (65.00-2.00)	4.45	24
12 Waterton	45	424.32	1682.40 (2195-1274)	43.34 (941.00-0.06)	8.02	60
13 Revelstoke	22	887.16	1902.27 (2332-1137)	2.45 (9.80-0.10)	2.59	21

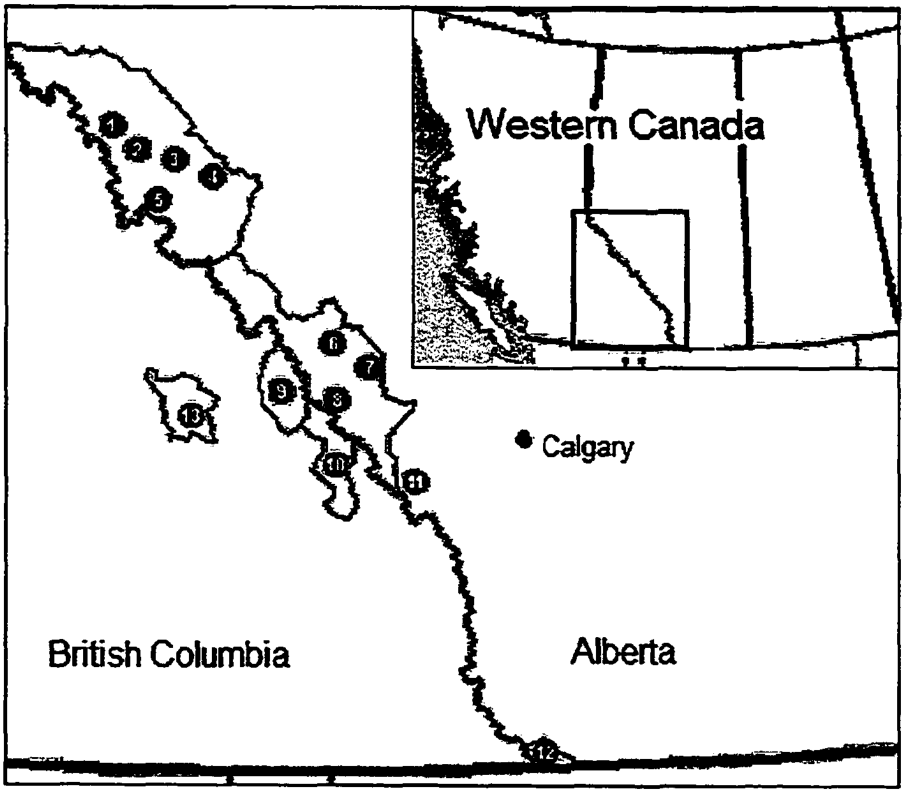

Figure 2-1 Map of the Canadian Rocky Mountains showing the locations of the 13 regions.

To develop a scale-independent test of the relationship between local and regional richness, I regressed regional richness against environmental variables and used the residuals as an explanatory variable for mean local richness. Backward stepwise regression was used to determine the physical variables (elevation, region area, number of lakes, mean surface area and mean depth) that significantly influenced regional richness. Mean local richness was plotted against residual regional richness, and linear regression analyses were performed to reduce the confounding influence of environmental heterogeneity on the relationship between mean local and regional richness.

The additive alpha-beta model (i.e. regional = alpha + beta; Gering and Crist 2002) was used to partition the contributions of local richness (alpha-richness) and species turnover (beta-richness) to regional richness. Regression analyses were performed to test the significance of the relationships between regional richness and alpha richness. Partitioning regional richness into alpha- and beta-richness components provided an estimate of the relative importance of local versus regional controls. For example, high beta-richness indicates that regional richness is primarily attributable to taxonomic differences among distinct local communities, suggesting pronounced dispersal limitation or environmental heterogeneity. Although previous investigations have demonstrated scale dependence of alpha and beta richness (Gering and Crist 2002), I did not examine these relationships because regional richness was not significantly related to total landscape area in my data (R^2=0.002, P=0.895).

The amount of environmental heterogeneity influencing beta richness was analyzed using direct gradient analyses. Redundancy analysis (RDA) was performed using CANOCO version 4.0 (ter Braak 1998) to examine the amount of variation in species composition among sites (i.e. beta richness) that could be explained significantly by environmental variables, including turbidity, alkalinity, chlorophyll *a*, temperature, total dissolved solids (TDS), conductivity, pH, dissolved organic carbon (DOC), total dissolved phosphorus (TDP),total phosphorus (TP), ammonia, nitrate, secchi depth, presence of fish (native and/or stocked), basin depth, volume, area, elevation and number of inflows and outflows. Forward selection and inspection of variance inflation factors were performed to identify significant and independent explanatory environmental variables. Monte Carlo permutation tests (499 unrestricted permutations) were used to test the significance of the redundancy analyses. Species that appeared in fewer than three lakes and lakes that contained fewer than two species were removed from the analysis. The magnitude and direction of influence for the significant environmental variables is indicated by the length and orientation of the arrows for continuous variables, and by the orientation and distance from the origin for categorical variables (e.g., fish presence/absence).

To minimize the statistical influence of environmental heterogeneity on the local-regional richness relationship across all mountain lakes, I used data from only alpine lakes (>2200 m above sea level) and repeated all of the above analyses. Collectively, alpine lakes represent a relatively homogeneous environment because they are characterized by cold and dilute abiotic conditions (Vinebrooke and Leavitt 2005).

RESULTS

A significant ($R^2 = 0.79$, $P < 0.001$) positive linear relationship existed between local and regional richness (Fig. 2-2A). A small regression coefficient ($b = 0.12$) reflected regional richness being typically two to four times greater than local richness (Table 2-1). The partial regression coefficient for a quadratic term was not significant, showing that local richness was not a curvilinear function of regional richness.

Stepwise multiple regression analysis identified mean elevation (Fig 2-2B; $R^2 = 0.52$, $P = 0.01$) and the number of lakes sampled in each region as significant predictors of regional richness (Table 2-2). When residual regional richness from this model was then used as a predictor of local richness, the previous linear relationship (Fig. 2-2A) was rendered non-significant (Fig. 2-2C). Regional richness was not significantly related to landscape area ($R^2 = 0.002$, $P = 0.89$); therefore, the size of the regional species pool was not scale-dependent.

Alpha richness was significantly related ($R^2 = 0.79$, $P < 0.001$) to regional richness (Fig. 2-3). Beta richness accounted for 85% of regional richness, estimated by the area under the curve. Also, beta richness contributed more than alpha richness to regional richness as the species pool increased in size (Fig. 2-3).

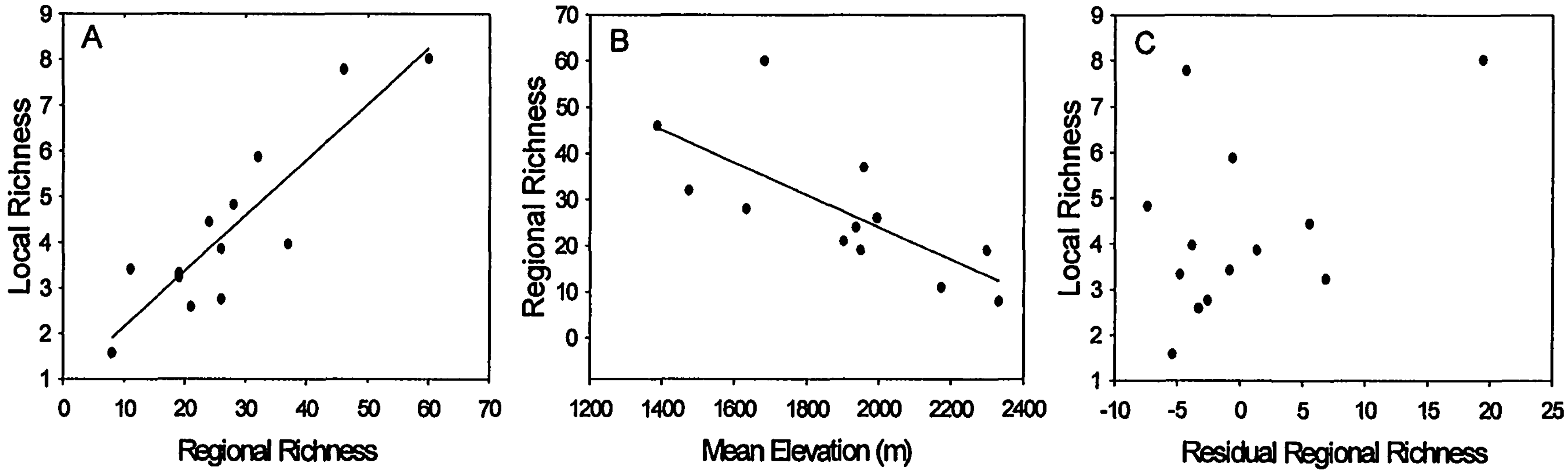

Figure 2-2 (A) Local vs. regional species richness for the 13 mountain lake regions is linear. $R^2 = 0.79$, $P < 0.001$, $y = 0.12x + 0.94$ (B) Regional richness vs. mean elevation (m) is negatively related. $R^2 = 0.52$, $P = 0.01$, $y = 93.91 - 0.04$ (C) Local vs. residual regional richness (influence of elevation and number of lakes removed) for the 13 mountain lake regions. $R^2 = 0.21$, $P = 0.11$.

Table 2-2 Multiple regression analysis results for the effect of environmental geographic variables on regional richness in the 379 mountain lakes in 13 regions. (A) ANOVA for the multiple regression model. (B) Parameter estimates and *t*- test results.

(A) Analysis of Variance

Source	SS	*df*	*F*	*P*	R^2
Model	1749.918	2	14.220	0.001	0.740
Error	615.313	10			
Total	2365.231	12			

(B) Parameter Estimates

Variable	Estimate	*df*	*t*	*P*
Intercept	71.106	1	4.197	0.002
Number of Lakes	0.152	1	2.904	0.016
Mean Elevation	-0.030	1	-3.703	0.004

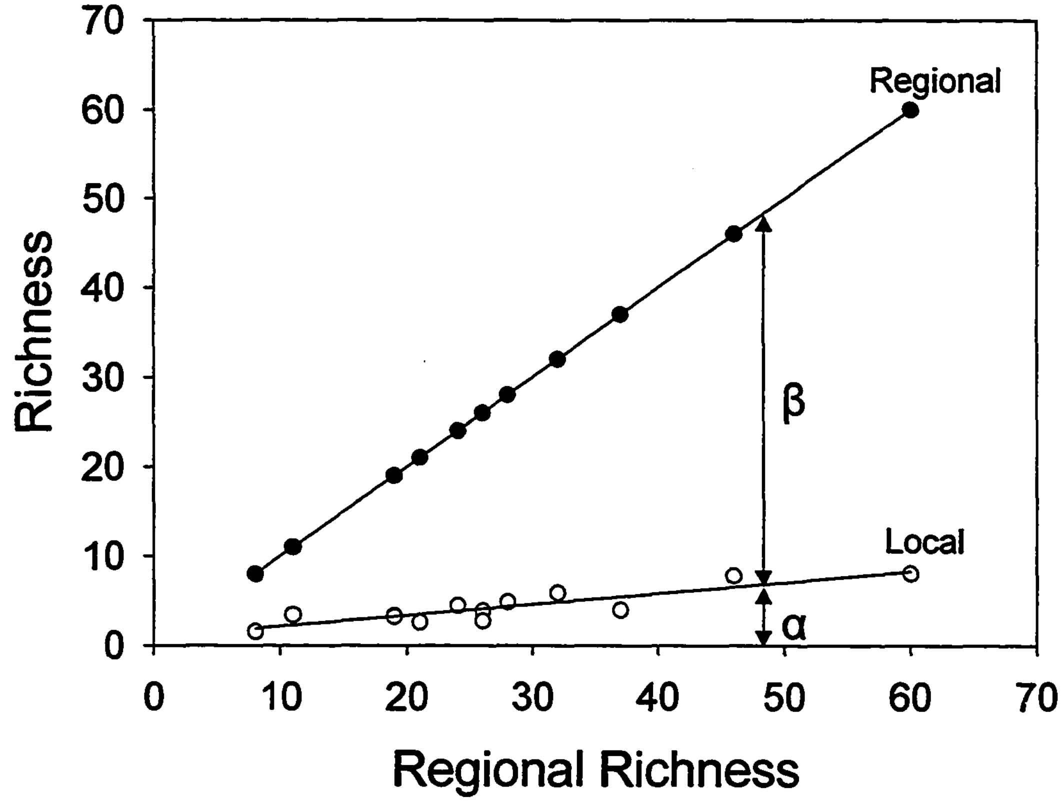

Figure 2-3 Partitioning of regional richness into alpha and beta richness components for the 13 mountain lake regions. Black circles represent the total regional richness values. Open circles are the alpha richness (local richness) estimates for each region. The regression equation for alpha richness is $y = 0.12x + 0.94$, $R^2 = 0.79$, $P < 0.001$. Beta richness accounts for 85% of the area under the regional richness line, and alpha richness accounts for 15%.

Redundancy analysis generated a significant (*F* = 12.50, *P* = 0.005) ordination that showed elevation best explained the influence of environmental heterogeneity on taxonomic variance of zooplankton communities among the 379 mountain lakes and ponds (Fig. 2-4A). The first RDA axis represented an elevation gradient while the second axis represented a water clarity gradient consisting of colour (DOC) and secchi depth, which together explained 11% of the variation in the species data. Chlorophyll *a* concentration and water temperature were significant negative covariables of elevation (Table 2-4) that were excluded from the final RDA because they did not exert independent influences on the ordination. The convergence of lakes (Fig. 2-4A) and species (Fig. 2-5) from right to left along RDA axis 1 showed that environmental heterogeneity and species richness decreased with increasing elevation. Zooplankton assemblages exhibited regionality as several waterbodies from certain mountain regions appeared tightly clustered, including Victoria Cross [region 1], Jasper [region 2], and Waterton [region 3] (Fig. 2-4B). Several zooplankton species also exhibited regionality. For example, *Diaptomus shoshone* [No.54] is present in alpine lakes in Waterton [No. 12] and Glacier [region 13] parks but not in the other parks, and *Acanthodiaptomus denticornis* [No. 44] occurs in the lakes of the Bow Valley [region 8] in Banff national park but not the other regions. Species-poor alpine communities were characterized by the presence of *Hesperodiaptomus arcticus* [No. 57] and *Daphnia middendorffiana* [No. 23] (Fig. 2-5).

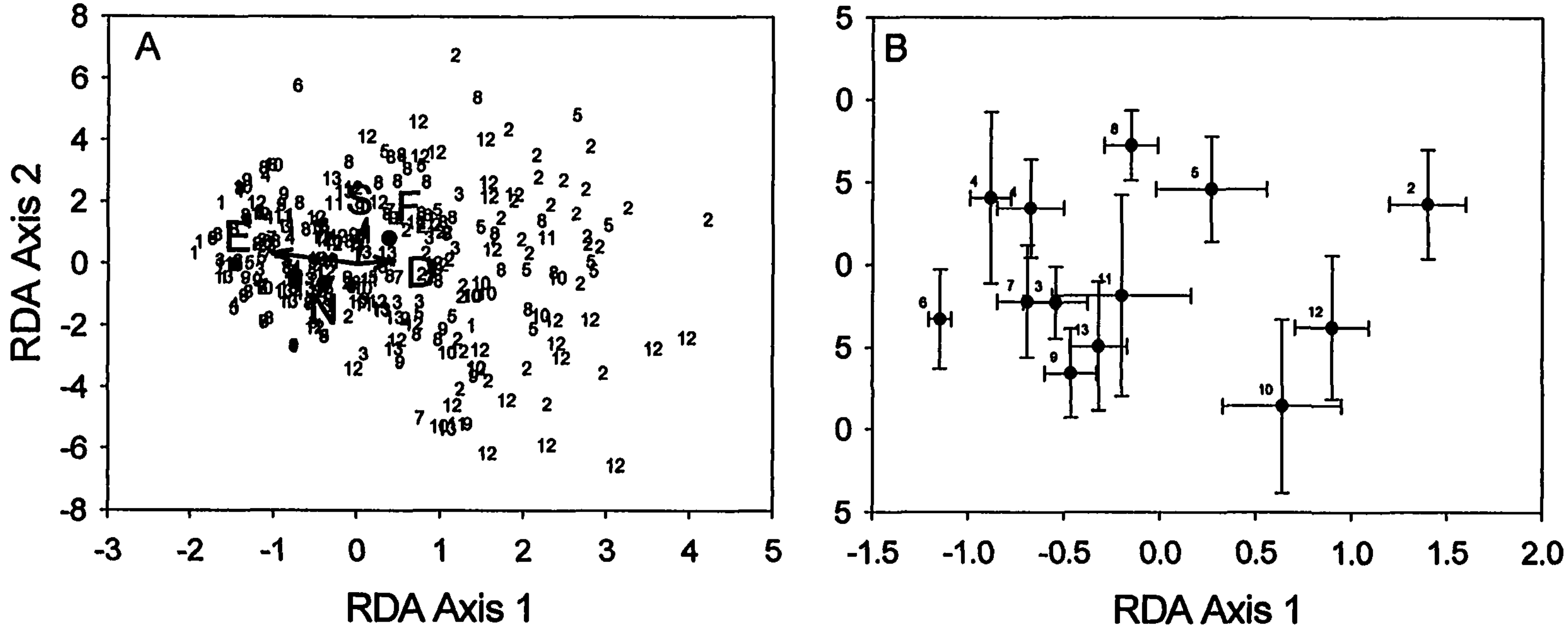

Figure 2-4 (A) RDA for 379 sample sites. The numbers on the samples points refer to the regions in Table 1. E = elevation, S = Secchi depth, F = fish present, D = DOC and N = no fish present. The first two RDA axes explained 11.8% of the variation in mountain zooplankton species data. (B) RDA plot showing the centroids of the 13 regions. The significant vectors are as shown in A. The point labels represented the regions shown in Table 2-1.

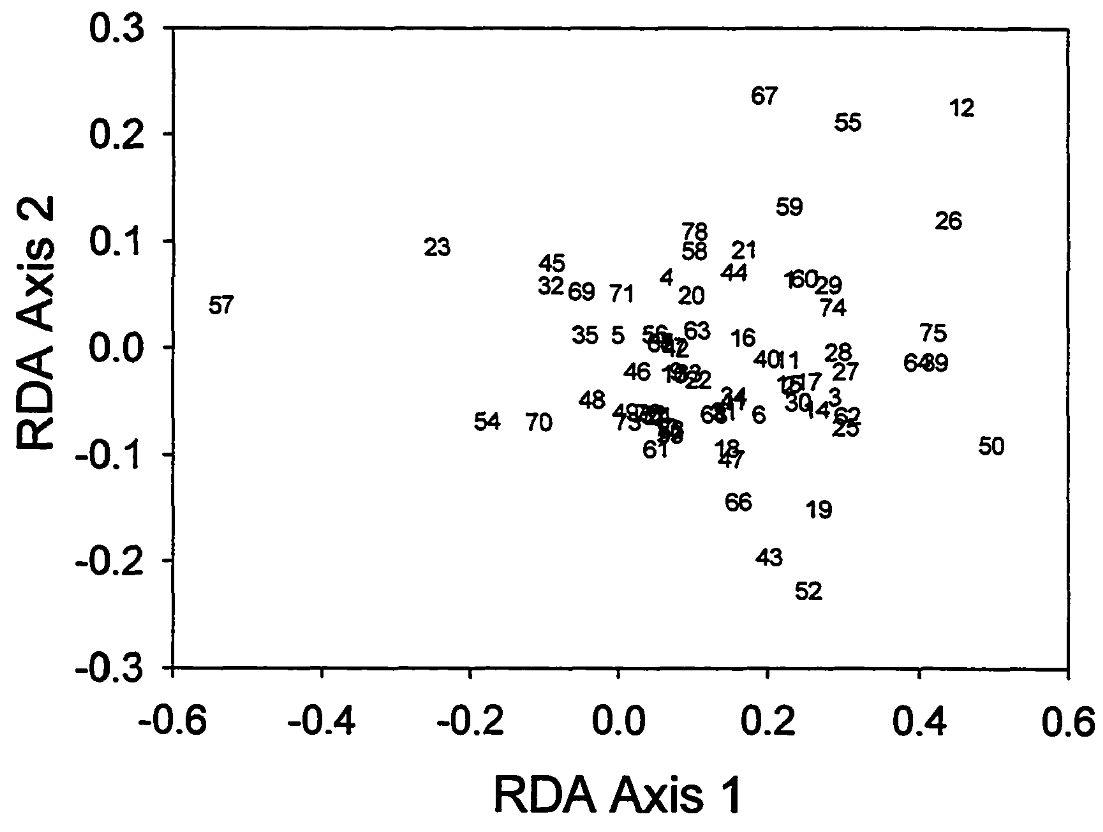

Fig. 2-5 RDA for 78 species present in the 13 regions. The significant vectors are as shown in 2-4A. The species points are represented by numbers which refer to the species in Table 2-3.

Table 2-3 Species codes for Figures 2-5 and 2-8B indicating the species number and the taxonomic group for each species.

Code	Species	Taxonomy
1	*Leptodora kindtii* (Focke 1844)	cladoceran
2	*Acroperus harpae* (Baird 1843)	cladoceran
3	*Alona affinis* (Leydig 1860)	cladoceran
4	*Alona circumfimbriata* (Megard 1967)	cladoceran
5	*Alona costata* (Sars 1862)	cladoceran
6	*Alona guttata* (Sars 1862)	cladoceran
7	*Alona intermedia* (Sars 1862)	cladoceran
8	*Alona quandrangularis* (Müller 1785)	cladoceran
9	*Alona rectangula* (Sars 1861)	cladoceran
10	*Alonella excisa* (Fischer 1854)	cladoceran
11	*Alonella nana* (Baird 1850)	cladoceran
12	*Bosmina longirostris* (Müller 1785)	cladoceran
13	*Ceriodaphnia acanthina* (Ross 1897)	cladoceran
14	*Ceriodaphnia affinis* (Lilljeborg 1900)	cladoceran
15	*Ceriodaphnia lacustris* (Birge 1893)	cladoceran
16	*Ceriodaphnia pulchella* (Sars 1862)	cladoceran
17	*Ceriodaphnia quadrangula* (Müller 1785)	cladoceran
18	*Ceriodaphnia reticulata* (Jurine 1820)	cladoceran
19	*Chydorus sphaericus* (Müller 1785)	cladoceran
20	*Daphnia catawba* (Coker 1926)	cladoceran
21	*Daphnia galeata mendotae* (Birge 1918)	cladoceran
22	*Daphnia longiremis* (Sars 1861)	cladoceran
23	*Daphnia middendorffiana* (Fischer 1851)	cladoceran
24	*Daphnia parvula* (Fordyce 1901)	cladoceran
25	*Daphnia pulex* (Leydig 1860/Richard 1896)	cladoceran
26	*Daphnia rosea* (Sars 1862/Richard 1896)	cladoceran
27	*Daphnia schødleri* (Sars 1862)	cladoceran
28	*Diaphanosoma brachyurum* (Liéven 1848)	cladoceran
29	*Diaphanosoma leuchtenbergianum* (Fischer 1850)	cladoceran
30	*Eurycercus lamellatus* (Müller 1785)	cladoceran
31	*Graptoleberis testudinaria* (Fischer 1848)	cladoceran
32	*Holopedium gibberum* (Zaddach 1855)	cladoceran
33	*Latona setifera* (Müller 1785)	cladoceran
34	*Leydigia quadrangularis* (Leydig 1860)	cladoceran
35	*Macrothrix hirsuticornis* (Norman and Brady 1867)	cladoceran
36	*Pleuroxus denticulatus* (Birge 1878)	cladoceran
37	*Pleuroxus procurvus* (Birge 1878)	cladoceran
38	*Pleuroxus striatus* (Schødler 1863)	cladoceran
39	*Polyphemus pediculus* (Linné 1761)	cladoceran
40	*Scapholeberis kingi* (Sars 1903)	cladoceran
41	*Sida crystallina* (Müller 1875)	cladoceran
42	*Simocephalus serrulatus* (Koch 1841)	cladoceran
43	*Simocephalus vetulus* (Schødler 1858)	cladoceran
44	*Acanthodiaptomus denticornis* (Wierzejski 1888)	calanoid copepod
45	*Diaptomus arapahoensis* (Dodds 1915)	calanoid copepod

46	*Diaptomus ashlandi* (Marsh 1893)	calanoid copepod
47	*Diaptomus forbesi* (Light 1938)	calanoid copepod
48	*Diaptomus franciscanus* (Lilljeborg 1889)	calanoid copepod
49	*Diaptomus hirsutus* (Wilson 1953)	calanoid copepod
50	*Diaptomus leptopus* (Forbes 1882)	calanoid copepod
51	*Diaptomus novemdecimus* (Wilson 1953)	calanoid copepod
52	*Diaptomus nudus* (Marsh 1904)	calanoid copepod
53	*Diaptomus sanguineus* (Forbes 1876)	calanoid copepod
54	*Diaptomus shoshone* (Forbes 1893)	calanoid copepod
55	*Diaptomus sicilis* (Forbes 1882)	calanoid copepod
56	*Diaptomus tyrrelli* (Poppe 1888)	calanoid copepod
57	*Hesperodiaptomus arcticus* (Marsh 1920)	calanoid copepod
58	*Senecella calanoides* (Juday 1923)	calanoid copepod
59	*Acanthocyclops vernalis* (Fischer 1853)	cyclopoid copepod
60	*Diacyclops bicuspidatus thomasi* (Forbes 1882)	cyclopoid copepod
61	*Diacyclops navus* (Herrick 1882)	cyclopoid copepod
62	*Eucyclops agilis* (Koch 1838)	cyclopoid copepod
63	*Eucyclops speratus* (Lilljeborg 1901)	cyclopoid copepod
64	*Macrocyclops albidus* (Jurine 1820)	cyclopoid copepod
65	*Macrocyclops ater* (Herrick 1882)	cyclopoid copepod
66	*Microcyclops varicans rubellus* (Lilljeborg 1901)	cyclopoid copepod
67	*Orthocyclops modestus* (Herrick 1883)	cyclopoid copepod
68	*Canthocamptus oregonensis* (Wilson 1956)	harpactacoid copepod
69	*Artemiopsis stephanssoni* (Johansen 1922)	anostracan
70	*Branchinecta paludosa* (Müller 1788)	anostracan
71	*Branchinecta zschokke* (Mackin 1952)	anostracan
72	*Eubranchipus intricatus* (Sars 1896)	anostracan
73	*Streptocephalus seali* (Ryder 1879)	anostracan
74	*Gammarus lacustris* (Sars 1865)	amphipod
75	*Hyalella azteca* (Saussure 1858)	amphipod
76	*Lepidurus apus* (Packard 1875)	notostracan
77	*Lynceus brachyurus* (Müller 1785)	conchostracan
78	*Mysis relicta* (Lovén 1861)	mysidacean

Table 2-4 Summary of significant linear regression analyses for the influence of elevation on chemical environmental variables. Regression equation $y = bx + c$.

Variable	*b*	*c*	*F*	*P*	R^2
Temperature	-0.009	28.186	124.254	<0.001	0.718
TDS	-0.074	225.186	94.802	<0.001	0.460
Turbidity	-0.060	187.515	42.643	<0.001	0.425
Conductivity	-0.107	360.635	37.713	<0.001	0.397
DOC	-0.005	12.213	20.805	<0.001	0.393
Chlorophyll *a*	-0.005	18.917	12.164	0.001	0.378

Because environmental heterogeneity overwhelmed the local-regional richness relationship for all of the mountain lake data, I also performed analyses on data from only relatively homogeneous alpine sites. I found a significant ($R^2 = 0.58$, $P = 0.05$) linear relationship between local alpine richness and regional alpine richness (Fig. 2-6). The quadratic term was not significant when it was included in the regression analysis. Stepwise multiple regression analysis showed that alpine regional richness was not scale-dependent because landscape area, number of lakes sampled, and elevation were not retained as significant explanatory variables (Table 2-5).

Alpha richness was significantly related ($R^2 = 0.58$, P = 0.05) to regional alpine richness (Fig. 2-7). Beta richness accounted for 77% of the variation in alpine species composition. Increased regional richness across alpine-lake regions was primarily attributable to beta-, rather than alpha-richness.

The first two RDA axes explained 50.2% of the taxonomic variation of zooplankton among the alpine sites (Fig. 2-8). Fish status best characterized the first axis as fishless lakes were contrasted from stocked lakes (Fig. 2-8A). The second axis was best explained by chlorophyll *a* concentration and pH. Monte Carlo permutation testing showed that the RDA analysis was significant ($F = 4.18$, $P = 0.002$). Zooplankton species composition showed very little variation across alpine lakes and ponds, though fewer zooplankton species were found in the presence of stocked sportfish (Fig. 2-8B).

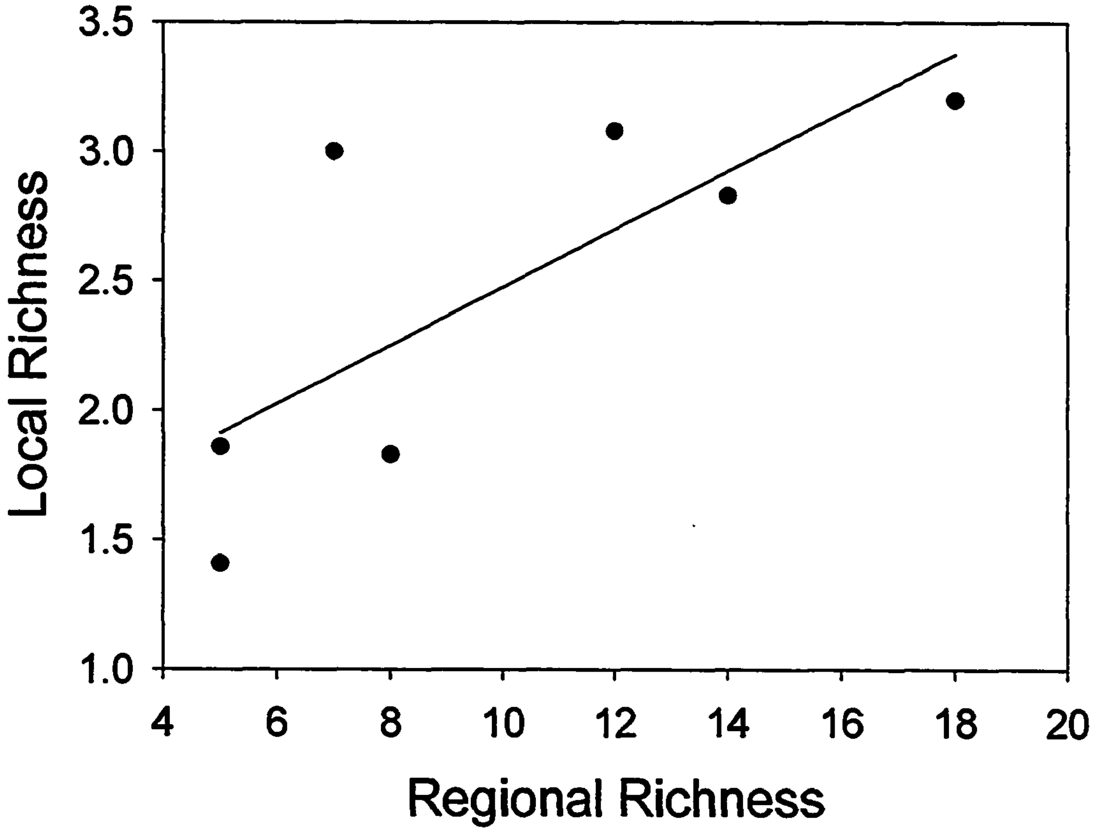

Figure 2-6 Local vs. regional species richness for 7 alpine lake regions. R^2 = 0.58, P = 0.05, y = 0.11x + 1.34.

Table 2-5 Multiple regression analysis results for the effect of environmental geographic variables on regional richness in the 102 alpine lakes in 7 regions. (A) ANOVA for the multiple regression model. (B) Parameter estimates and *t*- test results.

(A) Analysis of Variance

Source	SS	*df*	*F*	*P*	R^2
Model	19.100	2	1.689	0.294	0.077
Error	22.614	4			
Total	41.714	6			

(B) Parameter Estimates

Variable	Estimate	*df*	*t*	*P*
Intercept	50.977	1	0.887	0.425
Number of Lakes	0.291	1	1.831	0.141
Mean Elevation	-0.022	1	-0.846	0.445

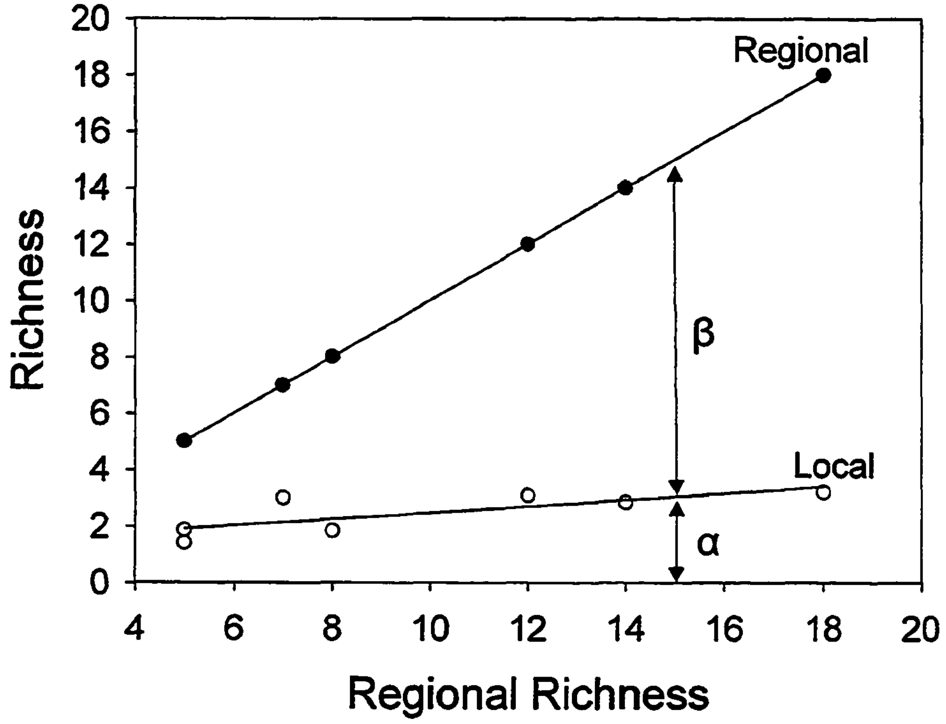

Figure 2-7 Partitioning of regional richness into alpha and beta richness components for the 7 alpine lake regions. Black circles represent the total regional richness values. Open circles are the alpha richness (local richness) estimates for each region. The regression equation for alpha richness is $y = 0.11x + 1.35$, $R^2 = 0.58$, $P = 0.05$. Beta richness accounts for 77% of the area under the regional richness line, and alpha richness accounts for 23%.

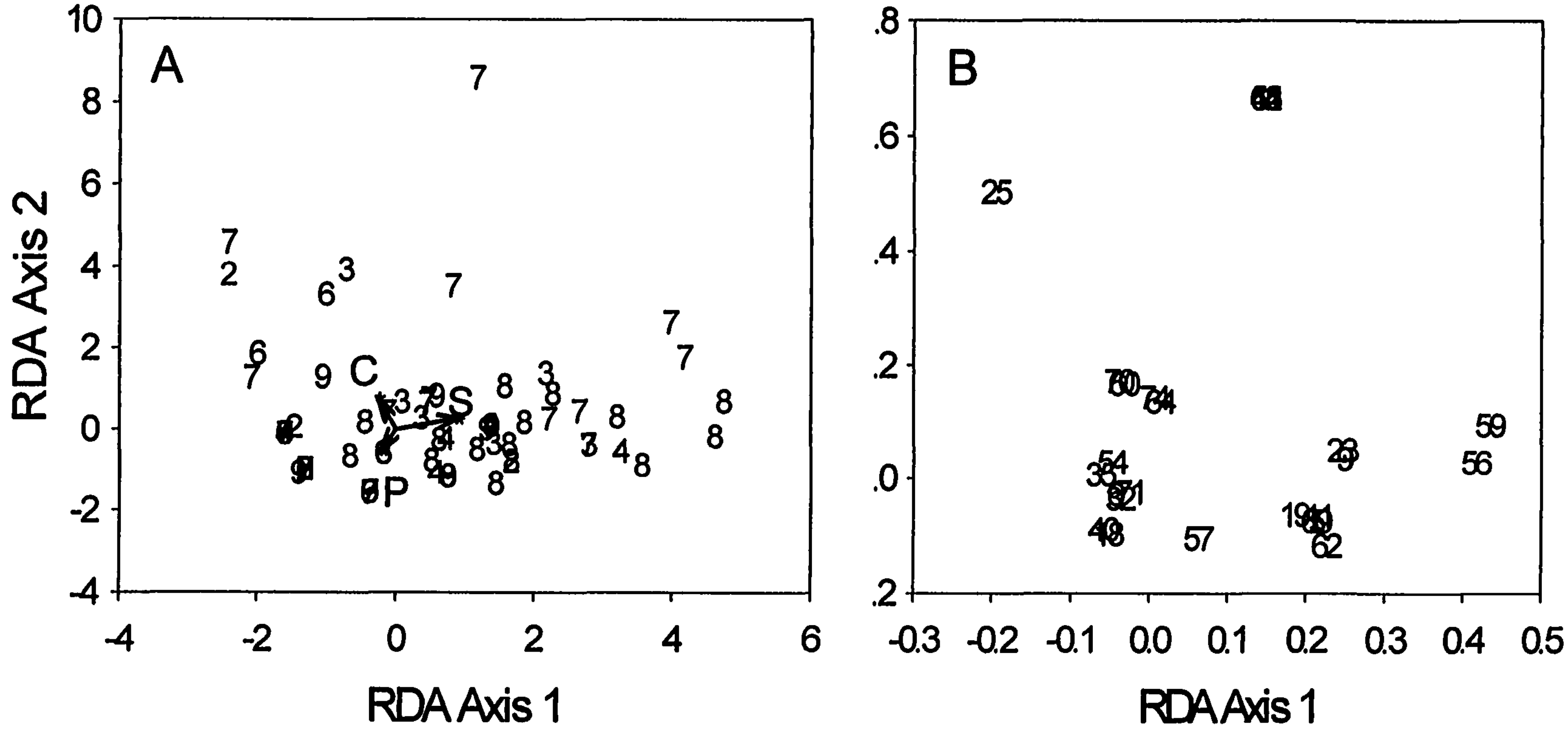

Figure 2-8 (A) RDA for 102 sample sites. The numbers on the samples points refer to the regions in Table 1. C = chlorophyll a concentration, S = presence of stocked fish, P = pH. The first two RDA axes explained 50.2% of the variation in the species data. (B) RDA for 26 species present in the 7 alpine lake regions. The significant vectors are as shown in A. The species points are represented by numbers which refer to the species in Table 3.

DISCUSSION

Zooplankton species richness in lakes and ponds of the Canadian Rocky Mountains was positively related to the size of the regional species pool, which could be interpreted as evidence of an unsaturated community structured by dispersal-limitation. However, the significant linear relationship between local and regional species richness may be attributable to the confounding influence of environmental heterogeneity. Specifically, zooplankton communities span a large altitudinal gradient consisting of a variety of distinct montane, subalpine, and alpine lakes and ponds.

In relatively homogeneous alpine environments, a significant positive local-regional richness relationship and high beta richness suggested that high-elevation communities were dispersal-limited. Unfortunately, I could not consider this relationship to be conclusive evidence of dispersal limitation because of the confounding influence of two factors. The first is that regional perturbations, namely widespread stocking of fishless alpine lakes with exotic sportfish occurred in the Canadian Rocky Mountains (Donald 1987). The second is regional zooplankton distributions, where the distributional range is restricted in spite of the relatively homogenous environmental conditions in alpine lakes across all regions. In both the mountain and alpine cases, regional richness consisted primarily of beta richness rather than alpha richness, suggesting that environmental heterogeneity, dispersal limitation, or both caused zooplankton communities to be distinct over short lateral distances. Therefore, I must place my findings in the context of other related findings to better understand how regional local factors can control mountain zooplankton communities and their adaptability to future environmental change.

Environmental heterogeneity, as a significant predictor of montane zooplankton richness, suggested that species are very responsive to environmental change. Therefore, dispersal limitation may have played a minor role in structuring low-elevation zooplankton communities. Similarly, findings from several surveys (Pinel-Alloul et al. 1995; Shurin et al. 2000; Donald and Anderson 2003) and experiments (Jenkins and Buikema 1998; Shurin 2000) support my expectation that zooplankton exhibit wide dispersal potential across relatively flat, low-elevation environments. Therefore, I hypothesize that zooplankton communities are adapt more readily to environmental change in mountain valleys because of the greater connectivity of higher-order lakes combined with a larger regional montane species pool than exists in alpine areas.

Local factors were expected to be significant explanatory variables of local richness and beta richness because resources and predation regulate zooplankton communities in other mountain and arctic lakes and ponds (McNaught et al. 1999; Winder et al. 2001, 2003; Dzialowski and O'Brien 2004). In particular, environmental influences on zooplankton richness, namely chlorophyll-inferred system productivity (Dodson et al. 2000; Winder et al. 2001) and temperature (Moore et al. 1996; Strecker et al. 2004) were positive covariables of elevation and species richness in my study. In turn, elevation may be considered an integrative metric of climate-related variables in mountainous regions (Vinebrooke and Leavitt 2005). Therefore, I hypothesize that interactions among climate-related variables and environmental heterogeneity override the influence of dispersal limitation in determining patterns in zooplankton richness along altitudinal gradients consisting of connected and unconnected lakes.

My findings provided some support for dispersal-limitation of zooplankton in abiotically similar alpine, but not in subalpine or montane, environments. A significant positive relationship between local and regional richness, together with high beta-richness and low environmental heterogeneity, agreed with the hypothesis that zooplankton are dispersal-limited in insular alpine and arctic settings owing to a heavy reliance on overland transport across extreme environments (Boileau and Hebert 1988). However, introduction of an exotic predatory fish into many of these fishless alpine lakes suppressed dominant large-bodied zooplankton, enabling colonization by smaller, inferior competitors and prey species (Knapp et al. 2001; Donald and Anderson 2003). Such a scenario should foster a positive relationship between local and regional richness (Shurin and Allen 2001) apart from that generated by dispersal limitation. In addition, selective stocking of only certain alpine lakes (Donald and Anderson 2003) together with relatively low connectivity likely accounted for high beta-richness among alpine lakes and ponds, despite a relatively small regional species pool. Therefore, I hypothesize that regional disturbance (i.e. introduction of exotic fish species) resulted in zooplankton communities being unsaturated in many alpine lakes.

Local zooplankton richness may have been affected by unmeasured local factors, such as competition (Winder et al. 2003; Dzialowski and O'Brien 2004) and predation by native and stocked fish (Donald et al. 2001; Donald and Anderson 2003) and invertebrates (Neill 1988; Paul et al. 1995). Consumption of zooplankton by fish declines with temperature (Jobling 1994) and basin depth and area, enabling large-bodied zooplankton to co-exist with introduced fish in cold, large mountain lakes by accessing depth refugia (Donald et al. 1994). As a result, variation in predation and a larger regional species pool could result in multiple stable states of zooplankton community structure (Chase 2003), thereby generating greater beta-richness among relatively species-rich montane lakes.

Evidence for zooplankton assemblages being unsaturated was stronger for those from insular alpine lakes and ponds than from low-elevation, montane sites. Consequently, alpine zooplankton communities should show less resistance to environmental perturbations because of limited colonization by non-resident tolerant species. Similarly, dispersal limitation would further reduce the resilience of alpine zooplankton as certain extirpated species are not able to readily colonize during ecosystem recovery. In addition, species-poor alpine zooplankton communities could have a poor chance of compensating functionally for extirpated species because of a low probability of resident tolerant species being present. Therefore, I hypothesize that alpine zooplankton communities will show poor adaptability to the increasing impacts of global change.

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CHAPTER 3: DOES ENVIRONMENTAL WARMING INCREASE INVASION OF ALPINE ZOOPLANKTON COMMUNITIES BY MONTANE SPECIES?

INTRODUCTION

In North America, many northern lakes have warmed by 2°C over a 20-yr period (Findlay et al. 2001), and are predicted to continue to warm by as much as 7°C by the year 2100 (Magnuson et al. 1997) based on a doubling of carbon dioxide and increases in other greenhouse gases (Intergovernmental Panel on Climate Change 2001). High-elevation lakes and ponds are considered especially sensitive to climate change as warming events reduce snowpack and ice cover, resulting in decreased albedo and increased heat absorption (Bradley et al. 2004; Strecker et al. 2004; Vinebrooke and Leavitt 2005). Consequently, climate warming is expected to cause loss of coldwater alpine habitats, possibly allowing upward migration by warm-water organisms (e.g., ~100-m ascent per +0.6°C) from lower montane sites (Körner 1999).

The capacity of zooplankton to migrate in response to environmental change is influenced by their dispersal potential. Zooplankton species are capable of dispersal across relatively flat, small (e.g., ~100 km) spatial scales (Shurin 2000; Cáceres and Soluk 2002; Bohonak and Jenkins 2003). However, dispersal limitation is expected to be more pronounced at larger geographic scales (Shurin et al. 2000), and in the presence of substantial topographical barriers, such as mountain ranges (Donald et al. 2001; Chapter 2). For instance, extirpated zooplankton species require decades to recolonize remote alpine lakes following the removal of stocked planktivorous fish (Donald et al. 2001; Knapp et al. 2001).

Local abiotic and biotic factors affect invasion success by zooplankton species. For example, if variation in water temperature exceeds the thermal tolerance of an invading species, reproductive failure and increased mortality may occur (Moore et al. 1996). Warming may also open communities to invasion by causing overexploitation of food resources, which results in the extinction of certain consumers (Beisner et al. 1997; Petchey et al. 1999; Strecker et al. 2004). Predation and competitive exclusion by resident species can also reduce invasion success by dispersing species (Shurin 2000). Alternatively, environmental warming may suppress populations of slow-growing zooplankton in coldwater environments (e.g., Hessen 1996) that favors invaders from warmer habitats.

I performed an experiment to determine the interactive effects of environmental warming and montane species invasion on the total abundance and taxonomic composition of alpine zooplankton communities. I hypothesized that environmental warming would suppress resident coldwater alpine species, thereby enhancing invasion success of montane species. Otherwise, alpine specialists, such as large-bodied omnivorous calanoid copepods (*Hesperodiaptomus arcticus*) and cladocerans (*Daphnia middendorffiana*), were expected to exclude montane invaders through predation and competition, respectively. Also, I anticipated that resting structures of montane species did not exist in alpine lake sediments owing to dispersal-limitation. Therefore, my experimental design consisted of two temperature treatment levels (13°C versus 20°C) crossed with three dispersal treatments (alpine species only, alpine + montane, and montane species only). Finally, I also expected that moderate warming would enhance primary production (e.g., Davison 1991), and therefore, increase food availability to consumers (e.g., zooplankton).

METHODS

In August 2003, zooplankton, sediment, and water were collected during a helicopter trip to a remote fishless alpine lake (Pipit Lake; 2217 m above sea level) located (51°36'N, 115°51'W) in the eastern front range of the Canadian Rocky Mountains in Banff National Park, AB. All collections were made from a boat at a mid-lake sampling location. Vertical hauls using a 64-µm mesh-sized net were performed to collect resident zooplankton, which consisted exclusively of the cladoceran *Daphnia middendorffiana* and calanoid copepod *Hesperodiaptomus arcticus.* Epilimnetic water samples were collected using 20-L plastic carboys, and later filtered through a 64-µm stainless steel sieve prior to the experiment. Lake sediments were collected using an Ekman dredge, and then pooled and transported in an 80-L insulated cooler.

All alpine samples were transported immediately to the University of Alberta, where zooplankton ("alpine-only") and zooplankton-free cultures were established in 8-L rectangular aquaria within a 24-h period. Each aquarium received 1 L of sediment and 7 L filtered water. Ambient densities of zooplankton collected from Pipit Lake were added randomly to 24 aquaria, while the other 12 contained only sediment and lake water. Specifically, 20 adult daphniids and 20 adult calanoid copepods were added to each zooplankton culture. Immature copepods and cladocerans were removed from the zooplankton-free cultures prior to the experiment. Densities were maintained for a one-week acclimation period, while invasion inocula were collected from montane lakes. Zooplankton were also collected from five low-elevation (< 1600 m asl) small lakes (Vista Lake, Kingfisher Pond, Copper Lake, Herbert Lake, and Sibbald Lake) located in the Bow Valley in Banff National Park. These collections were later pooled to create a single montane-invasion culture.

The 2-factor (warming x dispersal) experimental design was replicated six times for a total of 36 aquaria. The two warming treatment levels were achieved by randomly assigning each aquarium to one of two environmentally controlled growth chambers. The temperature in one growth chamber was maintained at the recorded ambient surface water temperature (13°C) of Pipit Lake, while the other was set at 20°C. A 12-h light:dark cycle was used during the 28-d experiment. Single well-mixed 500-mL aliquots of the invasion culture were added to "alpine + montane" and "montane-only" aquaria. In addition, 500 mL of filtered (64-μm mesh) invasion-culture water was added to the non-invaded "alpine-only" aquaria to standardize all aquaria for the effects of introduced nutrients and microplankton. The water level was maintained in the mesocosms throughout the experiment using filtered water from Pipit lake.

On Day 29, all of the water from each mesocosm was filtered through a 64-μm mesh screen to collect all the zooplankton. Zooplankton were preserved in a 4% sugared formalin solution (Prepas 1978) to prevent the expulsion of eggs by the cladoceran species. Zooplankton were identified and enumerated using a Leica MZ9.5 dissecting scope, and photographs were taken using a Micropublisher 3.3 digital camera. All species identifications followed Edmondson (1959). Length measurements were made from the digital photographs in Openlab version 3.1.5 (Improvision 2004), and the average length was calculated. Biomass estimates were then calculated using standard length-weight regression equations (Downing and Rigler 1984). Following removal of zooplankton, one litre of water from each aquarium was filtered to concentrate phytoplankton on to glass-fibre filters (0.45-μm pore size), which were then analyzed for chlorophyll using standard fluorometric procedures (Wetzel and Likens 2000).

Two-factor analyses of variances (ANOVAs) were performed to test for significant interactive and direct effects of warming and dispersal on response variables, including invasion success, resident species and total zooplankton biomass, and chlorophyll. Invasion success was measured as the abundance of montane species present in the "invasion" aquaria (alpine + montane, montane only) that were not present in the controls (alpine only). Statistically significant treatment effects were examined using Tukey multiple comparison tests to identify significant differences between treatment groups. All data were 1+ $\log_{10}$-transformed prior to statistical analyses using SYSTAT version 10.0 (SPSS 2000).

RESULTS

The dispersal treatment increased invasion success as several introduced montane species thrived under both ambient and warmed alpine conditions (Fig. 3-1; Table 3-1). Warming did not have a significant effect on invasion success of montane species (Table 3-1). The montane species that were observed in the invaded mesocosms included the cladocerans *Daphnia rosea, Daphnia pulex, Bosmina longirostris, Chydorus sphaericus,* and *Alona rectangula* and the copepods *Diaptomus sicilis, Diacyclops bicuspidatus thomasi* and *Macrocyclops albidus.* The abundance of *A. rectangula* and *M. albidus* in the invaded treatments were not significantly different from the un-invaded alpine-only treatment (Fig. 3-2; $F = 1.00$, $P = 0.38$ for both species). However, eggs were observed in 28% of these individuals.

The presence of alpine species suppressed total montane species abundance in invaded treatments (Fig.3-1; $F = 452.08$, $P < 0.001$). Invasion by *D. pulex* was suppressed by the presence of alpine species (Fig. 3-2; $F = 15.88$, $P < 0.001$). The abundance of *D. rosea* and *D. sicilis* in the invaded treatments were significantly different from the un-invaded treatments (Fig. 3-2; $F = 80.19$, $P < 0.001$; $F = 112.09$, $P < 0.001$ respectively) but were not significantly different in the presence or absence of alpine species.

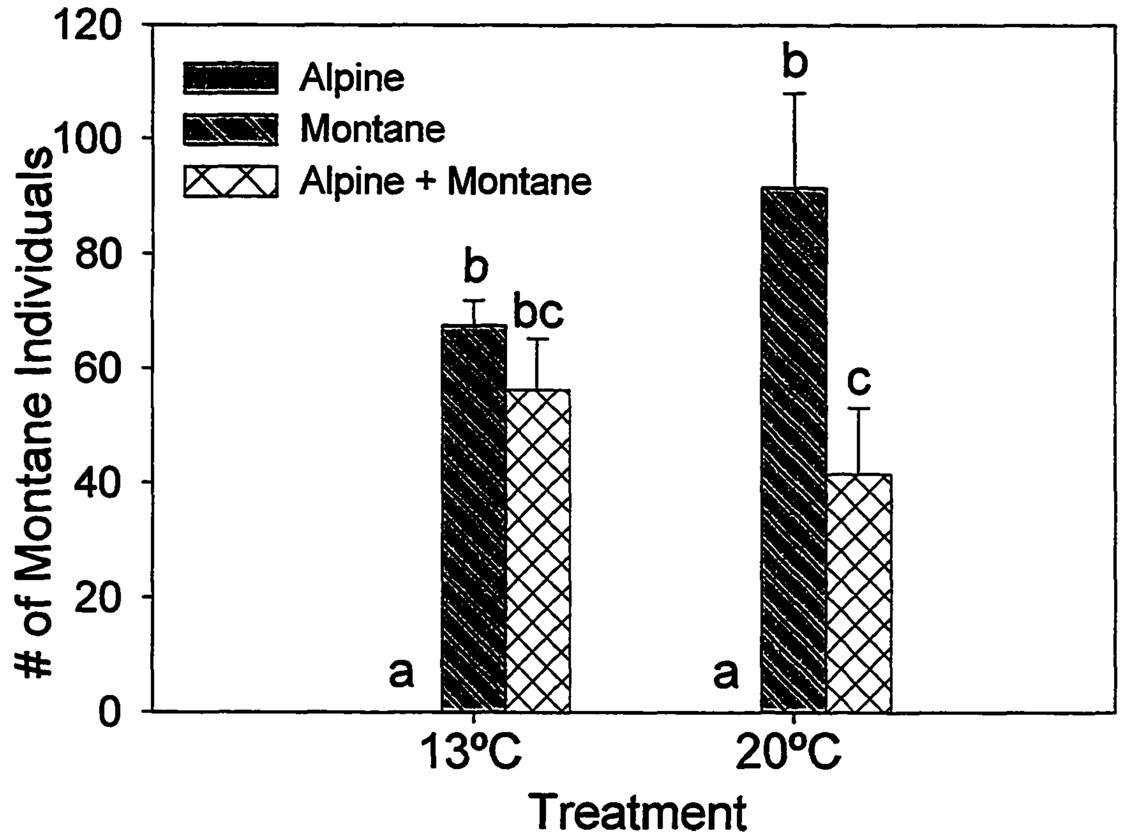

Figure 3-1 Abundance of total montane zooplankton individuals in the presence and absence of alpine species under control (13°C) and warmed (20°C) conditions. Different letters over bars (a – c) indicate differences among treatment means for the total montane invader abundance ($P < 0.05$).

Table 3-1 ANOVA results for effects of temperature and invasion treatment on total abundance of montane species.

Source	df	SS	F	P
Temperature	1	0.04	0.30	0.59
Invasion	2	133.06	452.09	<0.001
Temperaturex Invasion	2	0.68	2.32	0.12
Error	30	4.42		

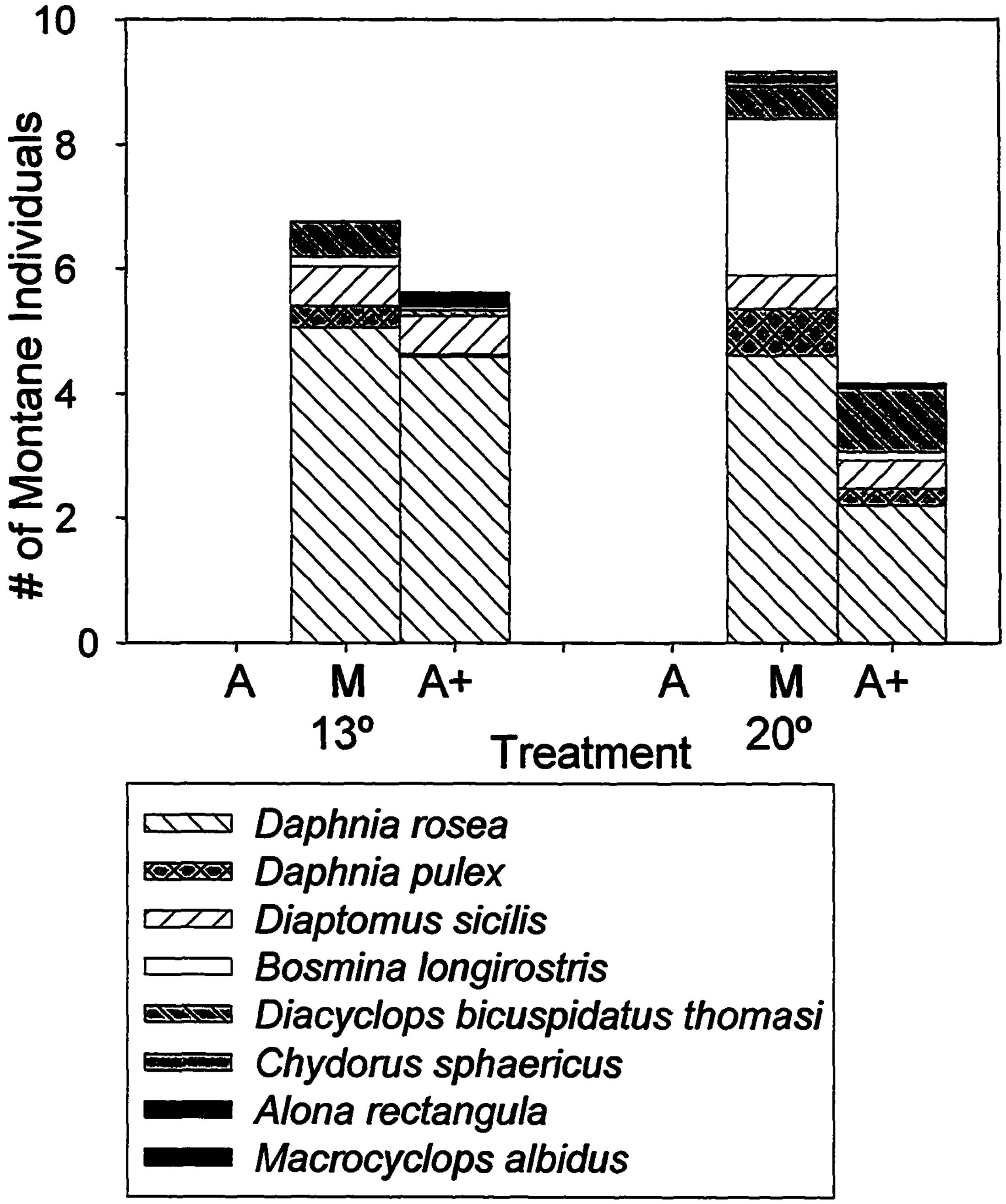

Figure 3-2 Total abundance of each montane zooplankton species in the presence and absence of alpine species under control (13°C) and warmed (20°C) conditions. The treatment symbols for the bars are (A) alpine only, (M) montane only and (A+M) alpine + montane.

There was a significant warming x dispersal treatment effect on *D. bicuspidatus thomasi, B. longirostris* and *C. sphaericus* (Fig. 3-2; $F = 5.88$, $P = 0.01$; $F = 4.79$, $P = 0.02$; $F = 5.21$, $P = 0.01$ respectively). *D. bicuspidatus thomasi* was more abundant in the presence of alpine species at 20°C than at 13°C and *B. longirostris* was more abundant in the absence of alpine species at 20°C than in the other treatments (Fig. 3-2). The presence of *C. sphaericus* was significant in the montane-only treatment at 20°C, however, it was only encountered in the 20°C montane-only and the 13°C alpine + montane mesocosms.

Emergence of montane species from alpine sediments was not detected in the alpine only mesocosms. *Acanthocyclops vernalis* consistently emerged from sediments including in the alpine only aquaria. As this species has been recorded in Pipit Lake, it was included in the alpine species biomass estimates. *Alona rectangula*, which has also been recorded in Pipit Lake, was included as an invading montane species because it was only present in the 13°C alpine + montane aquarium.

Warming suppressed *D. middendorffiana* ($F = 19.53$, $P < 0.001$) and *H. arcticus* ($F = 46.28$, $P < 0.001$) populations (Fig. 3-3). In addition, introduced montane species had a negative effect on *D. middendorffiana* (Fig. 3-3A; invasion effect; $F = 35.82$, $P < 0.001$) while not affecting *H. arcticus* (Fig. 3-3A). There was a significant warming x dispersal treatment effect on *H. arcticus* ($F = 12.70$, $P < 0.001$), resulting in a slight decline in *H. arcticus* population in the presence of montane species with warming. *D. middendorffiana* populations increased by 300%, while adult *H. arcticus* abundance declined by 25%, under control conditions (alpine-only at 13°C), during the experiment (Fig. 3-3).

Total alpine zooplankton biomass was negatively affected by warming ($F = 6.76$, $P = 0.01$) and montane species (Fig. 3-4A; $F = 24.55$, $P < 0.001$). Similarly, warming decreased total zooplankton biomass (Fig. 3-4B; $F = 7.25$, $P = 0.01$), however, total montane zooplankton biomass did not differ significantly between controls and warmed aquaria (Fig. 3-4B). Both *D. middendorffiana* and *H. arcticus* had slightly lower fecundity in the warmed mesocosms, as estimated by the number of individuals with eggs (*D. middendorffiana:* 19.5% at 20°C vs. 22.2% at 13 °C and *H. arcticus:* 13.7% at 20°C vs. 18.4% at 13°C), while *A. vernalis* had higher fecundity at 20°C (27.1% at 20°C vs. 2.3% at 13°C). All montane species showed evidence of reproduction in all invaded aquaria at both 13°C and 20°C, though on average more eggs were observed at 20°C (27.2% at 20°C vs. 15.7% at 13°C).

Total chlorophyll *a* concentrations showed a significant warming x dispersal treatment effect (Fig. 3-5; $F = 4.58$, $P = 0.02$). Chlorophyll *a* was significantly higher in the absence of alpine species at 13°C, and there was no difference between treatments at 20°C. Regression analysis showed that total zooplankton biomass and chlorophyll *a* were significantly inversely correlated across all aquaria ($R^2 = -0.22$, $P = 0.004$, $n = 35$).

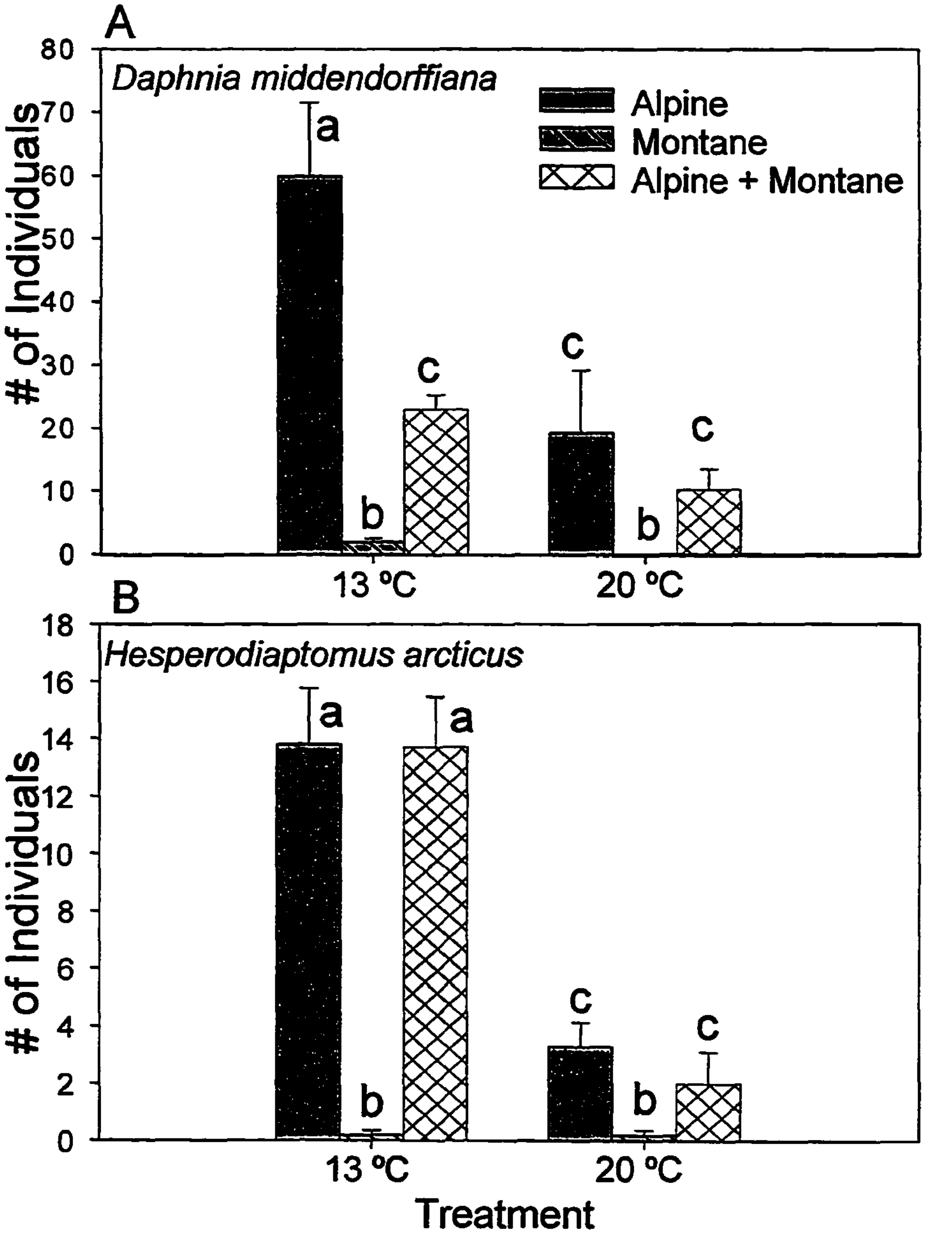

Figure 3-3 Number of individuals of (A) *Daphnia middendorffiana* and (B) *Hesperodiaptomus arcticus* in 3 dispersal treatments (alpine only, montane only, alpine + montane) at 13°C and 20°C. Different letters over bars (a – c) indicate differences among treatment means ($P < 0.05$). Error bars show 1 SE ($n = 6$).

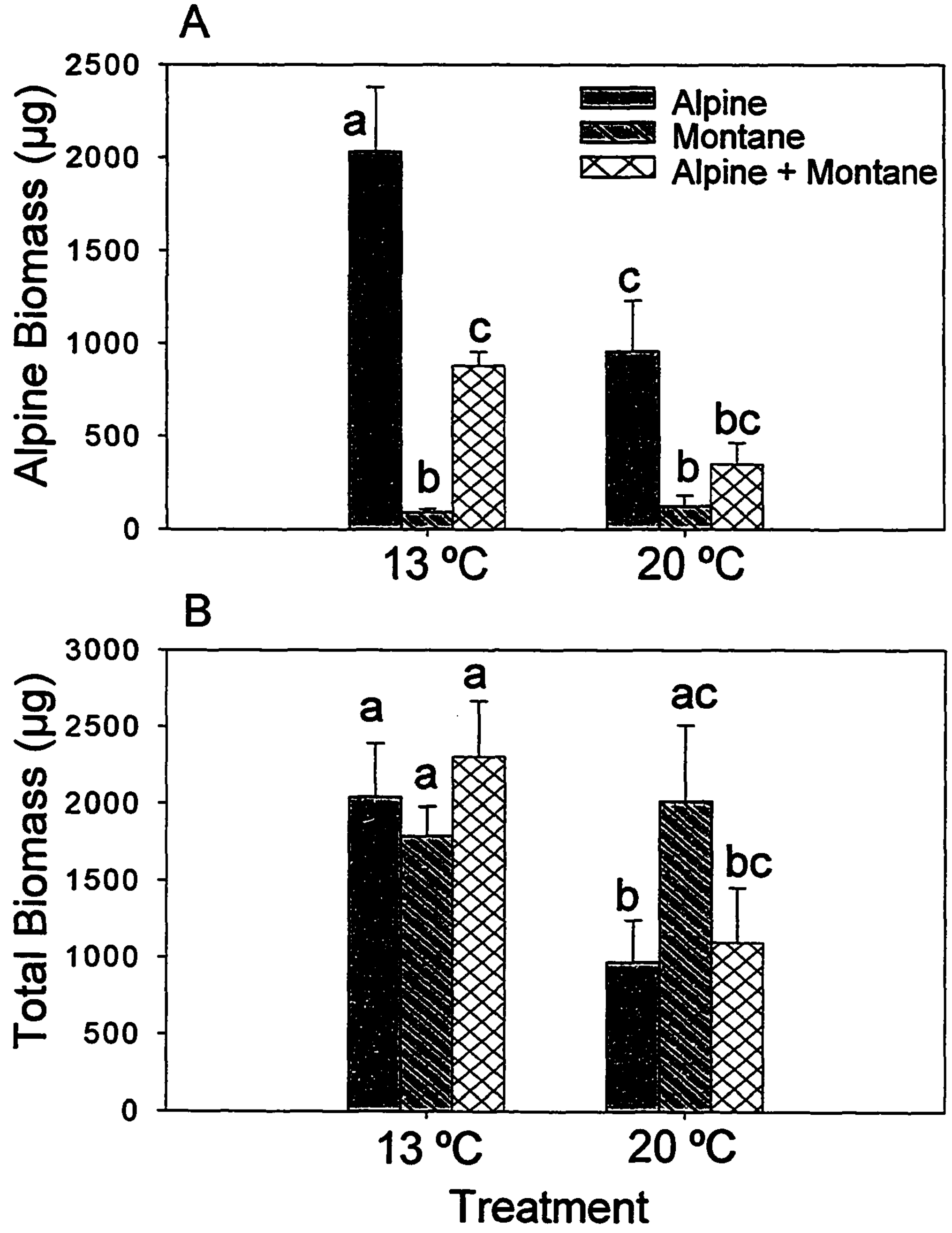

Figure 3-4 Zooplankton biomass estimates for (A) alpine species and (B) all species in 3 dispersal treatments (alpine only, montane only, alpine + montane) at 13°C and 20°C. Different letters over bars (a – c) indicate differences among treatment means ($P < 0.05$). Error bars show 1 SE (n = 6).

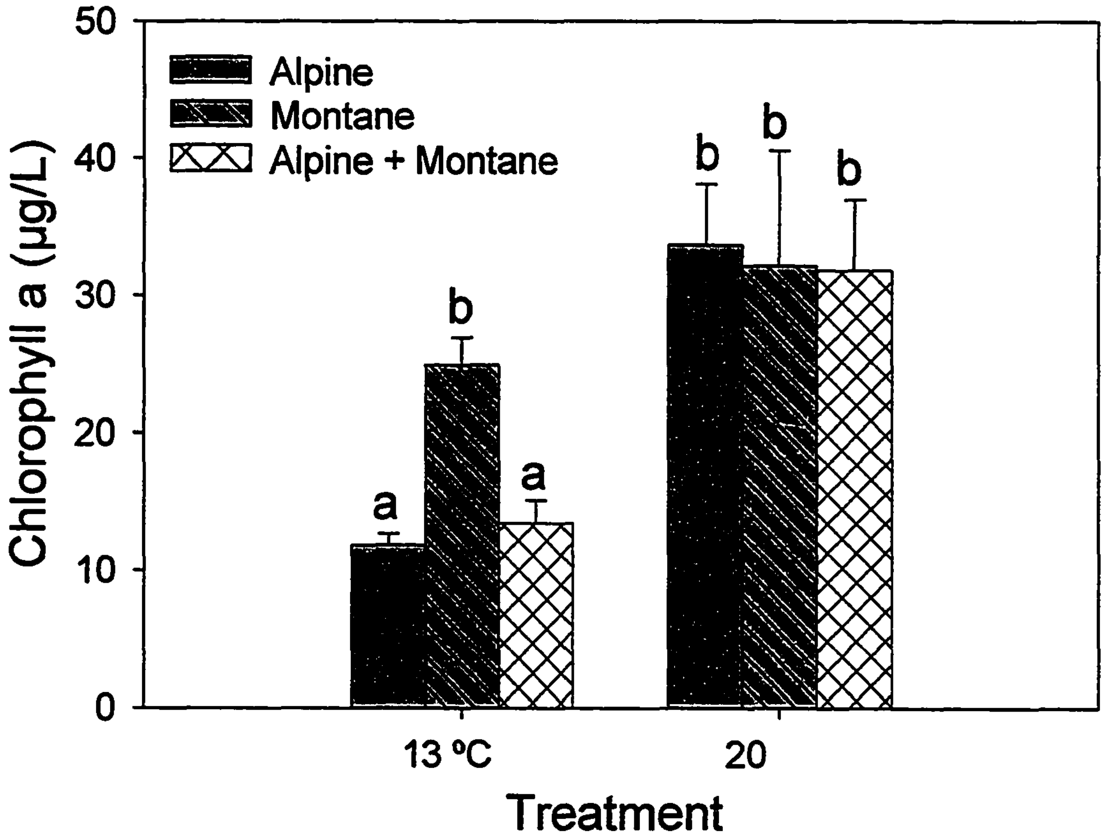

Figure 3-5 Chlorophyll *a* concentrations in the 3 dispersal treatments (alpine only, montane only, alpine + montane) at 13°C and 20°C. Different letters over bars (a, b) indicate differences among treatment means ($P < 0.05$). Error bars show 1 SE ($n = 6$).

DISCUSSION

My findings showed that dispersal would be more important than temperature as a determinant of invasion of alpine zooplankton communities by montane species. Unexpectedly, several montane species were able to survive and reproduce when introduced into cold alpine conditions. In addition, mean invasion success by montane zooplankton was greater in the absence of resident alpine species. Alpine species were suppressed by warming. Therefore, warming should reduce exclusion of invaders by resident alpine zooplankton, thereby increasing the likelihood of invasion by montane species that can overcome dispersal-limitation. Below I consider the relative importance of dispersal potential and local factors that will likely determine the future adaptability of zooplankton communities to climate warming at high elevations.

Dispersal limitation could explain why several zooplankton species do not inhabit alpine lakes despite their observed tolerance of cold, dilute conditions. Mountain zooplankton rely heavily on overland transport as a primary means of dispersal across insular alpine and arctic lakes owing to a lack of connectivity (Jones et al. 2003). However, species must disperse across both long lateral and vertical distances between montane and remote alpine lakes. Consequently, invasion success by mountain zooplankton species may be best attributed to distance between montane and alpine sites, rather than dispersal vectors (e.g., Cáceres and Soluk 2002). Further, animal dispersal vectors of zooplankton are likely weak in mountains because waterfowl seldom visit alpine lakes (Vinebrooke, personal observation). Mountain zooplankton show slow colonization rates in alpine lakes (Donald et al. 2001) likely because their dispersal is dictated by wind and rain events (e.g., Cáceres and Soluk 2002) and infrequent waterfowl visits.

Local biotic factors may also explain the discrepancy between the observed abiotic tolerance of montane zooplankton and their absence from alpine lakes. Specifically, my findings suggested that the alpine copepod *H. arcticus* suppressed invasion by some montane species. This large omnivore is a keystone predator preying on smaller copepods, daphnids, rotifers, and algae in fishless alpine lakes (Paul and Schindler 1994; Paul et al. 1995). Therefore, relative high densities of *H. arcticus* (~3.2 individuals/litre; Paul and Schindler 1994) could prevent establishment of dispersing montane species through predation, and perhaps competition. In remote alpine lakes, low propagule pressure would further reduce the probability of colonization by montane species in the presence of large resident zooplankton.

My findings suggest that montane zooplankton may compete with certain alpine species if they are able to disperse to high-elevation sites. The presence of montane invaders at 13°C reduced the abundance and reproduction of *D. middendorffiana,* suggesting that smaller montane daphnids out-compete larger alpine species. Dzialowski and O'Brien (2004) demonstrated that *D. middendorffiana* was competitively inferior to the smaller bodied *Daphnia pulex* in low resource environments. If smaller bodied montane species are superior competitors, the question becomes why they are not found in alpine lakes. Perhaps there exists an ecological trade-off involving competitive ability and susceptibility to predation (e.g., Leibold 1991). While montane daphnids may be better competitors than larger alpine species, their smaller size increases their susceptibility to predation by other resident alpine zooplankton, such as *H. arcticus*.

Warming is often hypothesized to negatively affect zooplankton due to thermal stress, especially for coldwater specialist species, and due to food limitations caused by shifts in algal communities to larger inedible species, which reduce growth and reproduction (Moore et al. 1996). Many coldwater zooplankton taxa experience thermal stress if water temperatures are above 15 – 18°C (Dadswell 1974). I found that a 7°C temperature increase reduced the abundance of resident alpine species, with a relatively larger impact on the daphnid *D. middendorffiana* than on *H. arcticus*. Strecker et al. (2004) found that an average 3.6°C temperature increase reduced daphnid abundance but did not affect copepod abundance in alpine ponds. This discrepancy in the effects of warming on copepod abundance may be explained by the larger temperature variability experienced in alpine ponds than is seen in alpine lakes and the higher temperature increase experienced in my experiment.

System productivity was expected to increase with warming because primary production increases with warming over certain temperature ranges (Davison 1991). In oligotrophic systems, such as alpine lakes, a moderate increase in primary production should increase resources for zooplankton thus increasing total zooplankton biomass (Flanagan et al. 2003). The mesocosm experiment showed that productivity and zooplankton biomass were negatively related in my experiment, which may be due to the shift in zooplankton species composition to smaller bodied, less efficient grazers, or a shift to larger inedible algal species (Beisner et al. 1997; Strecker et al. 2004).

Recent research has suggested that alpine zooplankton communities may be dispersal limited due to topographical barriers (Donald et al. 2001, Chapter 2). The results of this experiment appear to support the hypothesis that alpine zooplankton communities are dispersal limited since a significant number of montane species were able to colonize the aquaria at 13°C in the absence and presence of the resident alpine species, and resting stages of montane species were not evident in the sediments of the alpine lake. To provide adequate support for the dispersal limitation hypothesis, further large-scale, longer-term, and full life-cycle experiments should be conducted to determine if the predatory *H. arcticus* will exclude montane species, and also to determine if montane species can tolerate the higher UV, and other conditions experienced in alpine lakes.

The results of my experiment lead me to the conclusion that environmental warming may increase invasion of montane species into alpine zooplankton communities due to a temperature-related decrease in abundance of resident alpine zooplankton. Reducing alpine resident populations may allow an increase in biomass and abundance of montane invaders, though not necessarily an increase in the number of invading species. Thus with environmental warming, if montane zooplankton are not dispersal limited, several montane species should have the ability to colonize alpine lakes.

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CHAPTER 4: GENERAL CONCLUSIONS

Survey-based and Experimental Findings

To address the question of whether alpine zooplankton will be able to adapt to environmental warming, I tested for dispersal-limitation and the direct and indirect effects of warming on resident and introduced montane species. Alpine communities appeared unsaturated due to dispersal limitation, predation by stocked sportfish, or both. If zooplankton dispersal is not limited, environmental warming could allow montane species to invade alpine communities more readily, by suppressing the large omnivorous copepod *H. arcticus*. However, I suggest that alpine zooplankton assemblages may not readily adapt to environmental warming as these assemblages appear to be dispersal-limited.

Based on my survey results for zooplankton species distributions across mountain lakes and ponds, local-regional richness relationships suggested that alpine zooplankton assemblages were unsaturated and showed pronounced species turnover between sites (i.e., high beta richness). The taxonomic composition of mountain zooplankton assemblages were best explained by elevation, secchi depth, DOC, and the presence of fish. Elevation was significantly related to multiple environmental variables, such as water temperature, turbidity, pH, and productivity (Chlorophyll a). Redundancy analysis indicated that alpine lakes showed less environmental variability than montane lakes. Alpine zooplankton communities were influenced by chlorophyll-inferred productivity, stocked sportfish, and pH (Chapter 2).

The mesocosm experiment supported the hypothesis that alpine zooplankton communities are unsaturated and dispersal limited, as several of the introduced montane species were able to colonize the mesocosms regardless of temperature or presence of alpine residents. However, the presence of alpine species did reduce colonization success by montane species. Warming suppressed alpine species, which may allow increased invasion by montane species. Increased dispersal had a greater influence on invasion than did warming (Chapter 3).

Comment on the use of the Local-Regional Richness Relationship

Published studies using the local-regional richness relationships suggest that linear relationships with a slope less than one are indicative of unsaturated, dispersal limited communities (Cornell 1985; Shurin et al. 2000; Gering and Crist 2002). This relationship is scale-dependent due to the species-area hypothesis (Srivastava 1999; Shurin et al. 2000). I found that the data used in my study were not scale-dependent, however there was a very strong influence of elevation as well as a minor influence of the number of lakes sampled. When I corrected the local-regional richness relationship for the influence of these factors, there was no relationship between local and regional richness.

The species richness of zooplankton communities in mountain lakes and ponds is strongly influenced by environmental heterogeneity as a result of an elevation gradient. The confounding influence of environmental heterogeneity obscured the interpretation of the local-regional richness relationship. The regional species pool included zooplankton species that are generalist species, alpine specialists and species endemic to specific areas of the Canadian Rocky Mountain parks. Though I was able to reduce the effects of environmental heterogeneity by analyzing alpine zooplankton communities separately, I found that the local-regional richness relationship was still confounded by the effects of widespread sportfish stocking. Thus, I concluded that the use of local-regional richness relationships, and alpha-beta partitioning, have limited ability to predict community saturation or dispersal limitation of mountain zooplankton, without investigating environmental heterogeneity and history of the region.

Future Research

My thesis research has left me with several unanswered questions. First, can montane species persist in alpine lakes following their initial colonization? My experiment suggests that alpine zooplankton communities are dispersal-limited since montane species were able to survive and reproduce at the 13°C control temperature. However, alpine lakes are characterized by many other extreme environmental variables, such as short ice-free seasons and high UV radiation (Anderson 1971; Sommaruga 2001). Alpine specialist species have photo-protective pigments, while montane species usually lack these pigments. Several daphnid species, including *Daphnia middendorffiana* produce cuticular melanin and several copepod species, such as *Hesperodiaptomus arcticus* have large carotenoid concentrations (Hessen and Sorensen 1990). A large-scale, long-term *in situ* experiment in an alpine lake would provide a stronger test of the ability of montane species to tolerate alpine conditions.

The second question that could be examined is whether alpine specialist zooplankton species can adapt physiologically to tolerate warmer water temperatures. Many large-bodied, cold-water zooplankton species can experience thermal stress in the form of reproductive failure and mortality when water temperatures exceed 15 – 18°C (Dadswell 1974; Moore et al. 1996). All of my mesocosms were set up at 13°C, then half of the mesocosms were moved to a 20°C growth chamber, where the invasion treatments were then applied. Thus, the 7°C increase in water temperature occurred very rapidly. I observed some egg production in both *D. middendorffiana* and *H. arcticus* at 20°C. As large increases in water temperature are expected over a period of several years or decades (Magnuson et al. 1997) future research could be done to determine if the eggs of alpine species can hatch at 20°C and if survival and reproductive success increase when warming occurs over several generations.

The third topic that could be addressed in future studies is to examine zooplankton dispersal in mountain regions, specifically the distance between sites required to detect dispersal limitation, or the frequency of dispersal events. Several studies have been performed in low relief systems, suggesting that zooplankton are only dispersal limited over large distances or short time-scales (e.g. Shurin 2000; Cáceres and Soluk 2002). The effect of dispersal barriers and low connectivity is not known, though it required several decades for *H. arcticus* to reappear in alpine lakes after the removal of stocked sportfish (Donald et al. 2001; Knapp et al. 2001).

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