

SCALING UP TO FOOD WEBS: EFFECTS OF TEMPERATURE ON  
STRUCTURE AND FUNCTION ALONG A LATITUDINAL GRADIENT

by

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DALHOUSIE UNIVERSITY

DEPARTMENT OF BIOLOGY

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## **ABSTRACT**

Global warming will affect every level of biological organization from the metabolism of individuals to the functioning of ecosystems. I explored the effects of warming on three rock-pool meioinvertebrate communities along a latitudinal gradient (temperate, tropical, and sub-Arctic regions) to determine effects on community and food-web structure and functioning. Warming affected regions differently, having a positive effect on sub-Arctic communities, a negative effect on temperate communities, and intermediate responses in tropical communities in terms of abundance, stability and extinction frequency. Differences in structural properties of the food webs supported the insurance hypothesis: that greater redundancy in webs results in greater stability, and helped to explain why the tropical community was more stable than the temperate community in warmed treatments. My study highlights the importance of considering differential response of species and communities from different latitudes and the importance of food web structure in predicting species response to global climate change.

## LIST OF ABBREVIATIONS USED

CV	Coefficient of variation
df	Degrees of freedom
SD	Standard deviation
GLM	General linear model
ANOVA	Analysis of variance
S	Species richness
L/S	Links per species
C	Connectance
%T	Fraction of top predators
%I	Fraction of intermediate predators
%B	Fraction of basal species
%H	Fraction of herbivores
GenSD	Standard deviation of generality
VulSD	Standard deviation of vulnerability
LinkSD	Standard deviation of mean links per species
Loop	Fraction of species in a feeding loop
SWTL	Short weighted mean trophic level
Omniv	Fraction of omnivorous species
MeanSim	Mean similarity
MaxSim	Maximum similarity
PredSim	Predator similarity
PreySim	Prey similarity
Cannibal	Fraction of cannibalism
CC	Mean clustering coefficient

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# CHAPTER 1     **Introduction**

## **1.1     General Introduction**

Current climate conditions and the potential consequences of the predicted global warming trends have inspired many studies to look at the impacts increasing temperature will have on ecological communities (McLaughlin *et al.* 2002; Callaghan *et al.* 2004b; Thomas *et al.* 2004; Perry *et al.* 2005; Abrahams *et al.* 2007; Parmesan 2007; Deutsch *et al.* 2008; Tewksbury *et al.* 2008; Woodward *et al.* 2010). However, despite the pressing importance of this issue, few studies to date have looked directly at the effects of temperature on entire food webs (Woodward *et al.* 2010). My research explores the role of temperature on food web structure at the individual species, population, community, and ecosystem levels in rock pool micro-ecosystems along a latitudinal gradient. The objective of my research is to determine how increases in temperature will alter patterns of energy flow in food webs and how these changes may differ among communities adapted to different thermal environments. I will begin this chapter by discussing expected abiotic changes in the environment due to global warming, and predicted responses of species and populations from the literature. Next, I will discuss the importance of scaling up climate change studies to the ecosystem and food web level, and what has been done in this area so far. Finally, I will describe the rock pool communities used as model systems, and outline each chapter of this thesis.

## **1.2     Climate Change**

### *1.2.1 Direct Effects*

The increase in carbon dioxide in the atmosphere has had several direct effects on the global climate. The most noticeable is the corresponding increase in mean temperature. Barnola *et al.* (1987) used gases trapped in air bubbles in ice core samples from Antarctica to obtain estimates of historical levels of carbon dioxide in the atmosphere and found that there was a strong positive correlation of CO<sub>2</sub> concentration with the Earth's temperature. To date, global mean temperature has increased by 0.6 °C

since 1960. If the current trend in carbon dioxide concentration increase continues, there is predicted to be a minimum global warming of 1.1 - 6.4 °C by the year 2100, using a conservative prediction model for climate change (IPCC 2007). This warming will not be distributed evenly around the Earth; at the equator much of the radiation is absorbed by water and an increase at the lower end of the spectrum is expected (2 °C) whereas at temperate latitudes the mean temperature could increase up to 10 °C (Harrington 1987).

### *1.2.2 Effects on Biota*

As a result of both the direct and indirect effects of increasing greenhouse gas concentration in the atmosphere, patterns and behaviour at all levels of biological organization are expected to change. Changes in species distributions (Parmesan *et al.* 1999; Callaghan *et al.* 2004a; Perry *et al.* 2005), local population extinctions (Parmesan *et al.* 1999; McLaughlin *et al.* 2002), migration patterns (Schweiger *et al.* 2008; van der Putten *et al.* 2010), the seasonal timing of biological events (Parmesan 2007; Hoppe *et al.* 2008) and community food web structure (Beisner *et al.* 1997; Harmon *et al.* 2009) are widely accepted as a consequence of increases in global temperature (Pörtner & Farrell 2008).

Species are predicted to move to higher latitudes, or higher altitudes, to remain in their optimal temperature range (Peters & Darling 1985). Many species which may have been able to tolerate slow changes in global climate will not be able to migrate or adapt quickly enough to survive these present changes (Bell & Collins 2008). In addition, physical barriers such as mountains or inhospitable land may prevent species from migrating to a new habitat with an acceptable climate range (Peters & Darling 1985). Species in a community respond differently to climate change. Motile species are able to move poleward, for example, while sessile or slower moving species may not be able to expand or change their range distributions. The consequences of these different responses include local extinction and changes in species interactions within communities (Callaghan *et al.* 2004a). A study covering 20% of the Earth's land surface and looking at extinction risk for both plants and animals under different predictions of future climate change found that up to 37% of species in their sample region would be committed to extinction in a maximum climate change scenario (Thomas *et al.* 2004). This study used a range of species with different mobility in the model, from completely sessile to having

no limits to dispersal, with the prediction that most species fall somewhere in the middle of this range.

### *1.2.3 Changes in Species Interactions*

Changes in temperature have also been found to change species interactions, from predation (Petchey *et al.* 1999), to parasitism (Pounds *et al.* 1999), to competitive interactions (Peters & Darling 1985). For example, Petchey *et al.* (1999) found that increasing temperature disproportionately decreased the number of top predators and herbivores in a community, and increased primary producers and bacterivores, thus changing the community structure from a top-down system controlled by predation, to a bottom-up system limited mainly by the amount of resources present in the community. Yachi & Loreau (1999) used the insurance hypothesis to support their prediction that greater biodiversity should allow a community to become more stable, even in the face of global climate change. With increased species richness there is a greater chance that two species will have similar roles in the community, therefore if one goes extinct due to climate change, there is still another species that fulfills a similar role, so the loss may not be felt as strongly by the community as a whole. The laboratory study by Petchey *et al.* (1999) supported these predictions as more diverse communities retained more species with increasing temperature, suggesting that high biodiversity buffered against the effects of environmental variation because more tolerant species were more likely to persist.

## **1.3 Scaling up to Food Webs**

The majority of previous research that has attempted to determine the effects of increasing temperature on ecological systems has focused on changes in species, population, and community properties. For example Thomas *et al.* (2004) used the concept of a species' 'climate envelope' to predict future extinctions due to global climate change. The climate envelope represents the current environmental conditions a species exists in. This is used to predict how a species will respond, assuming that their climate envelope will not change over time, so a species must migrate to stay within their envelope in the face of global climate change or else they will be unable to persist. The climate envelope approach is only able to make predictions by looking at each individual

species' distributions separately, but Parmesan *et al.* (1999) point out that changes in distribution do not necessarily occur from an individual species' changes in movement patterns but from changes in the ratios of extinctions to colonisations at the boundaries of a population's range.

A population is a group of organisms of the same species inhabiting a given area. A shift in any given populations' range northward may either be due to movement of all individuals northward, or a result of extinction of individual species at the southernmost boundaries and colonisation of species at the northern end of the range (Parmesan *et al.* 1999). However, predictions of changes in distribution based on the species and population level are still inaccurate, because a population's distribution is not only based on their optimal 'climate envelope', but also on their interactions with competitors, predators, and prey (Davis *et al.* 1998). Therefore, consequences of climate change on interactions at the community level should also be considered.

A community is an assemblage of populations of different species interacting with one another. Climate change has been found to alter interactions at the community level (Sanford 1999) so any accurate predictions of changes in species distribution must take interactions between populations into account. One such study by Davies *et al.* (1998) compared the climate envelope of a population of *Drosophila* species in isolation, versus in a habitat with other *Drosophila* species in both cold and warmed environments, and found that competitive interactions significantly changed the distribution and abundance of all species (Davis *et al.* 1998). Changes in competitive interactions are thus important to take into account as changes in distribution and abundance will alter community composition and consequently the food web structure at the regional level (Davis *et al.* 1998; Pounds *et al.* 1999). More accurate predictions can be made by expanding the resolution of the study. The next critical step is to scale-up to an understanding of how increasing temperature might influence the structure and functioning of entire food webs.

Food webs, networks of predator-prey interactions, are a fundamental way of viewing the structure of ecological communities. Since the 1970's, researchers have attempted to characterize generalities in food web networks' structure in order to find underlying 'laws' governing community assembly (Dunne 2005). Connectance ( $C=L/S^2$ ) can be calculated as the number of realized links in the web divided by the total number

of possible links, including cannibalism and looping. Once diversity (species richness) and complexity (connectance) are accounted for, other properties such as the fraction of omnivores, cannibals, and links per species generally have similar values regardless of the size of the web, or the habitat it describes (Dunne *et al.* 2004). The widespread patterns observed in these properties suggests that there are fundamental characteristics in how food webs may be structured in nature. Therefore, by understanding the way in which these properties change with changes in the environment we can begin to understand how the structure of the community is being altered, and subsequently make more effective conservation plans in the face of global warming.

Several studies have used food web theory to make predictions about effects of warming at the ecosystem scale. Warming has been predicted to result in extinction of top predators (Petchey *et al.* 1999; Voigt *et al.* 2003) and subsequent shortening of food chain length (Arim *et al.* 2007; Woodward *et al.* 2010), as well as changes in predator-prey interactions (Walther *et al.* 2002; Calliari *et al.* 2003; van der Putten *et al.* 2004; Beveridge *et al.* 2010; Sarmiento *et al.* 2010) which can have cascading effects throughout the food web (Winder & Schindler 2004; Wohlers *et al.* 2009). However, the vast majority of research on food web change with temperature increase has focused on the effects of species extinction on population and community variability (Raffaelli 2004; O'Connor *et al.* 2009). The next step is to look at how other food web structural properties change with temperature, such as connectance, trophic position and generality/vulnerability, because different properties give us different insights into the structure and function of the communities (Table 3.1).

## **1.4 Rock Pools as Model Systems**

The model systems I use are the communities that inhabit supralittoral rain-fed rock pools. Rock pools are typically small in size, ranging from 250 mL to 500 L, and hundreds can often be found within a few kilometres of coastline. Rock pool communities contain algae, microbes, and small micro-crustacean invertebrates (60µm-5mm). Rock pool communities are ideal systems to study because their small size and contained structure is easily replicated in the lab (Romanuk & Kolasa 2002; Romanuk *et*



*al.* 2010), and they are found on rocky shores around the world, so similar communities adapted to different climates can be used to separate intrinsic from extrinsic responses to the temperature treatments.

Three communities were obtained along a latitudinal gradient: from a tropical region, Jamaica (18°28'N, 77°25'W), a temperate region, Nova Scotia (44°28'N, 63°47'W), and a sub-Arctic region, Churchill, Manitoba (58°46'N, 94°11'W). Regional species richness in the three communities varies, with the regional richness in Jamaica spanning from ~3 to ~70 species, to ~ 1 to 10 species communities from the arctic (T. Romanuk, *pers. comm*). Species richness within individual rock pools is similar for all three regions, varying from 1-10 (Romanuk & Kolasa 2002; Romanuk *et al* 2010). The identity of the species from these different latitudes also differs, however the community composition is very similar, with similar functional and phylogenetic groups (copepods, ostracods, daphnids, chydorids). Key differences between the regions lies in the daily and annual range of temperatures they experience. The sub-Arctic region experiences a daily range of up to 10.2 °C, and a yearly difference between the coldest and warmest month of 39.5 °C (Danks 1999). The tropical region on the other hand has only a 10 °C difference between the coldest and warmest month, and a daily range of 2.5 °C (Anonymous 2009).

## **1.5 Thesis Outline**

The first question I addressed (Chapter 2) is the effect of increasing temperature on population and community dynamics, focusing on the differences between regions. Using the mean annual summer temperature from each region as a baseline, and the worst case scenario predictions of IPCC for the warmed treatments (IPCC 2007), I looked at relative change in abundance, extinction frequency, and stability at both the community and functional group levels. Implications of cold adaptation and the use of metabolic theory to predict response of different regions to warming are discussed.

Chapter 3 uses data from the temperature increase experiment discussed in Chapter 2, but analyzes the results from an ecosystem and food web perspective. Through feeding

trials, visual observations and primary literature, I constructed food webs for the tropical, temperate, and sub-Arctic regions. I looked at changes in food web structural properties, as well as changes in abundance of basal species/resources, ecosystem productivity and respiration rates, and mean community body size. I then explored whether predictions based on single trophic level communities can be scaled up to complete ecosystems, and whether there were any predictable responses along a latitudinal gradient that could indicate intrinsic responses to warming.

Finally, I conclude with a discussion synthesizing the main results from each chapter in the context of the main goals of my research, which were to track changes at multiple levels of biological organization to determine how effects of warming scale up through a system, and to see how communities adapted to different climates respond differently to warming.

## **CHAPTER 2     Robustness of Ecological Communities to Environmental Warming along a Latitudinal Gradient**

### **2.1     Abstract**

Species extinctions have been predicted to be one of the main consequences of environmental warming. The robustness of ecological communities to warming induced extinction has been predicted to differ based on latitude. Physiological adaptations of polar organisms may increase the metabolic consequences of warming for polar organisms relative to those from temperate and tropical regions. Here I show that sub-Arctic meiofaunal communities are more robust to experimentally induced environmental warming than similar temperate or tropical meiofaunal communities. Warming led to non-linear biotic responses along the latitudinal gradient, with temperate populations becoming less stable and losing more species than tropical or sub-Arctic communities. My results provide the first empirical evidence that environmental warming may lead to non-linearities in the biotic responses of communities along latitudinal gradients. My results also suggest that the main consequences of warming may be different in temperate and tropical communities with temperate communities losing more species with warming than tropical communities and tropical communities experiencing greater changes in productivity than temperate communities.

### **2.2     Introduction**

Investigating the impact of climate change on entire ecosystems is becoming increasingly important. The average temperature of the Earth has increased by 0.6°C since the 1960s and by 2100 the average temperature of the Earth is expected to have increased by 1.1 to 6.4°C (IPCC 2007). It has been predicted that climate change, independent of other stressors, will result in the premature extinction of between 15% and 37% of extant species in the next 50 years (Thomas *et al.* 2004). Warming induced species extinctions can occur both directly, by raising environmental temperature above physiological tolerance limits (Pörtner 2002), as well as by increasing metabolism (Seibel & Drazen 2007), leading to rapid population growth, resource depletion and population crashes (McLaughlin *et al.* 2002), as well as indirectly by changing species phenologies (Winder & Schindler 2004; Hays *et al.* 2005; Parmesan 2007), ranges (Perry *et al.* 2005; Parmesan 2006; Schweiger *et al.* 2008), and interactions (Callaghan *et al.* 2004b; Suttle

*et al.* 2007; Harmon *et al.* 2009; Walther 2010). The possibility that the magnitude of species extinctions will differ along latitudinal gradients due to physiological adaptations to different thermal regimes has also been predicted (Strathdee & Bale 1998; Callaghan *et al.* 2004a). Because cold-adapted species have higher metabolic rates relative to species from lower latitudes (Clarke 2003; Pörtner *et al.* 2005), sub-Arctic communities may be less robust to warming induced extinction than communities at lower latitudes (Blackburn & Gaston 1999). I experimentally manipulated temperature of aquatic rock pool communities from different latitudes to answer this question. Rock pool communities are ideal to study complex effects such as those due to climate change because they are comprised of a manageable set of species with known feeding interactions, and conditions in their natural environment can be easily simulated in the lab (Romanuk & Kolasa 2002).

## **2.3 Methods**

### *2.3.1 Sample Collection*

I used aquatic meiofaunal communities collected from supralittoral rock pools located along Eastern North America on a latitudinal gradient from a sub-Arctic habitat, a temperate habitat and a tropical habitat. Supralittoral rock pool communities are a common habitat type located on rocky shores around the world. The pools form by either dissolution of limestone or in granite depressions and are above the high-tide line and therefore primarily rain-fed. Despite wide geographical separation, the biotic composition of rock pool communities is highly constrained due to the relatively extreme environmental conditions the communities are subjected to, which include frequent desiccation events and wide variations in salinity.

Sub-Arctic species were collected from granite rock pools located near the Churchill Northern Research Station (58°46'N, 94°11'W), temperate species were collected from granite rock pools located in either Prospect Point or Herring Cove, Nova Scotia (44°28'N, 63°47'W), and tropical species were collected from limestone rock pools located near the Discovery Bay Marine Laboratory on the North Coast of Jamaica (18°28'N, 77°25'W). Communities from Churchill and Nova Scotia were collected in

the summer 2009 (July-August). Communities from Jamaica were collected in May 2009. Communities were maintained in the lab for different lengths of time before being used in the experiment.

Rock pool meiofauna differ strongly in functional traits related to feeding (Romanuk *et al.* 2010). Rock pool species were classified into functional groups based on their trophic role as herbivores, detritivores, omnivores, or predators based on pair-wise feeding trials. Three individuals of each species were placed in a small (20 mL) container with three individuals of another species. Ten replicates were conducted for each feeding trial and all species were crossed with all other species including itself (temperate n=7 spp., tropical n=7 spp., sub-Arctic n= 6 spp.). All trials were performed at 24°C with a 12 hour light/dark cycle. The feeding trials were checked regularly until all individuals of one species were missing or dead (~5 days). If the average of all 10 replicates had at least one individual less of one species than the other this suggested a consumer-resource link between the species. If the average number of both species was the same, it suggested they feed upon basal resources. In the case where the species was crossed with itself it was considered cannibalism if the average of all ten replicates had one less individual from the initial number (n=6).

For the species used in the experiment, the functional groups correspond to the following taxonomic classifications: herbivores (Daphniidae (*Daphnia magna*, *Daphnia ambigua*, and *Ceriodaphnia lacustris*) and Ostracoda (*Cypridinae Eucypris sp.*, and *Cypridopsis cf. mariae Rome*)), detritivores (Chydoridae (primarily *Alona* and *Alonella* spp.)), omnivores (Ostracoda (*Cypridinae Megalocypris sp.*, *Candona sp.*, *Cypricercus sp.*, *Potamocypris sp.*)), and predators (Cyclopoid copepods (*Microcyclops Varicans*, *Paracyclops sp.*). Rock pool communities from all three regions contained representative species from each of these functional groups. Initial species richness averaged 7 ( $\pm$  0.49 SD) species for the tropical communities, 6.5 ( $\pm$  0.51 SD) species for the temperate communities, and 5.5 ( $\pm$  0.62 SD) species for the sub-Arctic communities.

### 2.3.2 Experimental Design

The zooplankton and meiofaunal communities were exposed to either a control temperature (adjusted to the seasonal average of mean temperature for the region) or a 4°C or 8°C temperature increase (sub-Arctic control =5°C, +4°C=9°C, +8°C=13°C;

temperate control= 20°C, +4°C=24°C, +8°C=28°C; tropical control=24°C, +4°C=28°C, +8°C= 32°C). For each of the three temperature treatments I used six 1.5 L replicates housed in plastic (16x12x9 cm) aquaria. In total 18 microcosms were assembled for each region (total n=54). Microcosms were maintained in water baths (for temperate and tropical communities) or in cold chambers (sub-Arctic communities) with 12 hours of full spectrum light and 12 hours of dark and were sampled weekly for eight weeks following a two week acclimation period. Each week the number of individuals of each species was determined by counts under a dissecting microscope from a 50 mL sample, taken after gently stirring the microcosm to homogenize the contents. All individuals in the sample were measured to determine body size using a Zeiss Axiovert 200 M microscope with an AxioCam HRC camera. Biovolume was estimated using these measurements and the equation for a cone for copepods, ellipsoid for daphnids, and irregular shape for chydorids and ostracods (Wetzel & Likens 1991; Hayward *et al.* 2009).

Detrital biomass was assessed by filtering the entire remaining contents of each microcosm through a 63µm mesh sieve. The detritus was then dried in a drying oven at 60°C for 48 hours and weighed.

After the final density count (week 8), dissolved oxygen was measured using a Data Sonde (YSI 650 Multiparameter Display System) to determine productivity and respiration using the light/dark bottle method (Gaarder & Gran 1927). Water from each microcosm was sealed in an airtight, 250 mL mason jar and placed back in its appropriate heating bath. Half of the replicates from each treatment were completely covered in tin foil to block out light to determine respiration and half were left uncovered to determine productivity. After 24 hours, a second oxygen reading was taken for the water inside the jars. Respiration was calculated as the difference between final and initial oxygen readings in the dark jars. Gross productivity was calculated as the difference between final oxygen readings in the dark minus light jars, and net productivity was calculated as the difference between gross productivity and respiration.

### 2.3.3 Data Analysis

To determine the relative effect of warming I normalized the biotic responses in the warmed treatments to the controls (variable control-variable treatment). This normalization allowed me to assess the extent to which the warmed treatments differed

from the controls over time as well as to determine whether the response represented a positive or a negative deviation from the control. Relative changes in robustness, productivity, and stability were then assessed across the three regions. To determine whether environmental warming and latitude affected robustness to species loss I calculated the relative change in extinction frequency (maximum no. spp - final no. spp)/maximum no. spp). Effects of environmental warming on productivity were assessed using abundance counts averaged over eight weeks. Differences in stability of warmed communities relative to controls were assessed using coefficient of variation (CV= standard deviation in abundance/mean abundance). CV was calculated for the community as a whole, as well as for mean abundances across functional groups for functional group variability (Romanuk *et al.* 2010). CV was used as it standardizes for differences in mean abundance so variability of abundances can be compared across communities and populations. Mean abundance was similar for all three regions (n= 1-20 individuals) therefore the CVs were not overly confounded by large differences in abundance. All analyses were conducted for total community properties as well as for the four functional groups defined according to their trophic role: herbivores, detritivores, omnivores, and predators, and assessed for significance using factorial analysis of variance (ANOVA) with a significance value of  $\alpha=0.05$  using Statistica (version 7.0, Statsoft 2004). Data were tested for normality using Shapiro-Wilk's test and homogeneity of variance using Levene's test.

## 2.4 Results

Warming increased extinction frequency in the temperate and tropical communities and decreased extinction frequency in the sub-Arctic communities (Fig. 2.1a). The greatest difference in extinction frequency relative to the controls was observed in the temperate communities followed by the tropical communities ( $F_{2,30}=39.14$ ,  $p<0.001$ ; Fig. 2.1a). Relative extinction frequency for the temperate and tropical communities was higher at +8°C than at +4°C ( $F_{1,30}=9.37$ ,  $p=0.005$ ; Fig. 2.1a). Sub-Arctic communities were highly robust to warming, retaining 25% more species at both +4°C and +8°C than in the controls (Appendix Table A.1).

Regional differences in relative extinction frequency occurred for all four functional groups (Fig. 2.2a-d). In the temperate communities, relative extinction frequency for all four functional groups increased as the magnitude of warming increased. In the tropical communities, a +4°C increase only increased extinction frequency for omnivores. In contrast, at +8°C extinction frequency for all four functional groups was higher than controls. In the sub-Arctic communities, extinction frequency was highest in the low temperature treatment for all four functional groups, suggesting that increasing temperature buffered functional groups in the sub-Arctic from losing species. This buffering effect of warming was particularly strong for detritivores, which lost 50% and 42% fewer species at +4°C and +8°C, and for predators, which lost 50% fewer species at +8°C (Appendix Table A.2).

Warming led to no change in community abundance in the sub-Arctic and decreases in community abundance in the temperate and tropical communities (Fig. 2.1b; Appendix Table A.3). Within the sub-Arctic communities, the abundance of detritivores and predators significantly increased with warming (Fig. 2.3a-d). Warming had no effect on the abundance of herbivores or omnivores in the sub-Arctic. The magnitude of warming only affected predator abundance in the sub-Arctic communities, which was greatest at +8°C. In contrast, abundances of all four functional groups either decreased or were unaffected by warming in the temperate and tropical communities. Herbivores showed similar responses to warming in the temperate and tropical communities, with abundance of herbivores decreasing with warming and the magnitude of warming in the tropical and temperate communities. For detritivores communities from different regions responded differently. In the tropical communities detritivores were unaffected by warming whereas in the temperate communities abundance of detritivores decreased at +8°C. In the temperate and tropical communities the abundance of omnivores declined with warming. Abundance of predators decreased with warming in the temperate communities at +8°C and in the tropical communities in both warming treatments (Appendix Table A.4).

The effects of warming on community and functional group stability differed along the latitudinal gradient (Fig. 2.4a-b). In the sub-Arctic communities the magnitude of warming did not have a statistically significant effect on either community or



functional group stability. In contrast, community stability in the temperate and tropical communities declined significantly with warming ( $F_{1,30}=4.36$ ,  $p=0.045$ ; Fig. 2.4a; Appendix Table A.5). In the tropical communities functional group stability was unaffected by warming, but temperate functional groups became destabilized with warming ( $F_{1,10}=12.5$ ,  $p=0.005$ ; Fig. 2.4b; Appendix Table A.6).

Detritus weight did not vary with temperature in the temperate region, increased with temperature in the tropical region ( $p=0.036$ ) and was significantly lower in the +8°C treatment than in the control in the sub-Arctic region ( $p=0.003$ ; Fig. 2.5a-b; Appendix Table A.7).

Mean biovolume of the community differed significantly across regions ( $p<0.001$ ), with temperate communities having a larger overall biovolume than communities from the tropical or sub-Arctic regions. In the tropical community, biovolume increased with increasing temperature ( $p=0.002$ ). In the temperate community there was a trend towards a decrease in biovolume with increasing temperature but the difference was not statistically significant ( $p=0.33$ ). There was no difference in biovolume between temperature treatments in the sub-Arctic community (Fig. 2.6; Appendix Table A.8). Across all functional groups there was a statistically significant difference in biovolume across both weeks and temperature treatments ( $p<0.001$ ). Herbivores had the largest biovolume in the temperate region, omnivores in the sub-Arctic and predators in the tropical region. Herbivores from the temperate region had the largest body size overall (Fig. 2.7). There was also a statistically significant difference between regions ( $p<0.001$ ; Appendix Table A.9).

There was a statistically significant difference in respiration across regions, with the tropical community having the highest rate and sub-Arctic having the lowest respiration rate ( $p<0.001$ ). The temperate region was the only one to experience a statistically significant change in respiration, with respiration decreasing with increasing temperature ( $p=0.013$ ; Fig. 2.8a; Appendix Table A.10).

There was a statistically significant difference in net productivity across regions ( $p<0.001$ ) with the tropical having the highest productivity and the sub-Arctic the lowest productivity. Increasing temperature only affected productivity in the temperate region,

with a decrease in productivity as temperature increased ( $p=0.029$ ; Fig. 2.8b; Appendix Table A.11).

## 2.5 Discussion

When making predictions in regards to the effects of climate change many factors must be taken into account. Effects can be observed as a result of changes occurring at the individual level, such as development and metabolism (Beisner *et al.* 1997; Gillooly *et al.* 2006), as well as indirect effects on the community as a whole, such as changes in competitive interactions, food availability, parasites, and invasive species (Callaghan *et al.* 2004b).

### 2.5.1 Stability Across Latitudes

My results present some intriguing trends in terms of the implications for global warming on whole ecosystems across latitudes. Sub-Arctic communities were more robust to warming than either temperate or tropical communities, having a lower extinction frequency in warmed treatments than in the control (Fig. 2.1a), higher abundance (Fig. 2.1b) and higher stability at both the functional group and community levels (Fig. 2.4). Contrary to initial predictions that temperate communities would prove to be more stable with increasing temperatures due to the higher level of fluctuations found in temperate environments (Newell 1969), extinction rate was significantly higher and stability significantly decreased with increasing magnitude of warming. Tropical communities showed intermediate results with extinction frequency, with abundance and stability mainly being affected only in the highest temperature treatment. It has been suggested that changes due to increased temperature seen across latitudes include significant population fluctuations, likely due to an increased growth rate due to increased metabolism (Halbach 1970). Greater fluctuations in population abundance lead to destabilized dynamics, because with larger amplitude fluctuations the population has a higher probability of decreasing closer to zero, increasing the risk of extinction due to demographic or environmental stochasticity (Lawton 1985).

### 2.5.2 *Effects of Increased Metabolic Rate*

The predictions of metabolic theory, that increases in temperature will lead to lower population densities resulting from increases in the rates of resource consumption at finite resource levels (Brown *et al.* 2004) and higher probabilities of extinction risk due to stochastic and demographic fluctuations in density when density is low (Blackburn & Gaston 1999) were not well supported for the sub-Arctic communities. Sub-Arctic communities achieved higher population abundances in the warmed treatments and were more robust to extinction than controls. For tropical and temperate communities my results generally matched those predicted by metabolic theory, although stability of functional groups in the tropical communities was not affected by warming. Non-linear responses along a latitudinal gradient to increasing temperature have previously been observed, for example increased abundance and species richness in the sub-Arctic, and decreased abundance and species richness in tropical communities (Walther *et al.* 2002; Callaghan *et al.* 2004a). Previous studies have found that the slope of the metabolic rate-temperature relationship becomes steeper as latitude increases (Irlich *et al.* 2009). This may explain why the temperate region was more vulnerable than the tropical region in terms of extinction frequency as well showing decreased community and functional group stability as temperature increased (Figs. 2.1a; 2.4a,b). The results from the sub-Arctic region do not follow this trend however, as these communities were much more robust in all above mentioned variables than either the tropical or temperate regions.

### 2.5.3 *Factors Affecting Response of Tropical Region*

Tropical communities may have been more sensitive to warming than initially predicted because tropical species are already living close to their thermal optimum, whereas sub-Arctic species are living below their optimum, therefore tropical species may be vulnerable to even small increases in temperature while sub-Arctic species may benefit (Somero 2005; Deutsch *et al.* 2008; Tewksbury *et al.* 2008). Species living in more constant environments, such as tropical regions, also have fewer behavioural or physiological traits that might provide relief from rising temperatures than species living in regions with seasonality that are adapted to surviving periods of thermal sub-optimal temperatures (Tewksbury *et al.* 2008). In addition, species living in constant environments may have lost the capacity for temperature-mediated shifts in gene

expression which may be critical to acclimatize to increases in temperature (Somero 2005).

#### *2.5.4 Factors Affecting Response of Sub-Arctic Region*

Sub-Arctic communities may have been the most stable with increasing temperature due to several adaptations occurring at the species level. Sub-Arctic species are more commonly generalists in terms of habitat selection and also have a higher metabolism than a warm adapted species at the same temperature, known as ‘cold adaptation’ (Fox 1936; Addo-Bediako *et al.* 2002). Cold adaptation allows for a faster generation time and therefore faster response to increasing temperature. The greater robustness of sub-Arctic communities compared to temperate or tropical communities is likely due in part to the higher metabolism of cold-adapted species at any given temperature. This physiological adaptation has been shown to operate even within sub-Arctic regions, with species from colder sites showing stronger responses to temperature increase than species from warmer sites (Hodkinson *et al.* 1998). Additional mechanisms, such as decreases in nutrient and enzyme concentrations (Clarke 2003; Wernberg *et al.* 2010), may be operating in sub-Arctic communities to regulate increases in the respiration rate with increases in temperature. In this way metabolism does not increase with temperature to the extent that sub-Arctic organisms need more energy than they are able to obtain.

Sub-Arctic species are also exposed to a much wider range in climatic variability annually than tropical species. Churchill, Manitoba experiences a daily fluctuation in temperature of up to 10.2 °C, and a yearly difference between the coldest and warmest month of 39.5 °C (Danks 1999). This variability may select for a larger environmental tolerance in sub-Arctic species, which is known as the climatic variability hypothesis (Stevens 1989; Addo-Bediako *et al.* 2000; Woodward *et al.* 2010).

#### *2.5.5 Factors Affecting Response of Functional Groups*

Effects of warming were also observed by comparing changes at the functional group level. Many studies have predicted a negative effect of warming on top predator species (Blackburn & Gaston 1999; Abrahams *et al.* 2007) due to the fact that top predators often have the largest body sizes of the communities, and therefore require

more energy (Voigt *et al.* 2003). As metabolism increases with increasing temperature, this increasing demand for energy often cannot be met (Pörtner & Farrell 2008). This prediction has been observed in a study by Petchey and colleagues (1999) who found a decrease in top predators and herbivores with increasing temperature, while detritivore and phytoplankton abundance increased. My results did not show a particularly negative effect on predators; extinction frequency decreased with increasing temperature in the sub-Arctic and in the +4 °C treatment in the tropics. Detritivores however did increase in abundance with increasing temperature in the sub-Arctic, and remained stable at both treatments in the tropics and the +4 °C treatment in temperate communities. This is likely due to the fact that the microbial food web that breaks down organic matter has a high tolerance for increased temperature and is predicted to have a higher abundance and increased metabolism in higher temperatures (Wrona *et al.* 2006). This breakdown of organic matter would also release more nutrients available for phytoplankton photosynthesis, thereby increasing community productivity (Flanagan *et al.* 2003). The pattern I observed for herbivores also matched Petchey's results, as extinction rate increased and abundance decreased with warming in both the temperate and tropical regions (Petchey *et al.* 1999). Omnivores were not significantly affected by magnitude of warming statistically; however they did have a higher extinction rate and lower abundance in the warmed treatments than in the control in the temperate and tropical regions.

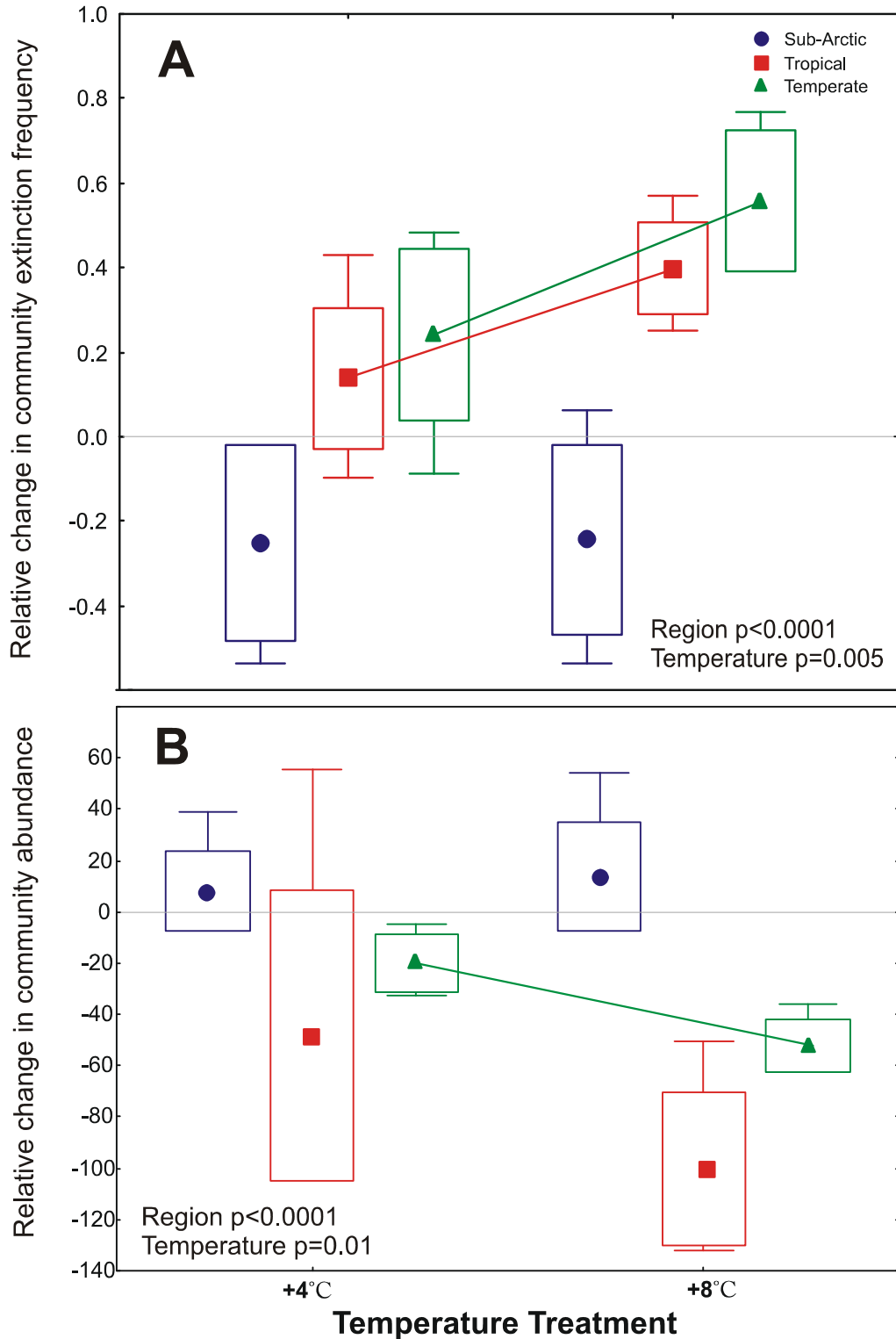
Several possibilities exist for the vulnerability of herbivores and relative robustness of detritivores including availability of resources and vulnerability of larger-bodied individuals. Detrital biomass increased with temperature in the tropical region (Fig. 2.5b), which may explain why abundance of detritivores did not decrease with temperature in the warmed treatments in the tropical region as it did in the temperate region. Resources for the herbivores however appeared to decrease, as net primary productivity decreased significantly with temperature in the temperate region (Fig. 2.8b), corresponding with the increased extinction frequency of herbivores with warming in the temperate region. Body size affects vulnerability to temperature increase as well, because larger organisms require more resources to sustain their increased metabolism (Gillooly *et al.* 2001). Community biovolume in microcosms from the temperate region

was significantly greater than community biovolume from tropical or temperate regions in the control and +4°C treatments (Fig. 2.6). Herbivores had the largest biovolume in the temperate region (Fig. 2.7), thus the temperate region and specifically temperate herbivores may have been more vulnerable to warming because they were not able to obtain enough resources to support their larger body size.

In summary, my results suggest that regions respond differently to warming along a latitudinal gradient, and the factors influencing this response are different for each region. The sub-Arctic communities were most robust due to cold adaptation and adaptation to climatic variability. Tropical communities were more vulnerable possibly due to the fact that they are already living at their optimal thermal tolerance level, and thus are more sensitive to even small increases in temperature. Finally, the high vulnerability of temperate regions to warming appears to have been due to decreases in available resources rather than a physiological intolerance of the temperature increase, as productivity significantly decreased with warming and larger-bodied functional groups, which require the most energy to support themselves, were lost disproportionately (Clarke & Fraser 2004). This latter pattern has been observed previously where stability and abundance decreased with increasing temperature even in the absence of predators (Pratt 1943; Wrona *et al.* 2006) or in the absence of competitors from the same functional group (Beisner *et al.* 1997). Instead the main factors causing the observed changes were thought to be limitations in either food resources (Beisner *et al.* 1997) or oxygen (Pratt 1943), due to heightened demands from an increased metabolism, which particularly affected individuals of larger body size (Petchey *et al.* 1999).

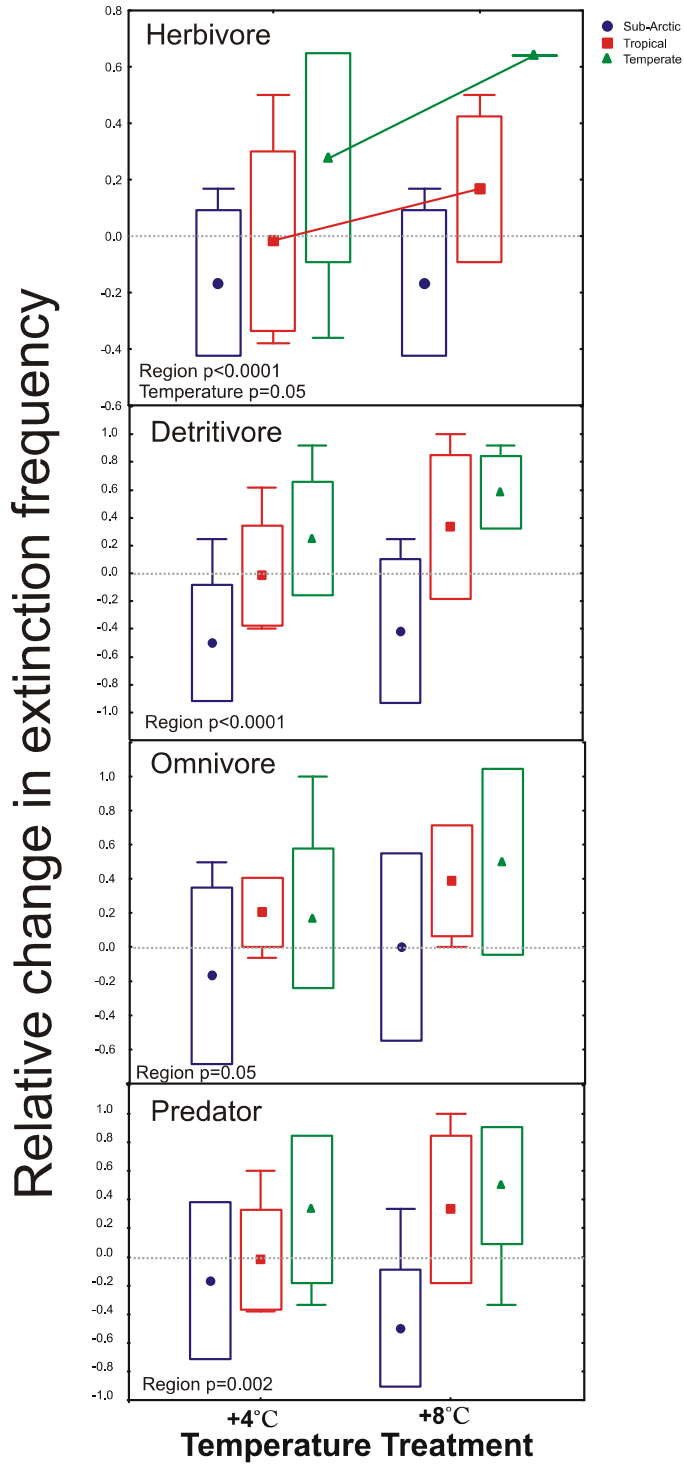
In conclusion, my results suggest that the potential for cascading effects of increased environmental temperature may be strongest in temperate regions. While my results are limited to poikilotherms such as zooplankton with small body sizes and small predator-prey ratios these results have potentially wide-reaching consequences as zooplankton are globally distributed and are a critical lower trophic level in aquatic systems. From a management perspective, the non-linearity of responses I observed across the latitudinal gradient caution against simply trying to extrapolate information

about the effects of environmental warming on populations and communities based simply on metabolic theory.

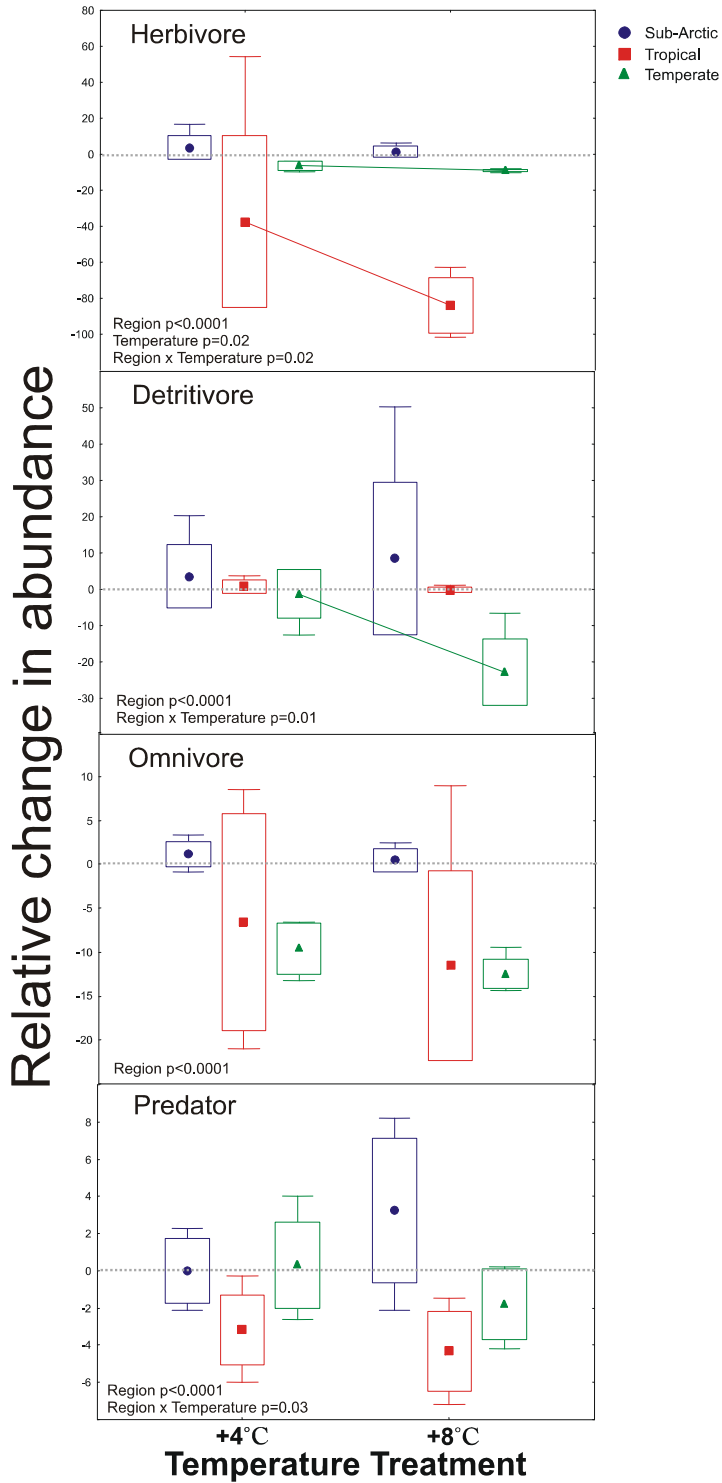


**Figure 2.1.** Relative change in **a)** extinction frequency and **b)** summed community abundance adjusted to control (grey line). Middle point shows mean, box shows standard deviation and whiskers show minimum and maximum values. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.

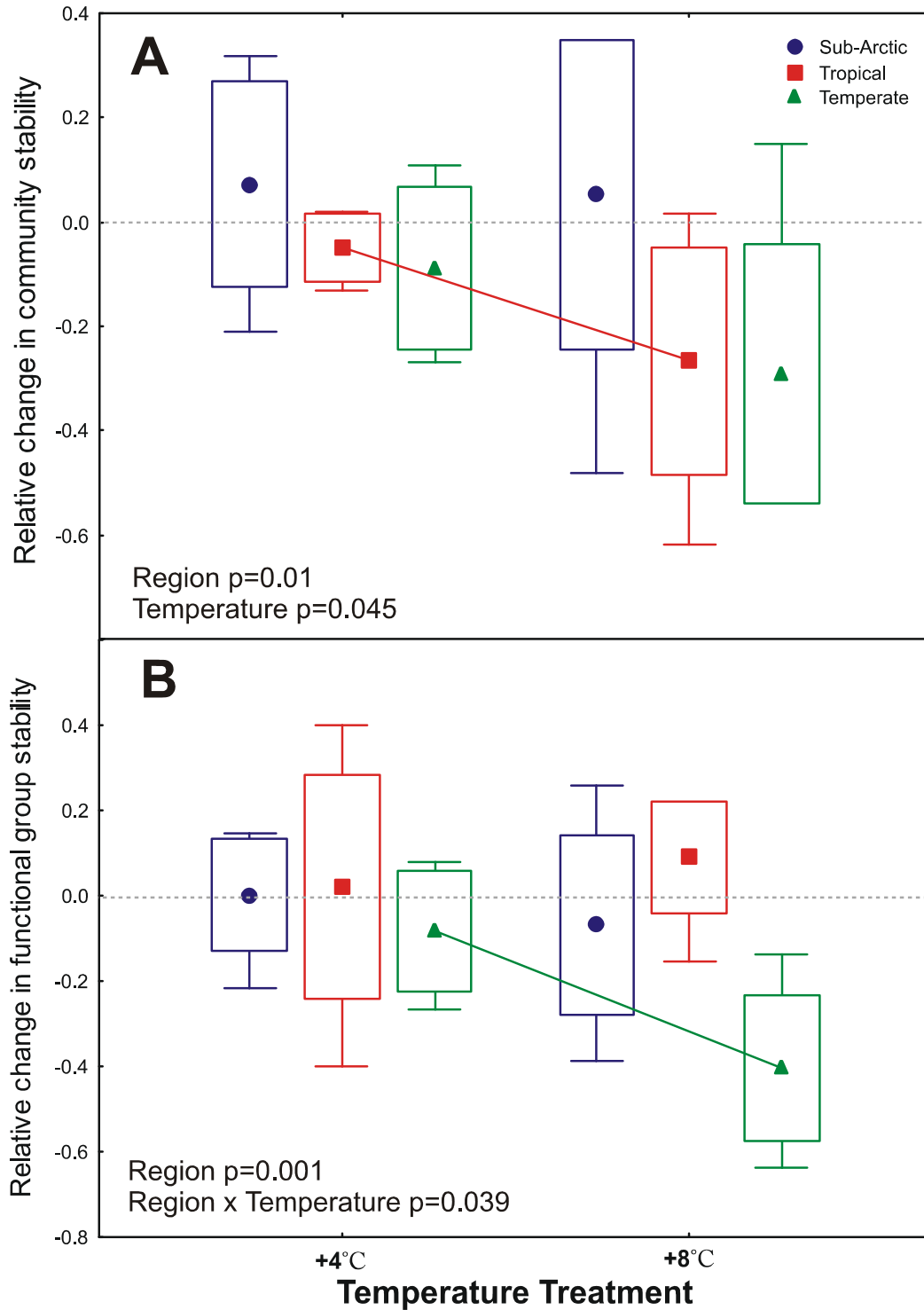




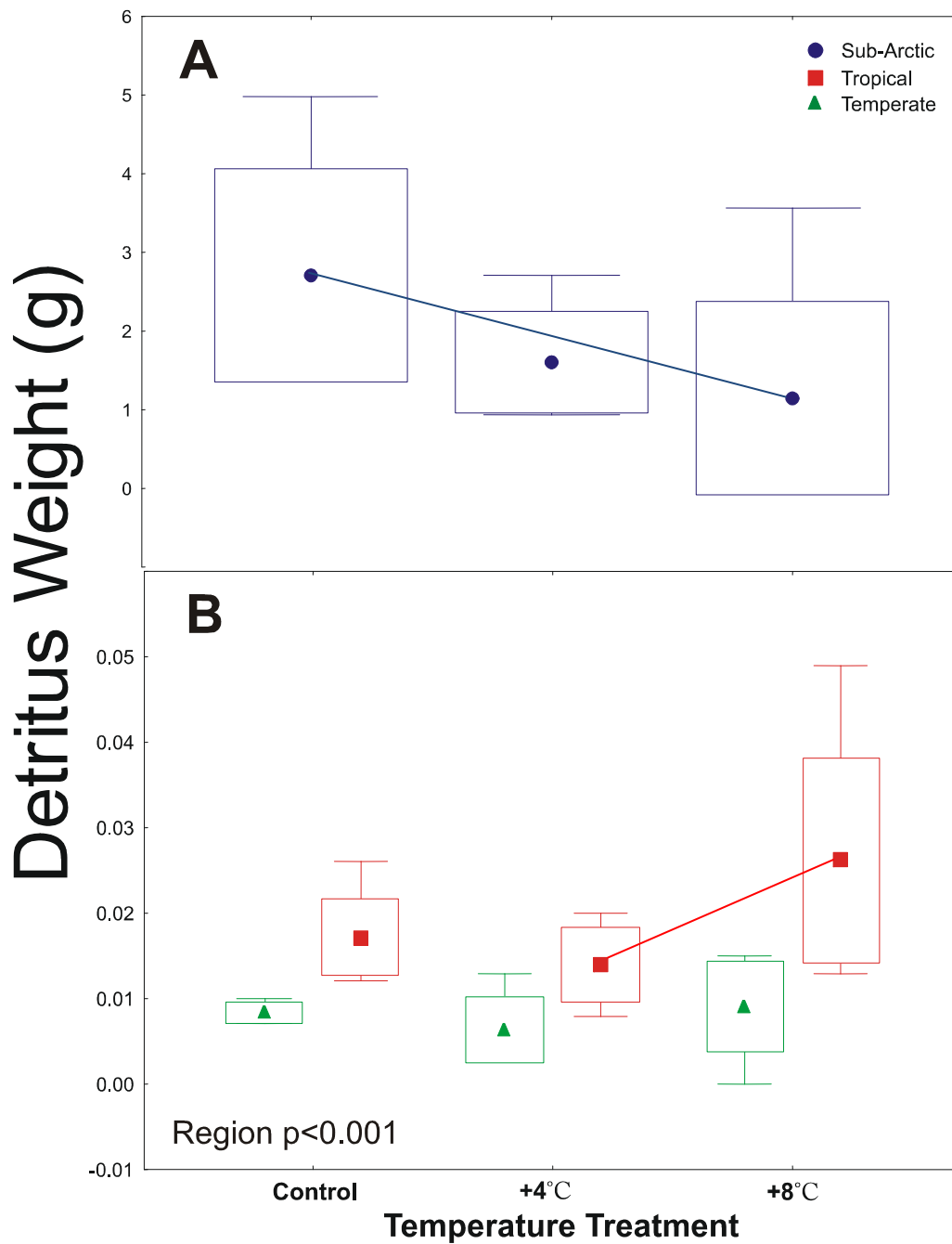
**Figure 2.2.** Relative change in extinction frequency within functional groups. Middle point shows mean, box shows standard deviation and whiskers show minimum and maximum values. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



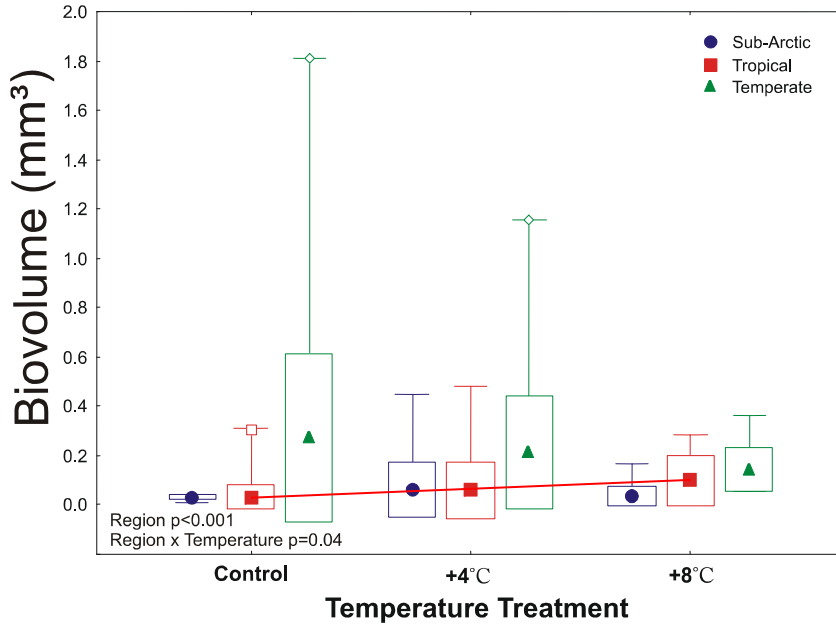
**Figure 2.3.** Relative change in abundance within functional groups. Middle point shows mean, box shows standard deviation and whiskers show minimum and maximum values. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



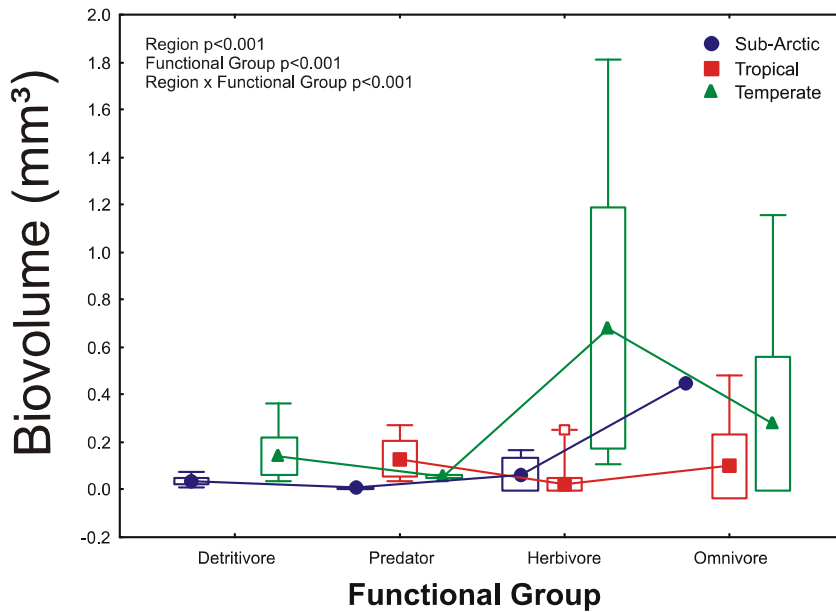
**Figure 2.4.** Relative change in a) community and b) functional group stability (coefficient of variation x -1). Middle point shows mean, box shows standard deviation and whiskers show minimum and maximum values. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



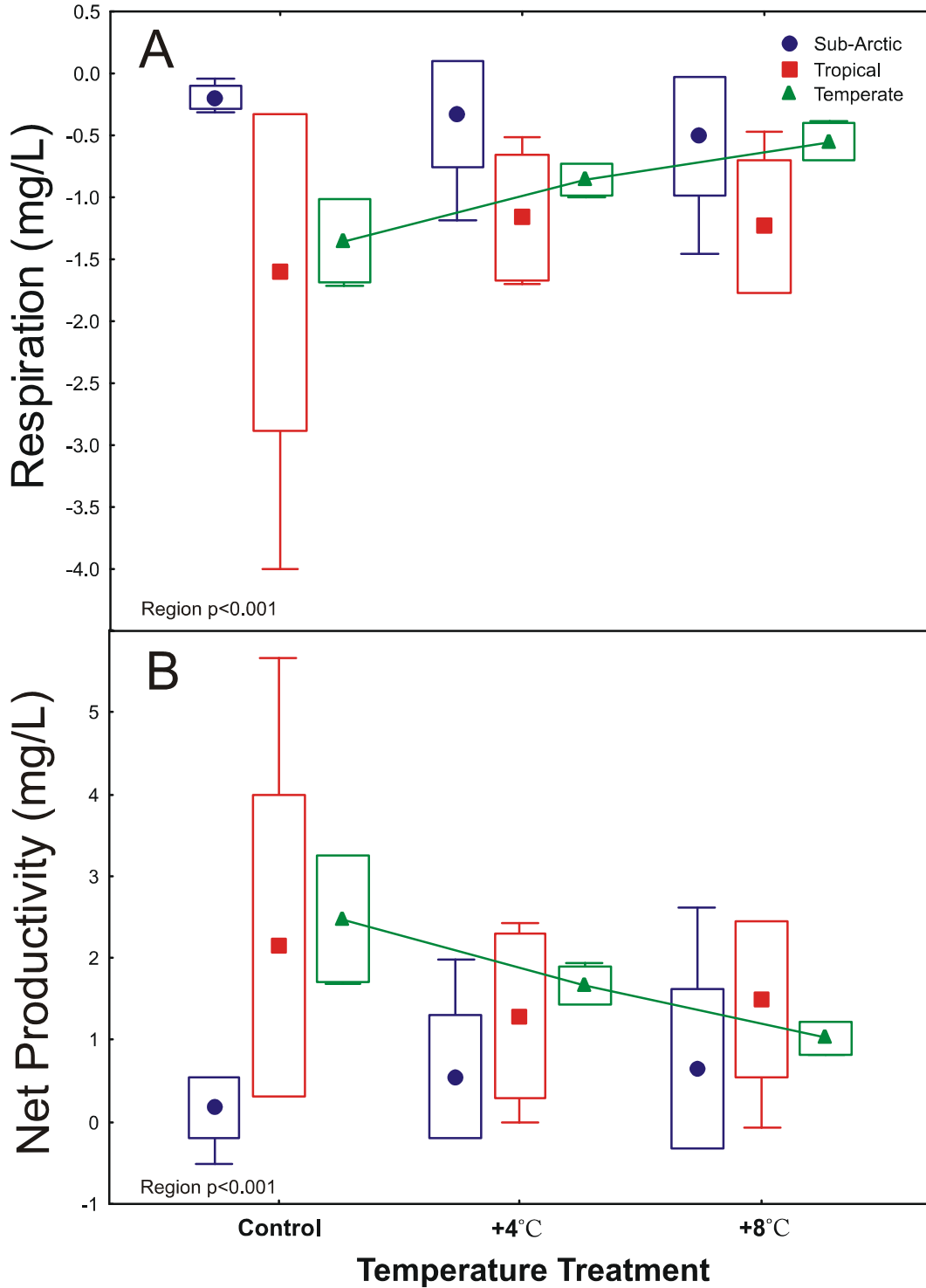
**Figure 2.5.** Detritus weight of **a)** sub-Arctic and **b)** tropical and temperate regions at final week of experiment. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



**Figure 2.6.** Community biovolume from samples taken at week 8. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



**Figure 2.7.** Mean biovolume across all weeks and temperature treatments of functional groups. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



**Figure 2.8.** Oxygen measurements for community a) respiration and b) productivity rates taken during week 8. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.

# CHAPTER 3      **The Effects of Temperature on Food Web Structure and Ecosystem Functioning in Rock Pool Communities along a Latitudinal Gradient**

## **3.1 Abstract**

Evidence is increasing that the current global warming trend will affect every level of biological organization from the metabolism of individuals, structure of populations and communities, to the functioning of ecosystems. The consequences of warming have also been predicted to have major effects on the structure of food webs, however to date few studies have attempted to unravel complex changes associated with warming in whole-ecosystems. Here, I construct food webs for a temperate, tropical, and sub-Arctic region, and track how food web structural properties, as well as abundance of basal species and community respiration and productivity, change over time following a 4°C and 8°C increase above summer mean temperatures. I show that rock pool communities do not follow predictions made based on metabolic theory that body size should decrease, respiration rate increase, and the fraction of top predators decrease with warming. Instead, no structural properties were affected by temperature except for connectance in the temperate region, which decreased with warming. Initial structural properties such as links per species, fraction of omnivory, and similarity supported the insurance hypothesis and helped to explain why the tropical community was more stable than the temperate community in warmed treatments.

## **3.2 Introduction**

The effects of increasing temperature on species metabolism (Addo-Bediako *et al.* 2002; Brown *et al.* 2004), body size (Calliari *et al.* 2003; Perry *et al.* 2005; Woodward *et al.* 2010), and population dynamics (Walther *et al.* 2002; Parmesan & Yohe 2003; Winder & Schindler 2004; Hays *et al.* 2005; Schweiger *et al.* 2008) have been well documented. In Chapter 2, I explored the effects of warming at the community level, as well as differential responses of functional groups adapted to different climate regimes. The next step is to scale up to the ecosystem level. This chapter will focus on the effects of warming on interactions between species, or food web dynamics, as well as ecosystem processes including community respiration and productivity.

Food webs, networks of predator-prey interactions, are a fundamental way of viewing the structure of ecological communities. Once diversity (species richness) and complexity (connectance) are accounted for, other properties such as the fraction of

omnivores, cannibals, and links per species generally have similar values regardless of the size of the web, or the habitat it describes (Dunne *et al.* 2004). The similarity across different ecosystems in the patterns seen in many food web properties suggests that there are fundamental characteristics in how food webs may be structured in nature. However, climate change and anthropogenic disturbances such as over-exploitation and destruction of habitat may shift the structural properties of food webs leading to webs that are more depauperate and less resistant and resilient to natural disturbance (Leary & Petchey 2009). By understanding the way in which these properties change with changes in the environment we can begin to understand how the structure of the communities is being altered, and subsequently make more effective conservation plans in the face of global warming.

The vast majority of research that has looked at the consequences of environmental change on food web structure has focused on the effects of species extinction on population and community variability (Romanuk & Kolasa 2002; Dunne *et al.* 2004). To date, little is known regarding how properties other than species richness might shift as environmental conditions such as increases in temperature occur. However, several predictions could be made based on previous findings and metabolic theory. Top predators and herbivores have been shown to decrease in warmed treatments (Petchey *et al.* 1999) and basal species such as phytoplankton and detritus are expected to increase due to increased metabolic rate (O'Connor *et al.* 2009; Moran *et al.* 2010; Sarmiento *et al.* 2010). Finally, warming is expected to favour generalist species over specialists, because warming causes increased fluctuations in biomass, and thus decreased predictability of resources (van der Putten *et al.* 2004).

Studying food web structure rather than simply its component species alone is essential in predicting secondary effects of warming. Changes in biomass of basal and low trophic level species such as detritus, algae, and bacteria could have cascading effects up the food web. For example, an increase in bacteria could cause an increase in the abundance of bacteriovores in the web. Previous studies have found an increase in bacterial growth rate with an increase in temperature (Delaney 2003; Beveridge *et al.* 2010; Sarmiento *et al.* 2010; van der Putten *et al.* 2010), however, if this is not coupled with an increase in algae, which is the bacteria's food source, bacterial abundance will



not increase and consequentially fraction of bacteriovore species may decrease (Lopez-Urrutia & Moran 2007).

Overall changes in ecosystem functioning can be determined by comparing community respiration and productivity rates, as well by assessing average community body size, as smaller body size is an indication of increased respiration rate (Brown *et al.* 2004). Warming has been found to affect both respiration and productivity rates, but not to the same degree. This difference is crucial to the functioning of the community. Different studies have found a disproportionate increase (Wohlers *et al.* 2009; Montoya & Raffaelli 2010), equal increase (Baulch *et al.* 2005), or increase in respiration but decrease in productivity (Hoppe *et al.* 2008) depending on the community under study. The general trend seen is that respiration is more sensitive to warming because productivity is limited in its magnitude of increase by the amount of available resources (i.e. nitrogen and phosphorous) (Lopez-Urrutia & Moran 2007; Yvon-Durocher *et al.* 2010).

To study these effects of temperature on ecosystem processes I used rock pool communities from a tropical, temperate, and sub-Arctic region. The species composition and feeding interactions of these communities have been well characterized (Tenberge 1978; Dole-Olivier *et al.* 2000; Romanuk & Kolasa 2002) and their small size allows for a fully functioning community to be maintained easily in the lab, making them an ideal study system. Rock pool communities were subjected to two warming treatments and effects on the structural properties of the food web, abundance of basal species, as well as community respiration, productivity, and body size were analyzed both within and between regions.

### **3.3 Methods**

#### *3.3.1 Data Collection*

Rock pool communities were collected from a temperate (Nova Scotia), sub-Arctic (Churchill, Manitoba), and a tropical (Jamaica) region. For each region, six replicates of 1.5 L rock pool microcosms were placed in temperature baths at three different temperatures. The control treatment was based on the summer mean annual

temperature for each region (sub-Arctic= 5°C, temperate= 20°C, tropical= 24°C). The other two treatments were 4°C and 8°C above the mean temperature. Every week for eight weeks density counts were made by taking a 50 mL sample after gently stirring the microcosm to homogenize the contents and recording number and identity of each species under a dissecting microscope (Fig. 2.1).

Basal resources, including bacteria and detritus, were measured following the final live sample count at week 8. To determine final bacterial abundance each microcosm was sampled for bacteria using an inoculation loop which was then smeared on a plate of marine agar. Plates were incubated at room temperature for 48 hours, at which point the number of colonies was counted as an estimate of bacterial density (Beveridge *et al.* 2010). Detritus size was determined by removing 2 mL of detritus using a pipette. Using a dissecting microscope, the ten pieces of detritus closest to the microscope scale were measured and the size of each piece was recorded. Detrital biomass was assessed by filtering the entire remaining contents of each microcosm through a 63µm mesh sieve. The detritus was then dried in a drying oven at 60°C for 48 hours and weighed. To determine the identity and abundance of algae an AlgaeAnalyzer was used to determine algal class from the stock cultures from each region. To sample algae a 20 mL sample was taken from each initial stock tank of rock pool water after gently stirring, and was then analyzed. Algae was not measured from samples subjected to warming treatments so this data was only used for construction of the food webs. Total algae concentration was highest in the tropics and lowest in the sub-Arctic in initial stock rock pool water ( $p=0.0459$ ). The dominant types of algae present in each region differed as well, with green and bluegreen algae dominating in the sub-Arctic and temperate regions, and bluegreen and cryptophyton in the tropical region (Appendix Fig. B.1a,b).

After the final density count (week 8), dissolved oxygen was measured using a Data Sonde (YSI 650 Multiparameter Display System) to determine productivity and respiration using the light/dark bottle method (Gaarder & Gran 1927). To determine productivity and respiration, water from each microcosm was sealed in an airtight, 250 mL mason jar and placed back in its appropriate heating bath. Half of the replicates from each treatment were completely covered in tin foil to block out light to determine

respiration and half were left uncovered to determine productivity. After 24 hours, a second oxygen reading was taken for the water inside the jars. Respiration was calculated as the difference between final and initial oxygen readings in the dark jars. Gross productivity was calculated as the difference between final oxygen readings in the dark minus light jars, and net productivity was calculated as the difference between gross productivity and respiration.

The 50 mL density count samples from weeks 1 and 8 were preserved and body size of every individual was measured using a Zeiss Axiovert 200 M microscope with an Axiocam HRC camera. Biovolume was estimated using these measurements and the equation for a cone for copepods, ellipsoid for daphnids, and irregular shape for chydorids and ostracods (Wetzel & Likens 1991; Hayward *et al.* 2009).

### 3.3.2 Feeding Links

To determine feeding links between species, feeding trials were performed. For the feeding trials, three individuals of each species were placed in a small (20 mL) container with three individuals of another species. Ten replicates were conducted for each feeding trial and all species were crossed with all other species including itself (temperate n=7 spp., tropical n=7 spp., sub-Arctic n= 6 spp.). All trials were performed at 24°C with a 12 hour light/dark cycle. The feeding trials were checked regularly until all individuals of one species were missing or dead (~5 days). If the average of all 10 replicates had at least one individual less of one species than the other this suggested a consumer-resource link between the species. If the average number of both species was the same, it suggested they feed upon basal resources. In the case where the species was crossed with itself it was considered cannibalism if the average of all ten replicates had one less individual from the initial number (n=6).

As added support for feeding links made through feeding trials, primary research was consulted (Dole-Olivier *et al.* 2000; Thorp & Covich 2001) and notes were made when any feeding interactions were observed during live density counts.

### 3.3.3 Food Web Construction

Using the species presence/absence, predator/prey lists were constructed for each replicate (n=6) and temperature treatment (n=3) for every week of the experiment for the

three regions, for a total of  $6 \times 3 \times 5 \times 3 = 270$  lists. Additional lists were made using the average abundance of all six replicates to represent a 'meta-web' for each temperature treatment (Meta-web species lists with all species present in Appendix Table B.1-3). Each list contained all species present in one replicate for one treatment and time period in the first column, and a list of all prey present in the second column. When a species was absent in a replicate it was deleted from the predator/prey list.

From the predator/prey lists, 270 food webs were constructed and 19 structural properties that describe important topological properties of food webs were calculated including species richness ( $S$ ), connectance ( $C$ ), and fractions of major trophic groups (Williams & Martinez 2000; Martinez & Dunne 2007). A list of the 19 topological properties and their definitions is given in Table 3.1.

Properties describing trophic level (%T, %I, %B, %H, Omniv, Cannibal, SWTL) or feeding chain length are central to determining ecosystem stability, because they depict how energy is distributed throughout the system. Changes in these properties are important to understand dominant energy flow pathways and trophic cascades, as well as how community organization will change in response to temperature increase. Properties such as connectance, link SD, and loop characterize both the amount, and type of connections between species in the web. Mean similarity, max similarity, and predator and prey similarity describe the extent of redundancy in the food webs. Greater similarity indicates that there are more species with similar trophic roles in the web, suggesting that the web may be more robust to extinctions because the web contains species with similar feeding niches. The mean clustering coefficient (CC) gives an indication of how compartmentalized the food web is, where a higher CC indicates more compartmentalization. Finally, generality (number of prey species) and vulnerability (number of predator species) have been found to correlate with species richness. As the number of species increases, vulnerability increases, while generality reaches a plateau because predators are limited in the number of prey species they can consume (Schoener 1989). An increase in temperature may decrease species richness, which should in turn result in a decrease in vulnerability.

### 3.3.4 Data Analysis

A general linear model (GLM) was used with region (tropical, temperate, and sub-Arctic) and temperature treatment (control, +4°C, and +8°C) as categorical variables and week (1 through 8) as a continuous predictor to determine significant changes in all 19 food web properties. Detritus size and weight, bacteria abundance, body size, and productivity and respiration rates were analyzed using a 3x3 between groups analysis of variance (ANOVA) for differences between treatments and regions. Data were tested for normality using Shapiro-Wilk's test and homogeneity of variance using Levene's test. All analyses were conducted using Statistica 7.0 (StatSoft 2004). Significance level was set at  $\alpha=0.05$ . Post-hoc Tukey tests were used to determine significant differences between regions and temperature treatments.

## 3.4 Results

Visual representations of meta-webs from week 1 and 8 for each region and temperature treatment are shown in Figures 3.1-3.3. Only one meta-web is presented from the sub-Arctic region because the meta-web for the sub-Arctic region did not change in either of the temperature treatments.

### 3.4.1 Initial Differences Between Regions

Eighteen of 19 food web properties differed significantly across regions at the start of the experiment (Week 1). The only food web property that had no statistically significant difference was mean prey similarity ( $p=0.205$ ). The number of species was highest in the temperate (mean 13.5) and lowest in the tropical region (mean 12.3;  $p<0.001$ ; Fig. 3.4c). In contrast, connectance was highest in the tropical region (mean 24.3%) and lowest in the temperate region (mean 17.7%;  $p<0.001$ ; Fig. 3.4a). While the sub-Arctic region had the highest fraction of top predators (mean 17.9%), the tropical region had none ( $p<0.001$ ). Instead, the tropical region had a high fraction of intermediate species (mean 67.4%) and omnivores (mean 57%), with a high mean similarity (mean 20%) and predator similarity (mean 28%), and links per species (mean 3; Fig. 3.4a). Sub-Arctic webs had the lowest fraction of basal species (mean 30.5%) across all regions ( $p=0.006$ ). Sub-Arctic webs also had the highest SD vulnerability

(mean 0.72) of the regions ( $p < 0.001$ ; Fig. 3.4b). Finally, the temperate webs had the highest fraction of basal species (mean 37%;  $p = 0.006$ ) and lowest fraction of omnivores (mean 40.6%;  $p < 0.001$ ; Fig. 3.4a).

#### 3.4.2 Changes in Food Web Structure with Temperature

Food web properties changed significantly over time ( $F_{18,7} = 11.5$ ;  $p < 0.001$ ) and by region ( $F_{36,2} = 225.04$ ;  $p < 0.001$ ). Across all food web properties there was a significant effect of temperature ( $F_{36,2} = 1.68$ ;  $p = 0.009$ ). There was no statistically significant interaction between region and temperature ( $F_{72,5} = 1.25$ ;  $p = 0.087$ ).

Univariate tests for differences in the 19 food web properties however showed that no individual food web property had a strong enough effect with temperature to be statistically significant ( $p > 0.05$  for all) and there were no statistically significant region  $\times$  temperature interactions for any food web property ( $p > 0.05$  for all). Of the 19 food web properties only five did not change significantly over time (%Cannibals, MaxSim, VulSD %H, %T; Table 3.2). Most food web properties changed in the same direction and to a comparable degree across the three regions. Fraction of basal, GenSD, LinkSD, MeanSim, PredSim, PreySim, and CC increased over time in all regions while S, L/S, C, %I, Loop, SWTL, and Omniv decreased over time. Only a few food web properties changed in different directions over time in the different regions. The sub-Arctic region showed a significant increase in fraction of basal species (35% increase;  $p < 0.001$ ; Fig. 3.5a), generality (21% increase;  $p < 0.001$ ; Fig. 3.5b), and mean similarity (16% increase;  $p < 0.001$ ; Fig. 3.5c) over time, while the tropical and temperate regions showed no statistically significant changes over time in these properties. The temperate region had a significant increase in its clustering coefficient over time (45% increase;  $p < 0.001$ ; Fig. 3.5d), while there was no statistically significant change in this property in the sub-Arctic or tropical regions (Appendix Table B.4).

To determine whether changes in food web properties were present on the final sampling date, I performed an additional GLM with region and temperature as categorical variables. In week 8, significant differences were observed based on region in 14 of the 19 properties, suggesting that initial differences in food web structure were maintained throughout the experiment. The only property that was significantly affected by temperature was connectance in the temperate region which was higher in the control

treatment (19.3%) than in the +4°C treatment (15.6%;  $p=0.038$ ) or +8°C treatment (15.7%;  $p=0.024$ ) showing that connectance had declined in the warming treatments from initial conditions and increased in the control from initial conditions (Fig. 3.6).

#### *3.4.3 Change in Bacteria and Detritus*

Bacteria abundance decreased with warming in the tropical ( $p=0.029$ ) region and was significantly lower in the +8°C treatment than in the control treatment in the temperate region ( $p=0.021$ ). There was no statistically significant difference between bacteria abundance in the different warming treatments for the sub-Arctic region ( $p=0.128$ ; Fig. 3.7; Appendix Table B.5). Detritus size did not change significantly with temperature for any of the regions, however there was a significant difference between size in each region ( $p<0.001$ ) with sub-Arctic communities containing detritus that was 15% larger than the temperate region (Fig. 3.8; Appendix Table B.6). Detritus weight did not vary statistically with temperature in the temperate region, increased with temperature in the tropical region ( $p=0.036$ ) and was significantly lower in the +8°C treatment than in the control in the sub-Arctic region ( $p=0.003$ ; Fig. 2.5a,b; Appendix Table A.7).

#### *3.4.4 Productivity and Respiration*

There was a significant difference in respiration between regions, with the tropical region having the highest rate and sub-Arctic having the lowest ( $p<0.001$ ). The temperate region was the only one to experience a statistically significant change in respiration, with respiration rate decreasing with increasing temperature ( $p=0.013$ ; Fig. 2.8a; Appendix Table A.10).

There was a significant difference in net productivity across regions ( $p<0.001$ ) with the tropical region having the highest and sub-Arctic the lowest productivity across all temperature treatments. Only the temperate region had a statistically significant difference between productivity levels in the different temperature treatments, with a decrease in productivity as temperature increased ( $p=0.029$ ; Fig. 2.8b; Appendix Table A.11).

#### *3.4.5 Body Size*

Mean biovolume of the community at week 8 was significantly different between regions ( $p<0.001$ ), with temperate communities having a larger biovolume overall than

the tropical or sub-Arctic region (Fig. 2.6). Only the tropical region had statistically significant difference in biovolume between temperature treatments. In the tropical region, biovolume increased with increasing temperature ( $p=0.002$ ). This increase appeared to be due to an increase in daphnia biovolume in the  $+8^{\circ}\text{C}$  treatment (Fig. 3.9). In the temperate community there was a trend towards a decrease in biovolume with increasing temperature, but the difference was not statistically significant ( $p=0.33$ ). There was no difference in biovolume between temperature treatments in the sub-Arctic community (Appendix Table A.8).

### 3.5 Discussion

Evidence is increasing that the current global warming trend will affect every level of biological organization from the metabolism of individuals (Gillooly *et al.* 2001; Brown *et al.* 2004; Clarke & Fraser 2004), structure of populations and communities (McLaughlin *et al.* 2002; Walther *et al.* 2002; Parmesan 2006), to the functioning of ecosystems (Lopez-Urrutia & Moran 2007; Hoppe *et al.* 2008; Wohlers *et al.* 2009; Woodward *et al.* 2010; Yvon-Durocher *et al.* 2010). The consequences of warming have been predicted to have major effects on the structure of food webs, however to date few studies have attempted to unravel complex changes associated with warming in whole-ecosystems. Whole-ecosystem manipulations of temperature are critical to determine how the structure and functioning of food webs might change in increasing temperature. Microcosm studies, such as the one presented here, represent a powerful approach to determining general effects of warming on ecosystems.

Three areas of ecological theory are directly relevant to understanding and predicting the effects of warming in ecological systems: metabolic scaling theory, food web theory, and theory related to the effect of biodiversity on ecosystem functioning (Montoya & Raffaelli 2010).

#### 3.5.1 Metabolic Scaling Theory

This theory predicts that metabolic rate scales with temperature increase, and furthermore that changes in ecosystem process rates ultimately depend on changes in the metabolic demands of individual organisms (Brown *et al.* 2004). An increase in



temperature should therefore cause an increase in individual metabolic rate and a corresponding increase in community respiration rate. Along with increased metabolism a decrease in body size should ensue, due in part to earlier development, and in part because larger organisms may not be able to acquire enough resources to support their increased metabolism (Arim *et al.* 2007). Therefore metabolic scaling theory predicts a decrease in mean community biovolume with increase in temperature.

Between regions, final respiration was highest in the tropical region and lowest in the sub-Arctic region, as metabolic scaling with temperature would predict. However, within regions only the temperate region had a statistically significant change in respiration with temperature, and this was a decreasing trend (Fig. 2.8a). The tropical region also appeared to have a decrease in respiration with increase in temperature, but this decline was not statistically significant. Body size also did not respond as predicted by metabolic theory and as observed in other studies (Atkinson *et al.* 2003; Falkowski & Oliver 2007; Moran *et al.* 2010). There was no change in body size with temperature in the sub-Arctic or temperate regions, and body size in the tropical region increased with temperature (Fig. 2.6). The overall decrease in respiration with temperature may be due to the fact that community abundance decreased significantly with increasing temperature (Fig. 2.1). Therefore individual metabolism may have increased as metabolic theory predicts, but because abundance was also affected, community respiration did not reflect this increase. Body size may not have changed as expected because this prediction is based on the assumption that the largest species in the community are also at the highest trophic levels (Arim *et al.* 2007; Petchey *et al.* 2010), however Figure 2.7 shows that in the temperate and sub-Arctic regions, herbivores and omnivores rather than top predators have the largest body size, respectively. The tropical region experienced an increase in community mean body size because daphnia increased in body size in the warmest treatment (Fig. 3.9). Body size of daphnia may have increased in the tropical region if they were not limited by availability of their resources: abundance of algae or oxygen.

The total concentration of algae was highest in the tropical region and lowest in the sub-Arctic at the beginning of the experiment (Appendix Fig. B.1a). This corresponds with productivity measurements, which displayed the highest productivity in the tropical region and the lowest productivity in the sub-Arctic. Final measurements of

algal abundance were not taken, but productivity measured by change in oxygen concentration in the light bottles did not change with temperature in the tropical or sub-Arctic region. Only the temperate region had a significant decrease in productivity with increasing temperature (Fig. 2.8b). Body size of daphnia may have increased with temperature in the tropical region because they were not limited by resource availability. Another food source for daphnia is bacteria (Dole-Olivier *et al.* 2000). Bacterial abundance decreased with temperature in the tropical and temperate regions (Fig. 3.7). This decrease may have been due to increased protist grazing, because temperature alone is predicted to increase bacteria abundance (Baulch *et al.* 2005; Sarmiento *et al.* 2010; van der Putten *et al.* 2010).

In summary, changes due to metabolism did not appear to be a large driving force behind ecosystem response to warming, because respiration, body size, and bacterial abundance responded opposite to predictions based on metabolic theory. Rather, changes appear to be dominated by availability of resources for consumers and level of grazing pressure on basal species.

### 3.5.2 Food Web Theory

Several studies have used food web theory to make predictions about effects of warming at the ecosystem scale. Warming has been predicted to result in a decrease in fraction of top predators (Petchey *et al.* 1999; Voigt *et al.* 2003) and subsequent shortening of food chain length (Arim *et al.* 2007; Woodward *et al.* 2010), as well as changes in predator-prey interactions (Walther *et al.* 2002; Calliari *et al.* 2003; van der Putten *et al.* 2004; Beveridge *et al.* 2010; Sarmiento *et al.* 2010) which have been shown to lead to cascading effects throughout the food web (Winder & Schindler 2004; Wohlers *et al.* 2009). A recent study by Petchey and colleagues (2010) developed a model based on metabolic theory and foraging biology and found that connectance could increase, decrease, or be unaffected by increasing temperature depending upon attack rate and handling time activation energies of the species in question (Petchey *et al.* 2010). They further found that web sensitivity to changes in temperature depended on body size structure of the web, specifically the mass scaling of resources (Petchey *et al.* 2010). Webs with greater differences in body size at different trophic levels had greater stability, whereas webs with more evenly distributed body sizes were more sensitive to warming

(Rall *et al.* 2008; Vucic-Pestic *et al.* 2010). In the rock pool webs considered here, body size did not follow the traditional allometric scaling pattern with herbivores having smallest body size and top predators being largest (Arim *et al.* 2007), suggesting these webs may be more vulnerable to warming than webs where predator:prey body size ratios are greater.

The only food web property that was statistically significant with temperature treatment was connectance in the temperate region at week 8 which was higher in the control treatment (19.3%) than in the +4°C treatment (15.6%;  $p=0.038$ ) or +8°C treatment (15.7%;  $p=0.024$ ) showing that connectance had declined in the warming treatments from initial conditions and increased in the control from initial conditions (Fig. 3.6). This lack of strong effects of temperature on food web structure was surprising as a number of properties have been predicted to be affected by increasing temperature. One possible reason for this is that the food webs were constructed based solely on presence or absence of species. Although warming significantly affected abundance of species, unless extinction occurred food web structure did not change with temperature. Another explanation is that food web properties differed so strongly regionally and showed similar trajectories over time across regions. The only food web properties that did not show similar directional change across the three regions were the fraction of basal species, generality, and mean similarity which increased over time in the sub-Arctic community and did not change over time in the temperate and tropical region. The clustering coefficient also did not show similar directional change across regions as it increased over time in the temperate region and did not change over time in the sub-Arctic or tropical regions (Fig. 3.5a-d). Thus, it appears that initial food web structure was strongly constrained across regions with increasing temperature despite the high extinction frequency observed in the temperate and tropical region relative to the sub-Arctic region (Chapter 2). Differences between the regions in food web structure however may partially explain the lower stability of the temperate region to warming as discussed in Chapter 2. In particular, connectance declined with increasing temperature in the temperate communities. Connectance and the number of links per species were lower initially in the temperate region than in the tropical or sub-Arctic region (Fig. 3.4a,c). A positive relationship between connectance and stability has previously been

suggested (Briand 1983). Thus, it is possible that the lower initial connectance of the temperate community and the decrease in connectance that occurred with warming may have led to the higher variability that was observed in the temperate communities in Chapter 2.

The fraction of omnivores in a web has also been linked to increased stability (Fagan 1997; McCann 2000). The reasoning is that omnivorous species feed on different trophic levels, so are able to respond to changes in prey abundance by feeding more intensively on a different trophic level. Predators have fewer options and therefore may have stronger interaction strengths with their prey. When species with strong interaction strengths go extinct there are greater consequences on species they are connected too than if they were connected with weak interactions (McCann *et al.* 1998; Berlow 1999). Many previous studies have observed a decrease in fraction of top predators with warming (Petchey *et al.* 1999; Voigt *et al.* 2003). None of the regional food webs in this study experienced a decrease in fraction of top predators, however the tropical region had a significantly greater fraction of omnivores than either the temperate or sub-Arctic webs (Fig. 3.4a) which may have contributed to the robustness of tropical webs to increasing temperature (Williams & Martinez 2002). The sub-Arctic region was found to be the most robust in terms of stability, abundance and extinction frequency (Chapter 2) and several changes in its food web structure over time may help explain this observation. Similarly to the benefits of omnivores, a high level of generality in a web helps in maintaining stability in unfavourable environments (Callaghan *et al.* 2004a). The sub-Arctic region experienced an increase in generality SD over time, as the effects of warming became more apparent at the population and community level (Fig. 3.5b). The temperate region was also the only region to show a statistically significant increase in the clustering coefficient over time (Fig. 3.5d). This increase suggests that the temperate region may have lost key species that were well connected, causing it to become more compartmentalized. This increase in clustering, along with the decrease in connectance and the fraction of omnivores may partially explain why the temperate web was less robust to warming than the tropical and sub-Arctic webs (Fagan 1997).

### 3.5.3 Biodiversity and Ecosystem Functioning

Diversity, or number of species within a community, has long been predicted to increase the stability of ecological communities (MacArthur 1955; Yachi & Loreau 1999; McCann 2000; McGrady-Steed & Morin 2000; Romanuk & Kolasa 2002). One mechanism that has been suggested to underlie this pattern is the insurance hypothesis: that species richness is associated with stability in part because a greater number of species increases the chance that they will have similar feeding roles, and thus if one goes extinct another will be able to occupy the same niche in the community (Petchey 2007; Leary & Petchey 2009). Although the temperate and tropical communities both lost species in the warmed treatments (Figs. 3.2 & 3.3), the tropical community had higher mean and predator similarity than the temperate community (Fig. 3.4a). Similarly, the sub-Arctic region increased in mean similarity over time (Fig. 3.5c) and was also the most robust to warming. This provides evidence for the insurance hypothesis and suggests that it is the identity of species that went extinct that is important, not just the total number of species lost (Raffaelli 2004).

### 3.5.4 Conclusions

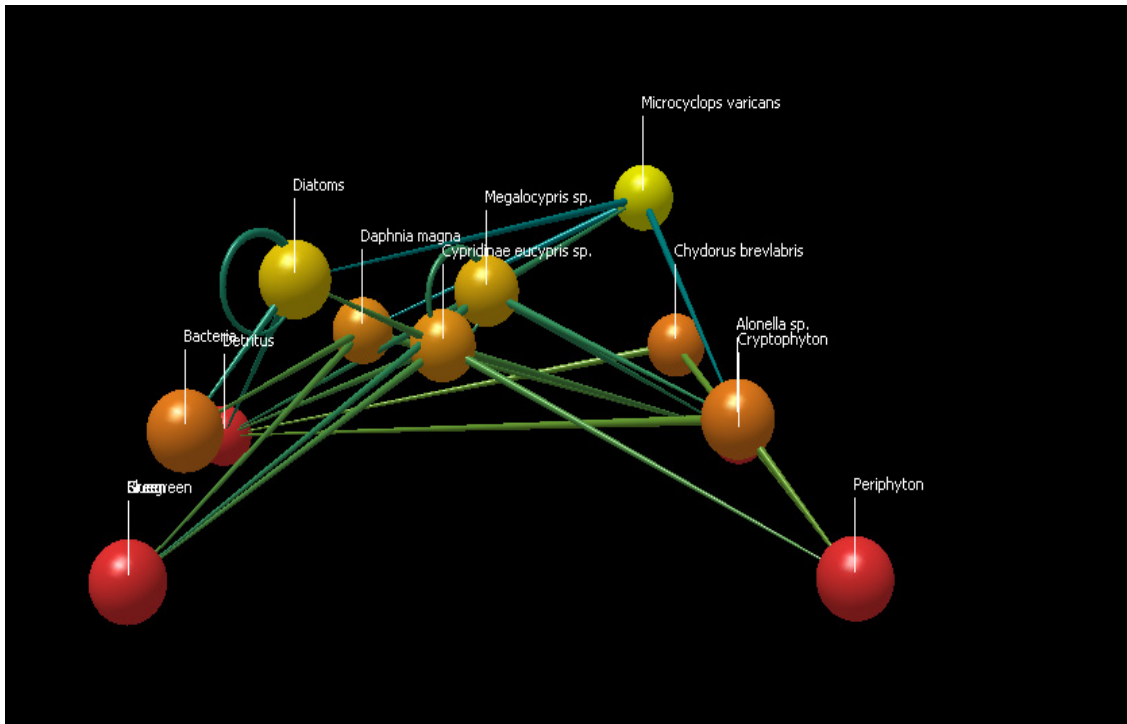
Temperature affects many levels of biological organization, and these effects are not easily predictable because response depends on many factors such as body size distribution of the community (Rall *et al.* 2008), trophic position of species in the community (Raffaelli 2004), strength of interactions between species (Berlow 1999), and availability of resources (Lopez-Urrutia & Moran 2007). Despite these factors, it is essential to study effects of temperature increase at the ecosystem level to begin to understand what changes may occur in the real world. Recent studies have called for a more holistic approach to climate change studies (Parmesan 2006; van der Putten *et al.* 2010; Walther 2010; Woodward *et al.* 2010), but very few have as yet responded. It is a daunting task, because at such a large scale many factors could be influencing the observed trends. However, by comparing very similar communities taken from different regions we are able to tease apart responses that may be unique to a community, and ones that may be universal to all ecosystems.

Here, I have shown that rock pool communities do not follow predictions made based on simple, single species models. Community respiration did not increase and

body size did not decrease with increasing temperature in any of the regions. Instead, a food web approach appears promising in making predictions at the ecosystem level. Structural properties of initial webs such as links per species, fraction of omnivory, and similarity supported the insurance hypothesis and helped to explain why the tropical community had a more stable abundance and lower extinction frequency than the temperate community in warmed treatments. Likewise, the decline in connectance observed in the temperate communities with warming along with the lower initial connectance of the temperate community may explain its low robustness to warming. Future studies would benefit from incorporating temperature variability and immigration into experimental design, as these factors also play a significant role in how species will respond to climate change.

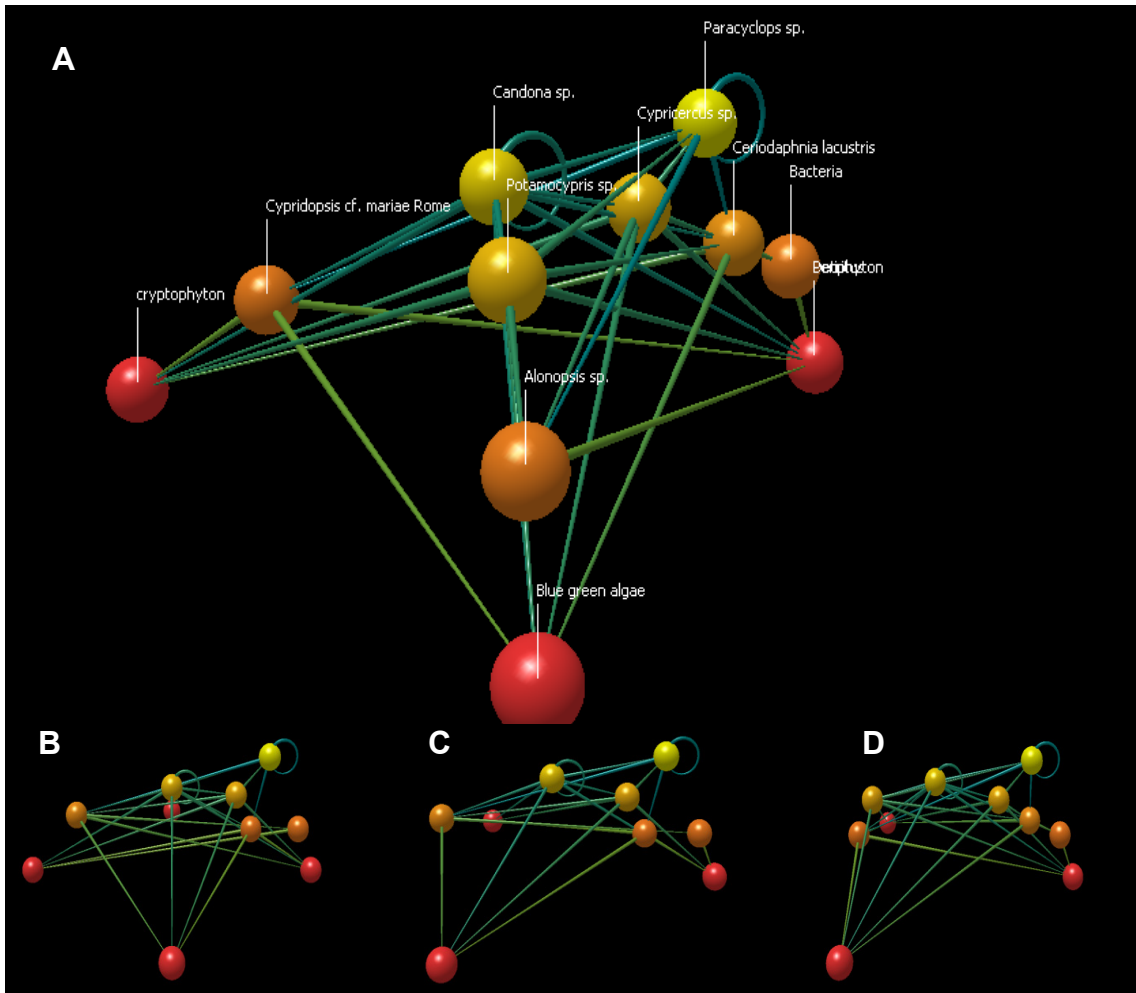
**Table 3.1.** Definitions of the food web properties

<b>Food web properties</b>	<b>Symbol</b>	<b>Description</b>
Species	S	Species richness or number of species (taxonomic or trophic) present in the web
Link/Species ratio	L/S	Linkage density: the number of all trophic links in the web (L) divided by S (species or ecological groups)
Connectance	C	Direct connectance or the proportion of all possible links ( $L/S^2$ ), 0= no species preys on any species, 1= every species preys on every other species including itself
Fraction of top predators	% T	Fraction of species with prey but no predators
Fraction of intermediate predators	% I	Fraction of species with both prey and predators
Fraction of basal species	% B	Fraction of species with predators but no prey
Fraction of herbivores	% H	Fraction of species feeding on the primary trophic level
SD Generality	GenSD	Standard deviation of generality (mean number of prey items by species)
SD Vulnerability	VulSD	Standard deviation of vulnerability (mean number of predators by species)
SD link	LinkSD	Standard deviation of mean number of links per species
Feeding Loops	Loop	Fraction of species in a loop chain
Short Weighted Mean Trophic Level	SWTL	Average of prey-averaged trophic level
Fraction of omnivorism	Omniv	Fraction of species that feed directly on more than one trophic level
Mean similarity	MeanSim	Average fraction of predators and prey shared between species
Maximum similarity	MaxSim	Average maximum fraction of predators and prey shared between species
Predator similarity	PredSim	Average fraction of predators shared between species
Prey similarity	PreySim	Average fraction of prey shared between species
Fraction of cannibalism	Cannibal	Fraction of species that feed directly on its own species
Mean Clustering Coefficient	CC	Mean of species pairs connected to the same species that are connected to each other

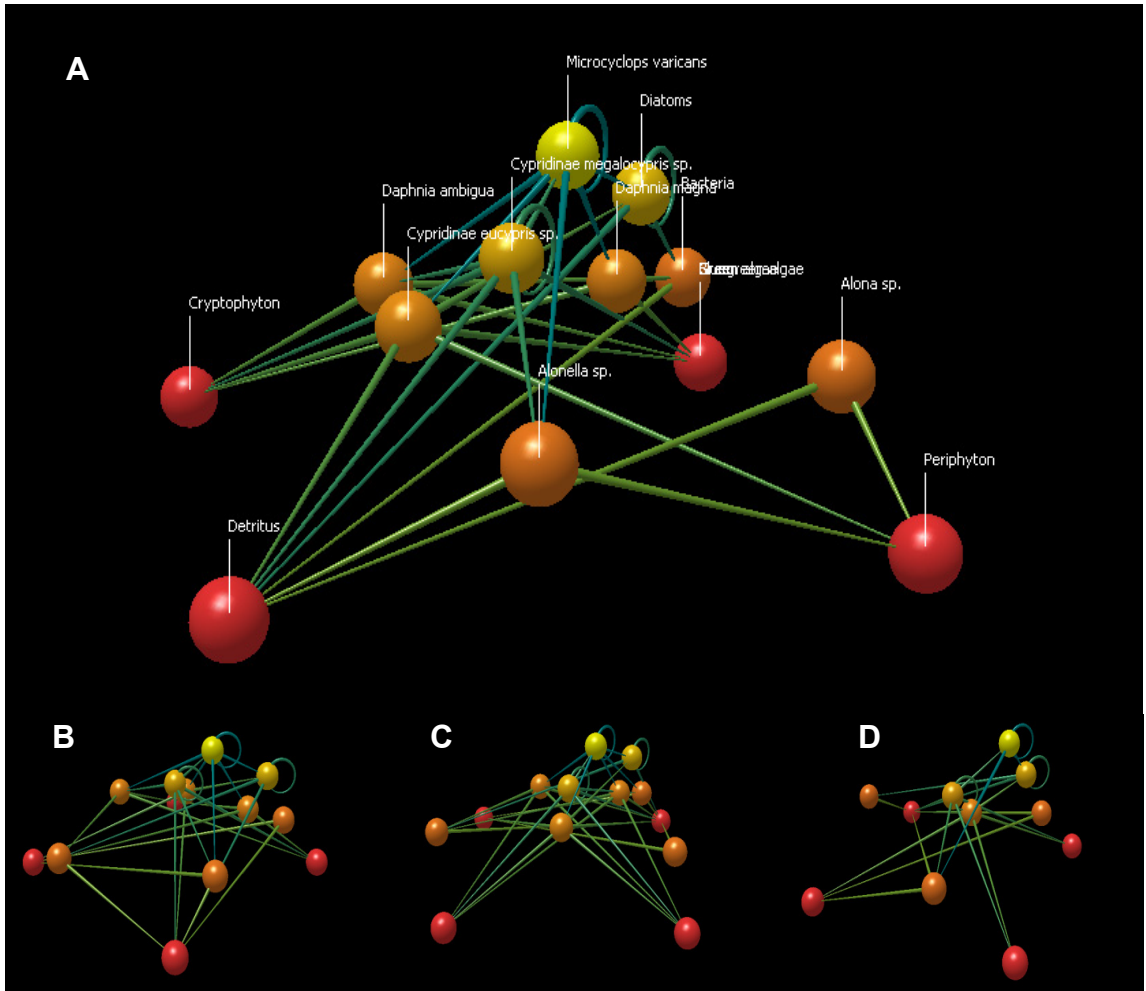


**Figure 3.1.** Visual representation of food web from sub-Arctic region. Web did not change over time in any temperature treatment. For all web representations here lower red nodes indicate basal species, middle orange nodes are intermediate species, and upper yellow nodes are top predators. Lines between nodes indicate a consumer-resource feeding link.

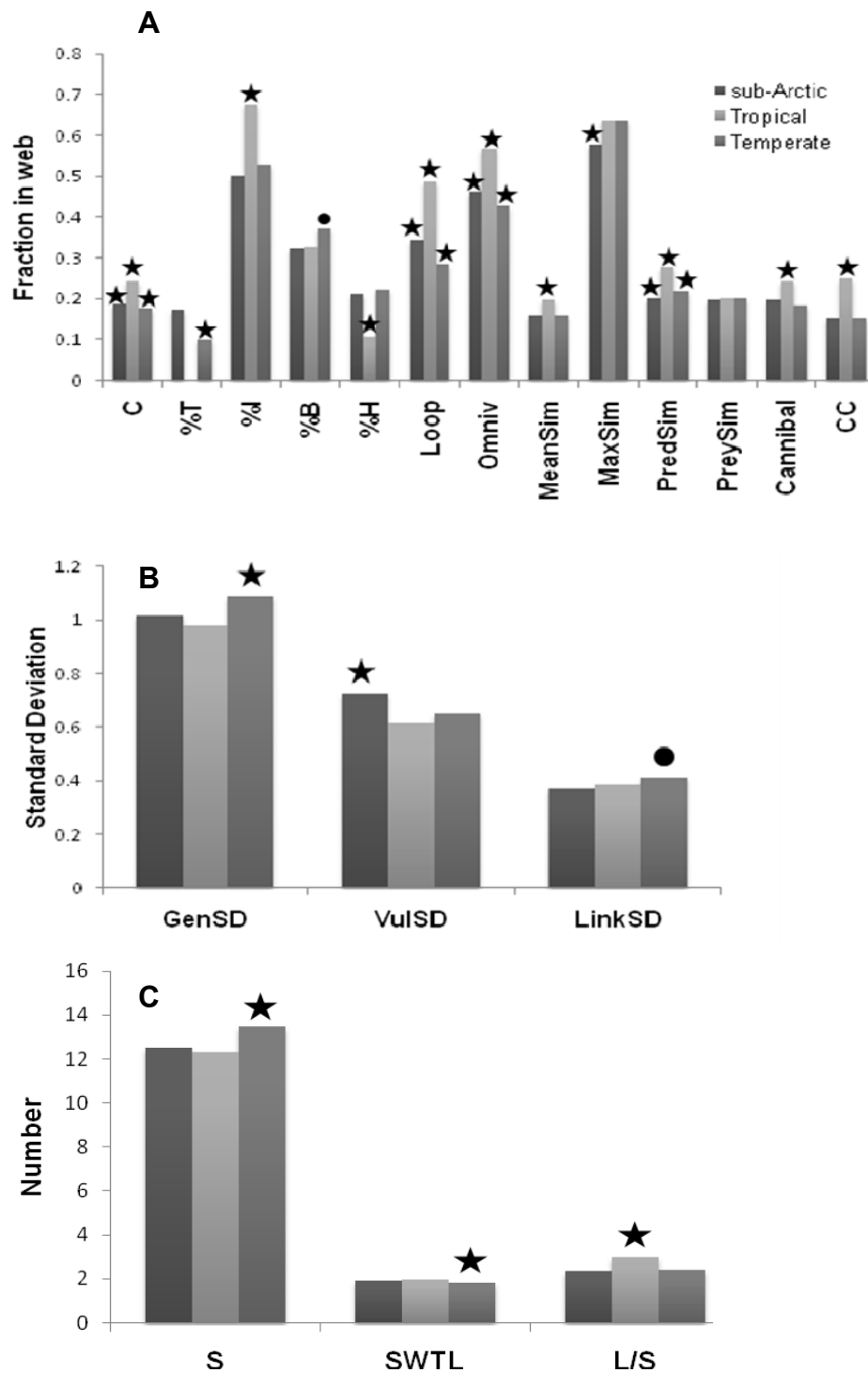




**Figure 3.2.** Visual representation of food web from tropical region at **a)** control, +4°C, and +8°C week 1 all species present **b)** control treatment week 8, **c)** +4°C treatment week 8, and **d)** +8°C treatment week 8.



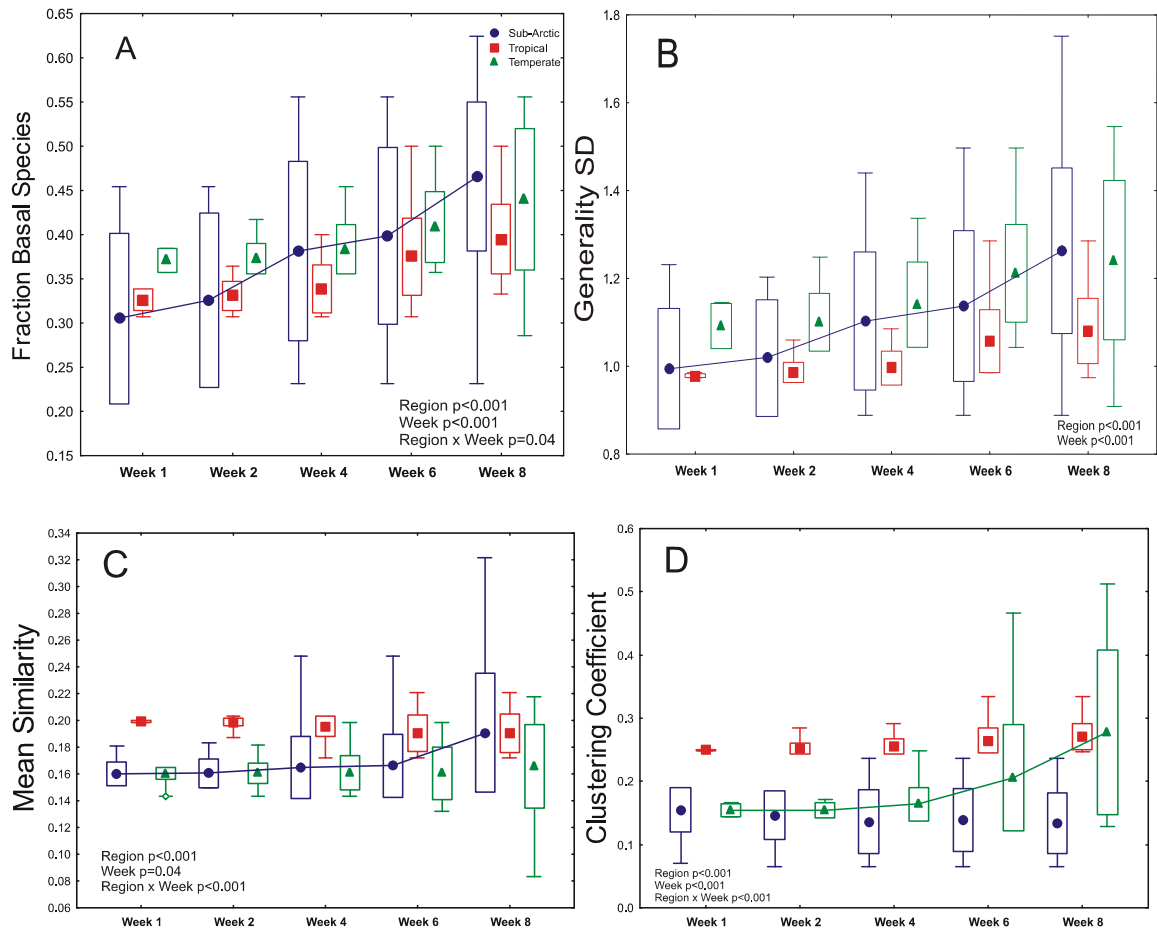
**Figure 3.3.** Visual representation of food web from temperate region at **a)** control, +4°C, and +8°C week 1 all species present **b)** control treatment week 8, **c)** +4°C treatment week 8, and **d)** +8°C treatment week 8.



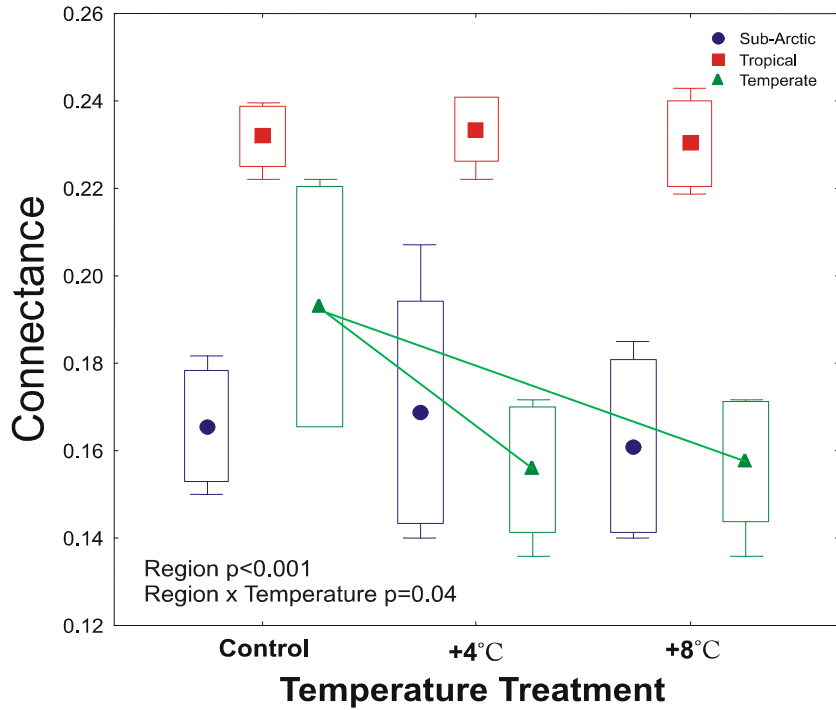
**Figure 3.4.** Initial differences between food web properties from each region, **a)** connectance, % top predators, % intermediate species, % basal species, %herbivores, fraction of loops, fraction of omnivores, mean similarity, maximum similarity, predator similarity, prey similarity, fraction of cannibals, clustering coefficient, **b)** standard deviation of generality, vulnerability and number of feeding links, **c)** species richness, short weighted trophic level, and fraction of links per species, taken from week 1 of control temperature treatment. Stars indicate significant differences from both other regions, a circle indicates a significant difference from one other region.

**Table 3.2.** General linear model (GLM) for changes in food web properties according to region, week, and temperature.

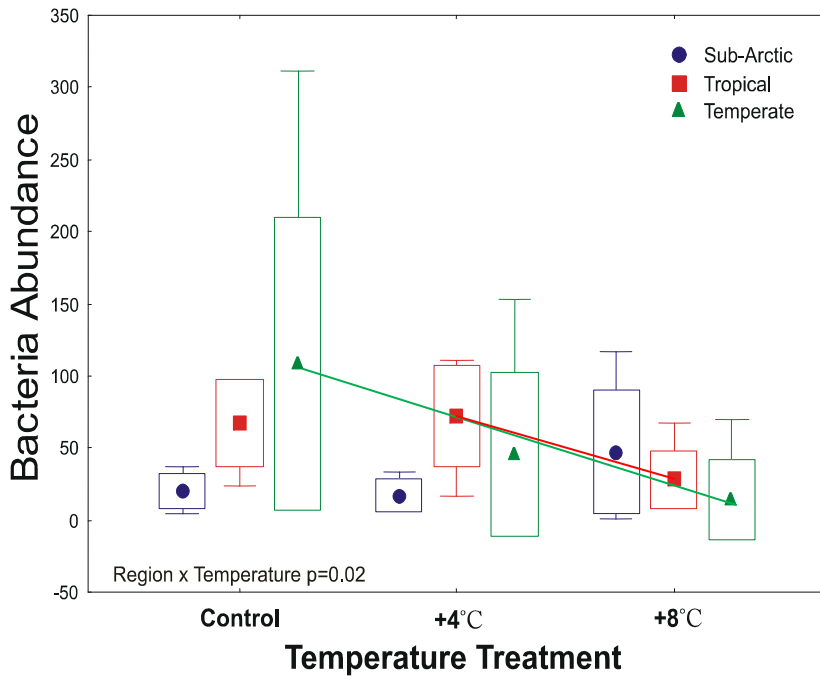
<b>Food web property</b>	<b>Region (df=2)</b>	<b>Week (df=1)</b>	<b>Direction of change</b>
S	<0.001	<0.001	Decrease
L/S	<0.001	<0.001	Decrease
C	<0.001	<0.001	Decrease
% T	<0.001	Not sig.	No change
% I	<0.001	<0.001	Decrease
% B	<0.001	<0.001	Increase
% H	<0.001	Not sig.	No change
GenSD	<0.001	<0.001	Increase
VulSD	<0.001	Not sig.	No change
LinkSD	<0.001	<0.001	Increase
Loop	<0.001	<0.001	Decrease
SWTL	<0.001	<0.001	Decrease
Omniv	<0.001	<0.001	Decrease
MeanSim	<0.001	0.04	Increase
MaxSim	0.02	Not sig.	No change
PredSim	<0.001	<0.001	Increase
PreySim	0.01	<0.001	Increase
Cannibal	<0.001	Not sig.	No change
CC	<0.001	<0.001	Increase



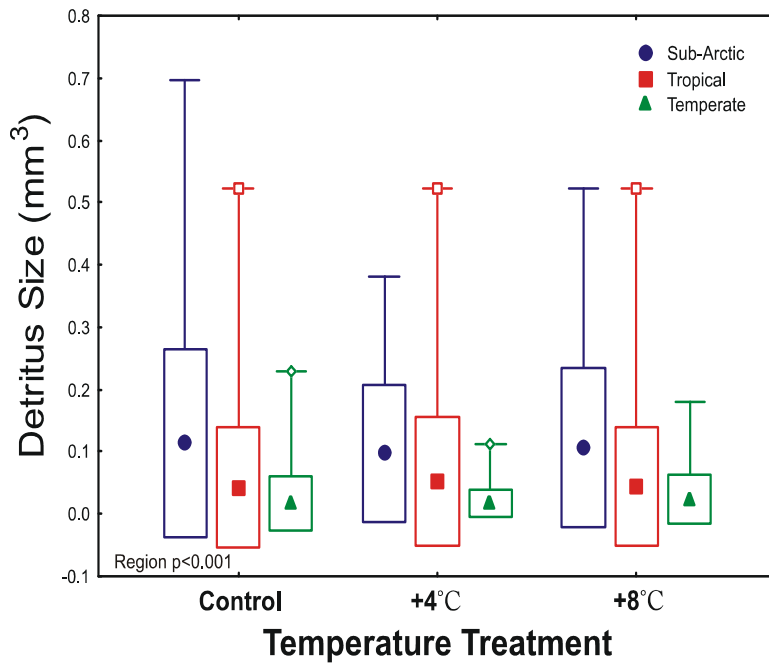
**Figure 3.5.** Change in **a)** fraction of basal species, **b)** generality SD, **c)** mean similarity, and **d)** clustering coefficient over time in the three regions. Significant changes between weeks 1 and 8 are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



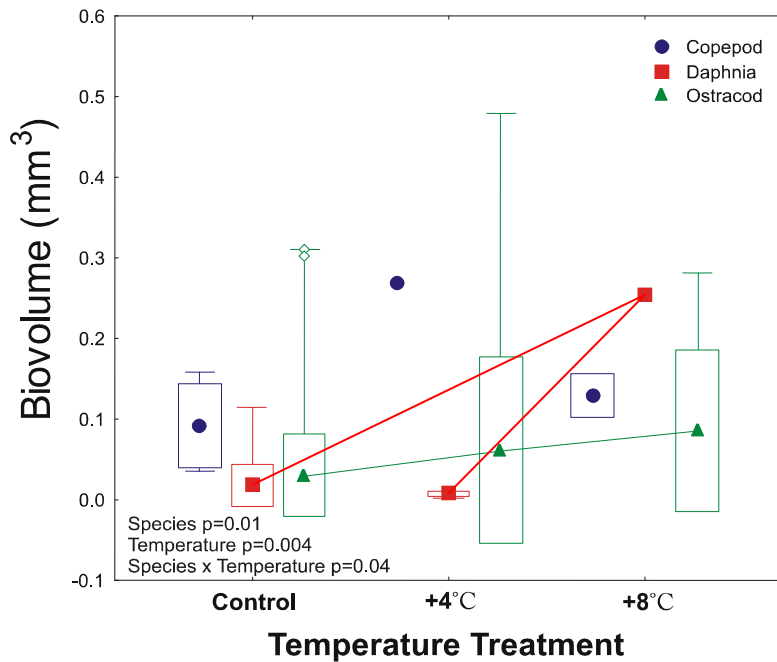
**Figure 3.6.** Connectance in final week of experiment. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



**Figure 3.7.** Bacteria abundance at final week of experiment. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



**Figure 3.8.** Detritus size at final week of experiment. Significant differences between temperature treatments within one region are connected with a line. P values for significant predictors in factorial ANOVA are also shown.



**Figure 3.9.** Mean biovolume of species in tropical region week 8. Significant differences between temperature treatments for a species are connected with a line. P values for significant predictors in factorial ANOVA are also shown.

## CHAPTER 4      **Conclusion**

Global warming is causing rapid species extinctions (Thomas *et al.* 2004; Parmesan 2006). The goals of my research were to track changes at multiple levels of biological organization to determine how effects of warming scale up through a system, and to see how communities adapted to different climates respond to warming. Here, I summarize the major results and conclusions of my findings.

Climate change affects individuals in many different ways, by raising temperature above physiological tolerance limits (Pörtner 2002), as well as by increasing metabolism (Seibel & Drazen 2007), leading to rapid population growth, resource depletion and population crashes (McLaughlin *et al.* 2002), as well as indirectly by changing species phenologies, (Winder & Schindler 2004; Hays *et al.* 2005; Parmesan 2007) ranges, (Perry *et al.* 2005; Parmesan 2006; Schweiger *et al.* 2008) and interactions (Callaghan *et al.* 2004b; Suttle *et al.* 2007; Harmon *et al.* 2009; Walther 2010). The interaction of these direct and indirect consequences of warming, which affect biological systems at all scales of organization, makes predicting the ecological consequences of climate change a challenging task. By comparing similar communities that are adapted to different climates, I was able to separate the effects of warming on physiological tolerance from effects due to changing species interactions. In Chapter 2, I showed non-linear responses to warming along a latitudinal gradient. Contrary to predictions based on cold-adaptation and metabolic theory (Gillooly *et al.* 2001; Addo-Bediako *et al.* 2002; Brown *et al.* 2004), the sub-Arctic region was most robust, lost fewer species, increased in abundance and increased in stability in warmed treatments. These results support the climatic variability hypothesis (Stevens 1989; Addo-Bediako *et al.* 2000) which states that organisms from high latitudes have a more broad thermal tolerance because they have evolved in an environment with greater climatic variations.

The temperate region was found to be most vulnerable to warming with the greatest increase in extinction rate and instability in abundance with increased temperature. The temperate region had the largest mean community biovolume of all regions, as well as a decreased productivity rate with increasing temperature.



Vulnerability of the temperate region to warming was linked to predictions based on metabolic theory, that organisms with larger body sizes require more energy as metabolic rate increases with temperature (Blackburn & Gaston 1999). If these increased resource requirements cannot be met larger organisms will not be able to survive in warmer temperatures (Beisner *et al.* 1997; Petchey *et al.* 1999). Thus, I concluded that temperate regions may have been the most vulnerable to warming due to a combination of a reduction in the amount of resources available and the larger size (and thus resource requirements) of the organisms (Hayward *et al.* 2009).

The effects of warming also differed between functional groups. The detritivore functional group was the most robust to warming over all regions and the herbivore functional group was the most vulnerable (Clarke 2003). Warming increased the biomass of detritus and decreased productivity, indicating that herbivores were limited by available resources while detritivores were not. My results did not show a particularly negative effect on predators; extinction frequency of predators decreased with increasing temperature in the sub-Arctic and in the +4°C treatment in the tropics. The omnivore functional group only had an increased extinction frequency in the +8°C in the temperate region. Omnivorous species feed on different trophic levels, and may have been more robust to increasing temperature as they are able to respond to changes in prey abundance by feeding more intensively on a different trophic level (Fagan 1997; McCann 2000). The weak effects on predators did not support predictions that predators should have been more affected by warming due to stronger interaction strengths with their prey than lower trophic level species (McCann *et al.* 1998; Berlow 1999). One possibility for the weak effect of warming on predators is that many rock pool predators are also scavengers, and thus can feed on both live and dead heterotrophs.

Scaling up to the food web and ecosystem level revealed further explanations for results reported in Chapter 2. The sub-Arctic region was most robust to warming with no change in any food web properties and no changes in respiration and productivity rates, while the temperate region experienced a decrease in connectance with warming, which may have lead to the higher instability that was observed in the temperate communities in Chapter 2. Previous studies on effects of warming at the food web and ecosystem level have found a decrease in top predators (Petchey *et al.* 1999; Voigt *et al.* 2003) and total

food chain length (Arim *et al.* 2007; Woodward *et al.* 2010), and an increase in respiration rate (Calliari *et al.* 2003; Lopez-Urrutia & Moran 2007; O'Connor *et al.* 2009). The results of my study did not support the results of previous research, as fraction of top predators did not decrease in any of the regions, and community respiration rate did not change in the sub-Arctic or tropical region, and decreased with increasing temperature in the temperate region. Food web theory provided a potential explanation for the greater stability of tropical communities in warmed treatments. Tropical food webs had higher links per species, omnivory, and similarity, thus although the tropical and temperate regions both lost species with warming, the tropical webs had higher redundancy so similar species could fill the same niche as any species that went extinct (Petchey 2007). My results show food web theory to be more promising than metabolic theory at making accurate predictions of realistic ecosystem responses to increasing temperature.

The goal of my research was to provide an empirical study testing predictions made from theory and single species experiments on response of complete ecosystems to warming. Global climate change is affecting all parts of the world at all levels of biological organization (Parmesan & Yohe 2003; Parmesan 2006; Walther 2010; Woodward *et al.* 2010), thus it is imperative to determine the differential response of ecosystems adapted to different thermal regimes. I have shown that communities from different regions along a latitudinal gradient do not respond as predicted based on metabolic theory and respond non-linearly to warming along the latitudinal gradient. Instead, studying structural properties of food webs provided the most coherent explanation of vulnerability of temperate communities and robustness of sub-Arctic communities to environmental warming.

## APPENDIX A SUPPLEMENTARY TABLES: CHAPTER 2

**Table A.1.** Univariate results of ANOVA for relative change in community extinction rate

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.704	0.704	19.687	<0.001
Region	2	2.799	1.399	39.142	<0.001
Treatment	1	0.335	0.335	9.368	0.004
Region*Treatment	2	0.162	0.081	2.269	0.120
Error	30	1.072	0.035		
Total	35	4.369			

**Table A.2.** Univariate results of ANOVA for relative change in functional group extinction rate

<b>Herbivore</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	0.537	1	0.537	7.342	0.011
Region	2.383	2	1.191	16.275	<0.001
Treatment	0.296	1	0.296	4.048	0.053
Region*Treatment	0.195	2	0.097	1.335	0.278
Error	2.197	30	0.073		
<b>Detritivore</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	0.054	1	0.054	0.305	0.584
Region	4.850	2	2.425	13.595	<0.001
Treatment	0.587	1	0.587	3.295	0.079
Region*Treatment	0.133	2	0.066	0.375	0.69
Error	5.351	30	0.178		
<b>Omnivore</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1.197	1	1.197	6.080	0.019
Region	1.278	2	0.639	3.246	0.052
Treatment	0.466	1	0.466	2.370	0.134
Region*Treatment	0.050	2	0.025	0.128	0.880
Error	5.909	30	0.196		
<b>Predator</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	0.233	1	0.233	1.087	0.305
Region	3.483	2	1.741	8.111	0.001
Treatment	0.033	1	0.033	0.156	0.695
Region*Treatment	0.750	2	0.375	1.747	0.191
Error	6.442	30	0.214		

**Table A.3.** Univariate results of ANOVA for relative change in community abundance

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	39700.56	39700.56	47.227	<0.001
Region	2	43537.13	21768.57	25.895	<0.001
Treatment	1	6259.45	6259.45	7.446	0.01
Region*Treatment	2	5182.32	2591.16	3.082	0.06
Error	30	25218.58	840.62		
Total	35	80197.48			

**Table A.4.** Univariate results of ANOVA for relative change in functional group abundance

<b>Herbivore</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	17525.35	1	17525.35	40.837	<0.001
Region	27693.17	2	13846.59	32.265	<0.001
Treatment	2657.4	1	2657.4	6.192	0.018
Region*Treatment	3863.31	2	1931.66	4.501	0.019
Error	12874.33	30	429.14		
<b>Detritivore</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	138.454	1	138.454	1.284	0.266
Region	2056.557	2	1028.279	9.537	<0.001
Treatment	306.25	1	306.25	2.840	0.102
Region*Treatment	1164.665	2	582.332	5.401	0.009
Error	3234.447	30	107.815		
<b>Omnivore</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1493.823	1	1493.823	31.544	<0.001
Region	967.355	2	483.678	10.213	<0.001
Treatment	73.102	1	73.102	1.543	0.223
Region*Treatment	27.522	2	13.761	0.290	0.749
Error	1420.702	30	47.357		
<b>Predator</b>	<b>SS</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	33.446	1	33.446	5.634	0.024
Region	173.093	2	86.546	14.580	<0.001
Treatment	0.000	1	0.000	0.000	0.994
Region*Treatment	48.770	2	24.385	4.108	0.026
Error	178.078	30	5.935		

**Table A.5.** Univariate results of ANOVA for relative change in community CV

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.326	0.326	7.396	0.01
Region	2	0.453	0.226	5.135	0.012
Treatment	1	0.192	0.192	4.358	0.045
Region*Treatment	2	0.072	0.036	0.818	0.45
Error	30	1.323	0.044		
Total	35	2.041			

**Table A.6.** Univariate results of ANOVA for relative change in functional group CV

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.197	0.197	6.026	0.02
Region	2	0.570	0.285	8.704	0.001
Temperature	1	0.102	0.102	3.136	0.086
Region*Temperature	2	0.236	0.118	3.609	0.039
Error	30	0.983	0.032		
Total	35	1.894			

**Table A.7.** Univariate results of ANOVA for detritus weight across treatments

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	20.774	20.774	50.534	<0.001
Region	2	39.431	19.715	47.958	<0.001
Temperature	2	2.630	1.315	3.198	0.05
Region*Temperature	4	5.251	1.312	3.193	0.021
Error	46	18.910	0.411		
Total	54	66.102			

**Table A.8.** Univariate results of ANOVA for community biovolume week 8

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	1.994	1.994	75.305	<0.001
Region	2	1.019	0.509	19.238	<0.001
Temperature	2	0.011	0.005	0.224	0.799
Region*Temperature	4	0.264	0.066	2.498	0.043
Error	271	7.177	0.026		
Total	279	9.374			

**Table A.9.** Univariate results of ANOVA for functional group biovolume week 8

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	0				
Region	1	1.003	1.003	63.967	<0.001
Functional Group	2	0.494	0.247	15.765	<0.001
Region*Funct. Group	5	2.234	0.446	28.501	<0.001
Error	530	8.311	0.015		
Total	540	13.769			

**Table A.10.** Univariate results of ANOVA for respiration rate week 8

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	27.623	27.623	106.467	<0.001
Region	2	12.022	6.011	23.169	<0.001
Temperature	2	1.276	0.638	2.459	0.113
Region*Temperature	4	1.047	0.261	1.009	0.428
Error	18	4.670	0.259		
Total	26	19.016			

**Table A.11.** Univariate results of ANOVA for net productivity week 8

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	60.121	60.121	87.985	<0.001
Region	2	22.750	11.375	16.647	<0.001
Temperature	2	3.833	1.916	2.805	0.086
Region*Temperature	4	1.690	0.422	0.618	0.654
Error	18	12.299	0.683		
Total	26	40.574			

APPENDIX B SUPPLEMENTARY FIGURES AND TABLES: CHAPTER 3

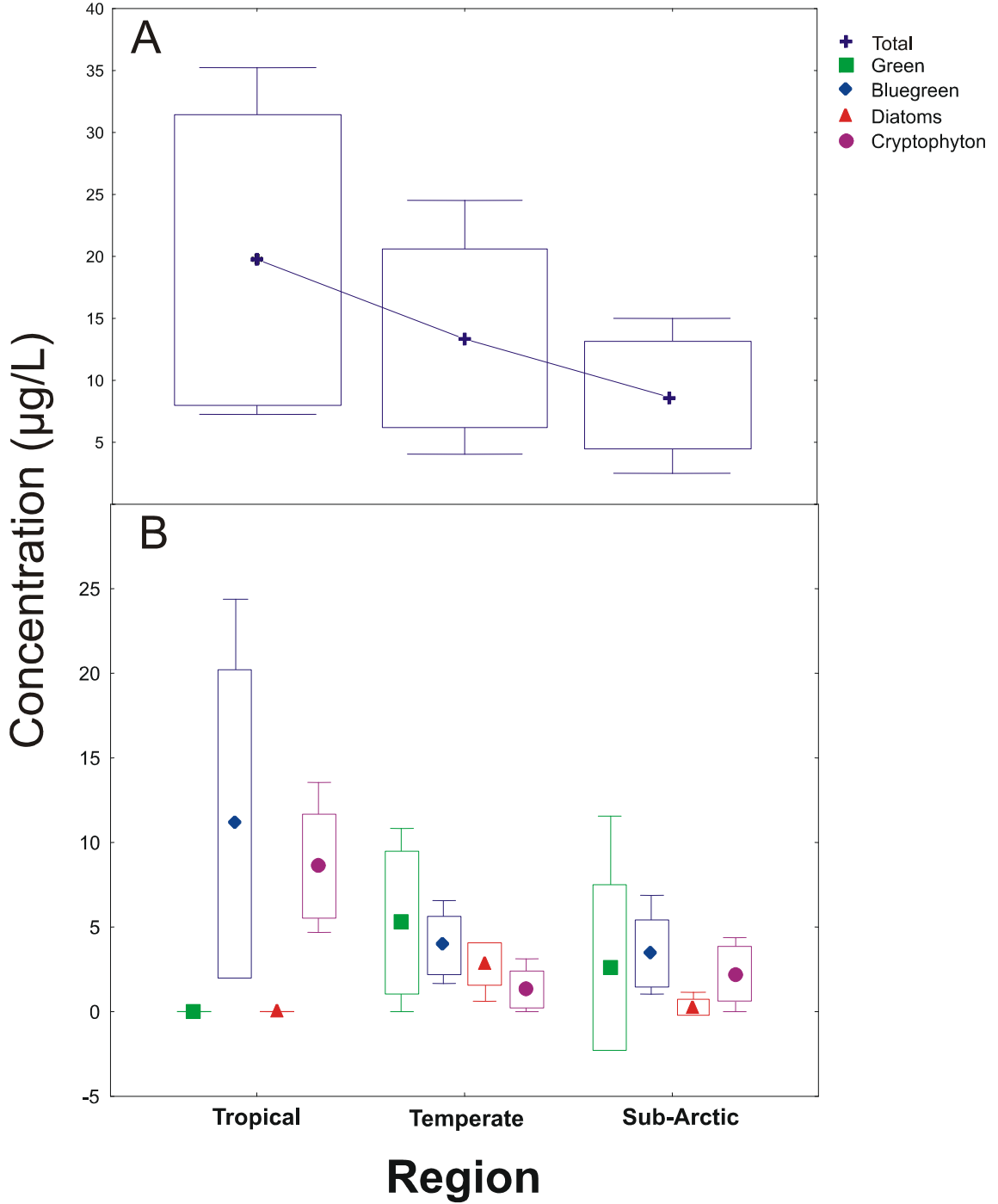


Figure B.1. a) Total algae concentration and b) concentration of each algal class at 24 degrees stock rock pool water

**Table B.1.** Sub-Arctic region predator-prey list

<b>Predator</b>	<b>Prey</b>
<i>Chydorus brevlabris</i>	Periphyton
<i>Chydorus brevlabris</i>	Detritus
<i>Alonella sp.</i>	Periphyton
<i>Alonella sp.</i>	Detritus
<i>Daphnia magna</i>	Phytoplankton
<i>Daphnia magna</i>	Bacteria
<i>Microcyclops varicans</i>	<i>Alonella sp.</i>
<i>Microcyclops varicans</i>	Protists
<i>Microcyclops varicans</i>	<i>Daphnia magna</i>
<i>Megalocypris sp.</i>	<i>Alonella sp.</i>
<i>Megalocypris sp.</i>	<i>Microcyclops varicans</i>
<i>Megalocypris sp.</i>	<i>Megalocypris sp.</i>
<i>Megalocypris sp.</i>	Detritus
<i>Megalocypris sp.</i>	Phytoplankton
<i>Cypridinae eucypris sp.</i>	Phytoplankton
<i>Cypridinae eucypris sp.</i>	Detritus
<i>Cypridinae eucypris sp.</i>	Protists
<i>Cypridinae eucypris sp.</i>	Periphyton
Protists	Protists
Protists	Detritus
Protists	Bacteria
Bacteria	Detritus
Phytoplankton	
Detritus	
Periphyton	



**Table B.2.** Temperate region predator-prey list

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<b>Predator</b>	<b>Prey</b>
<i>Microcyclops varicans</i>	<i>Alonella sp.</i>
<i>Microcyclops varicans</i>	Protists
<i>Microcyclops varicans</i>	<i>Daphnia magna</i>
<i>Microcyclops varicans</i>	<i>Daphnia ambigua</i>
<i>Cypridinae megalocypris sp.</i>	<i>Microcyclops varicans</i>
<i>Cypridinae megalocypris sp.</i>	<i>Alonella sp.</i>
<i>Cypridinae megalocypris sp.</i>	<i>Cypridinae megalocypris sp.</i>
<i>Cypridinae megalocypris sp.</i>	<i>Daphnia ambigua</i>
<i>Cypridinae megalocypris sp.</i>	Detritus
<i>Cypridinae megalocypris sp.</i>	Phytoplankton
<i>Cypridinae eucypris sp</i>	Phytoplankton
<i>Cypridinae eucypris sp</i>	Detritus
<i>Cypridinae eucypris sp</i>	Protists
<i>Cypridinae eucypris sp</i>	Periphyton
<i>Daphnia magna</i>	Phytoplankton
<i>Daphnia magna</i>	Bacteria
<i>Daphnia ambigua</i>	Phytoplankton
<i>Daphnia ambigua</i>	Bacteria
<i>Alona sp.</i>	Periphyton
<i>Alona sp.</i>	Detritus
<i>Alonella sp.</i>	Periphyton
<i>Alonella sp.</i>	Detritus
Protists	Protists
Protists	Detritus
Protists	Bacteria
Bacteria	Detritus
Phytoplankton	
Detritus	
Periphyton	

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**Table B.3.** Tropical region predator-prey list

<b>Predator</b>	<b>Prey</b>
<i>Ceriodaphnia lacustris</i>	Phytoplankton
<i>Ceriodaphnia lacustris</i>	Bacteria
<i>Alonopsis sp.</i>	Periphyton
<i>Alonopsis sp.</i>	Detritus
<i>Cypridopsis cf. mariae Rome</i>	Phytoplankton
<i>Cypridopsis cf. mariae Rome</i>	Detritus
<i>Cypridopsis cf. mariae Rome</i>	Periphyton
<i>Cypridopsis cf. mariae Rome</i>	Protists
<i>Paracyclops sp.</i>	<i>Alonopsis sp.</i>
<i>Paracyclops sp.</i>	Protists
<i>Paracyclops sp.</i>	<i>Ceriodaphnia lacustris</i>
<i>Paracyclops sp.</i>	<i>Cypridopsis cf. mariae Rome</i>
<i>Paracyclops sp.</i>	<i>Paracyclops sp.</i>
<i>Potamocypris sp.</i>	<i>Alonopsis sp.</i>
<i>Potamocypris sp.</i>	<i>Ceriodaphnia lacustris</i>
<i>Potamocypris sp.</i>	Detritus
<i>Potamocypris sp.</i>	Phytoplankton
<i>Potamocypris sp.</i>	<i>Paracyclops sp.</i>
<i>Cypricercus sp.</i>	<i>Alonopsis sp.</i>
<i>Cypricercus sp.</i>	<i>Ceriodaphnia lacustris</i>
<i>Cypricercus sp.</i>	Detritus
<i>Cypricercus sp.</i>	Phytoplankton
<i>Cypricercus sp.</i>	<i>Paracyclops sp.</i>
<i>Candona sp.</i>	<i>Alonopsis sp.</i>
<i>Candona sp.</i>	<i>Ceriodaphnia lacustris</i>
<i>Candona sp.</i>	Detritus
<i>Candona sp.</i>	Phytoplankton
<i>Candona sp.</i>	<i>Paracyclops sp.</i>
<i>Candona sp.</i>	<i>Cypridopsis cf. mariae Rome</i>
<i>Candona sp.</i>	<i>Cypricercus sp.</i>
<i>Candona sp.</i>	<i>Potamocypris sp.</i>
<i>Candona sp.</i>	<i>Candona sp.</i>
Protists	Protists
Protists	Detritus
Protists	Bacteria
Bacteria	Detritus
Phytoplankton	
Detritus	
Periphyton	

**Table B.4.** General linear model (GLM) for changes in food web properties according to region, week, and temperature.

<b>S</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	248.170	248.170	218.598	<0.001
Week	1	171.216	171.216	150.814	<0.001
Region	2	57.265	28.632	25.220	<0.001
Temperature	2	2.442	1.221	1.075	0.342
Region*Temperature	4	3.210	0.802	0.707	0.587
Error	257	291.767	1.135		
Total	266	527.760			
<b>L/S</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	18.493	18.493	182.683	<0.001
Week	1	14.292	14.292	141.184	<0.001
Region	2	22.309	11.154	110.190	<0.001
Temperature	2	0.250	0.125	1.239	0.291
Region*Temperature	4	0.393	0.098	0.971	0.423
Error	257	26.016	0.101		
Total	266	62.740			
<b>C</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.021	0.021	80.371	<0.001
Week	1	0.010	0.010	39.793	<0.001
Region	2	0.254	0.127	474.601	<0.001
Temperature	2	0.000	0.000	0.440	0.644
Region*Temperature	4	0.000	0.000	0.917	0.454
Error	257	0.068	0.000		
Total	266	0.333			
<b>%T</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.006	0.006	2.196	0.139
Week	1	0.010	0.010	3.716	0.054
Region	2	1.647	0.823	300.915	<0.001
Temperature	2	0.005	0.002	0.941	0.391
Region*Temperature	4	0.003	0.000	0.321	0.863
Error	257	0.703	0.002		
Total	266	2.370			

<b>%I</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.624	0.624	81.217	<0.001
Week	1	0.454	0.454	59.087	<0.001
Region	2	2.214	1.107	143.948	<0.001
Temperature	2	0.001	0.000	0.076	0.926
Region*Temperature	4	0.030	0.007	0.982	0.417
Error	257	1.976	0.007		
Total	266	4.657			
<b>%B</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.239	0.239	59.188	<0.001
Week	1	0.328	0.328	81.062	<0.001
Region	2	0.078	0.039	9.735	<0.001
Temperature	2	0.011	0.005	1.370	0.255
Region*Temperature	4	0.028	0.007	1.77	0.135
Error	257	1.042	0.004		
Total	266	1.484			
<b>%H</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.000	0.000	0.133	0.715
Week	1	0.000	0.000	0.284	0.594
Region	2	0.688	0.344	165.618	<0.001
Temperature	2	0.004	0.003	1.145	0.319
Region*Temperature	4	0.010	0.002	1.246	0.291
Error	257	0.534	0.002		
Total	266	1.239			
<b>GenSD</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.612	0.612	46.716	<0.001
Week	1	1.053	1.053	80.327	<0.001
Region	2	0.855	0.427	32.639	<0.001
Temperature	2	0.039	0.019	1.506	0.223
Region*Temperature	4	0.106	0.026	2.034	0.090
Error	257	3.369	0.013		
Total	266	5.397			
<b>VulSD</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.002	0.002	0.220	0.639
Week	1	0.041	0.041	3.689	0.055
Region	2	1.271	0.635	57.207	<0.001
Temperature	2	0.015	0.007	0.696	0.499
Region*Temperature	4	0.025	0.006	0.581	0.675
Error	257	2.856	0.011		
Total	266	4.210			

<b>LinkSD</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.360	0.360	62.971	<0.001
Week	1	0.485	0.485	84.928	<0.001
Region	2	0.184	0.092	16.092	<0.001
Temperature	2	0.010	0.005	0.961	0.383
Region*Temperature	4	0.045	0.011	1.986	0.097
Error	257	1.469	0.005		
Total	266	2.189			
<b>Loop</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.214	0.214	92.038	<0.001
Week	1	0.148	0.148	63.527	<0.001
Region	2	1.692	0.846	363.065	<0.001
Temperature	2	0.004	0.002	1.013	0.364
Region*Temperature	4	0.011	0.002	1.266	0.283
Error	257	0.598	0.002		
Total	266	2.438			
<b>SWTL</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	1.827	1.827	130.873	<0.001
Week	1	0.883	0.883	63.293	<0.001
Region	2	1.126	0.563	40.360	<0.001
Temperature	2	0.016	0.008	0.584	0.558
Region*Temperature	4	0.059	0.014	1.058	0.377
Error	257	3.588	0.013		
Total	266	5.650			
<b>Omniv</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.545	0.545	106.967	<0.001
Week	1	0.411	0.411	80.564	<0.001
Region	2	1.363	0.681	133.652	<0.001
Temperature	2	0.003	0.001	0.354	0.701
Region*Temperature	4	0.014	0.003	0.696	0.595
Error	257	1.311	0.005		
Total	266	3.084			
<b>MeanSim</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.000	0.000	0.000	0.980
Week	1	0.001	0.001	3.953	0.047
Region	2	0.055	0.027	74.412	<0.001
Temperature	2	0.000	0.000	0.859	0.424
Region*Temperature	4	0.000	0.000	0.568	0.685
Error	257	0.096	0.000		
Total	266	0.155			

<b>MaxSim</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.017	0.017	10.620	0.001
Week	1	0.000	0.000	0.009	0.924
Region	2	0.039	0.019	11.775	0.000
Temperature	2	0.000	0.000	0.286	0.751
Region*Temperature	4	0.003	0.000	0.467	0.759
Error	257	0.431	0.001		
Total	266	0.474			
<b>PredSim</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Week	1	0.011	0.011	21.682	<0.001
Region	2	0.240	0.120	224.015	<0.001
Temperature	2	0.000	0.000	0.911	0.403
Region*Temperature	4	0.000	0.000	0.299	0.877
Error	257	0.137	0.000		
Total	266	0.392			
<b>PreySim</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.033	0.033	34.743	<0.001
Week	1	0.053	0.053	55.102	<0.001
Region	2	0.008	0.004	4.557	0.011
Temperature	2	0.001	0.000	0.636	0.529
Region*Temperature	4	0.005	0.001	1.505	0.2
Error	257	0.250	0.000		
Total	266	0.320			
<b>Cannibal</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.012	0.012	8.925	0.003
Week	1	0.004	0.004	3.133	0.077
Region	2	0.342	0.171	123.323	<0.001
Temperature	2	0.000	0.000	0.252	0.777
Region*Temperature	4	0.003	0.000	0.585	0.673
Error	257	0.356	0.001		
Total	266	0.706			
<b>CC</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.031	0.031	11.239	<0.001
Week	1	0.049	0.049	17.466	<0.001
Region	2	0.612	0.306	108.859	<0.001
Temperature	2	0.001	0.000	0.202	0.816
Region*Temperature	4	0.004	0.001	0.361	0.835
Error	257	0.723	0.002		
Total	266	1.393			

**Table B.5.** Univariate results of ANOVA for bacteria abundance across treatments

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	119402	119402	58.213	<0.001
Region	2	9465.9	4732.9	2.307	0.110
Temperature	2	11515.6	5757.8	2.807	0.070
Region*Temperature	4	26356.8	6589.2	3.212	0.020
Error	46	94350.2	2051.1		
Total	54	141684.4			

**Table B.6.** Univariate results of ANOVA for detritus size across treatments

	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
Intercept	1	0.884	0.884	95.094	<0.001
Region	2	0.355	0.177	19.111	<0.001
Temperature	2	0.000	0.000	0.018	0.981
Region*Temperature	4	0.006	0.001	0.185	0.945
Error	261	2.427	0.009		
Total	269	2.789			

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