

Chapter 1:
The wind field does not improve predictions of annual average zooplankton abundance in Harp Lake, Ontario

Abstract

Zooplankton ecologists have generated a large number of multi-decade, mid-lake, zooplankton datasets, but the long-term dynamics of zooplankton heterogeneity induced by wind-driven currents has never been explored. If wind speed or direction changes over time, then the distribution of animals may also change, and abundance assessed at a single station may have changed with the wind field. In this study, I determine if changes in the annual averages of the abundance of 4 Cladoceran, 2 Calanoid and 2 Cyclopid species in Harp Lake, Ontario, were related to the wind field (speed and direction) between 1980 and 2004. Zooplankton data were generated from a volume-weighted composite of multiple vertical hauls taken from a single station at the deepest point of the lake. Wind speed has decreased, on average by 25%, while wind direction has shifted by 21 degrees towards the north. In order to assess if the variation in abundance was influenced by this change in the wind field, I first needed to correct for the other known long-term changes in lake's zooplankton. Hence, to consider how annual climatic differences might have influenced the community, I began by regressing zooplankton abundance against the presence/absence of *Bythotrephes*, the average number of days since spring ice break-up, and the average surface temperature on sampling days. I then determined if the residual variation in average zooplankton abundance from these models was correlated with the wind. Despite long-term changes in the wind field, linear-linear (speed) and linear-circular (direction) correlations of annual residual abundance of 7 of

the 8 species were not predictable from the wind fields using the averages of the sample day. The exception was *D. mendotae*, for which residual abundance was correlated with wind direction ($r^2=0.2300$, $p=0.005$) meaning that the high residual abundance was correlated with a particular wind direction. *D. mendotae* is a large, fast swimming cladoceran that may be predictably responding under turbulent mixing and the resulting thermocline tilting in the hypolimnion. In summary, on an annual basis, long-term changes in zooplankton abundance were not improved by changes in the wind field.

Introduction

Because of predictable responses to anthropogenic stressors, zooplankton have been used to document both the damage caused by, and subsequent recovery from various pollutants, such as acid rain (Marmorek and Korman 1993; Arnott *et al.* 2001). However, failure to consider spatial dynamics may reduce the usefulness of zooplankton as bioindicators of damage and recovery (MacKenzie and Leggett 1991). The distribution of zooplankton varies vertically and horizontally in lakes, and this distribution should be understood if we are to use them as indicators. The horizontal distribution of zooplankton is influenced by predation by littoral fish (Glizicz and Rykowska 1992), and wind-induced currents (Burkes *et al.* 2002). The diel vertical distribution of many species changes in response to a warming climate (Pinel-Alloul 1995; Lampert *et al.* 2003; Semyalo *et al.* 2009), to predation pressure from macroinvertebrates (Young and Yan 2008), fish (Dodson *et al.* 1997; Larsson and Lampert 2011), and to UV radiation (Lampert 1989; Leech and Williamson 2001).

Hence, to understand the impacts of both natural and anthropogenic drivers on zooplankton we need to understand the determinants of their spatial heterogeneity.

In comparison with other biota, the correlations of zooplankton community structure with many environmental stressors (e.g., shoreline disturbance, altered water chemistry, riparian disturbance, littoral macrophyte coverage and human development) are relatively weak (Allen et al. 1999; O'Connor et al. 2000). Thus, zooplankton have not been routinely recommended for inclusion in large scale, bioassessment programs (Jeppesen et al. 2011). However, the majority of zooplankton sampling procedures would not capture the patchiness or heterogeneous distributions known to occur (Folt and Burns 1999; Pinel-Alloul and Ghadouani 2007). Typical zooplankton monitoring programs use short-term studies with few sampling stations (Allen et al. 1999). Thus accurate zooplankton community distributions are unlikely. Patchiness is indeed the normal expectation (Folt and Burns 1999). For example, Malone and McQueen (1983) found that horizontal distributions of zooplankton were patchy even in small, single-basin lakes (Pinel-Alloul and Ghadouani 2007). Yan and Strus (1980) found that this patchiness could commonly include the standing stock of the entire community, not just individual species. Thus, we should not be surprised by low correlations of zooplankton assemblage structure with environmental factors in 186 northeastern United States lakes when sampling involved a single mid-lake station (Allen et al. 1999). As patchiness may contribute a large portion of the unexplained variance in large-scale assessments, it may be too soon to conclude that correlations of zooplankton community structure with environmental drivers are weaker than similar relationships for other groups of biota.

The risks of ignoring zooplankton patchiness in studies of zooplankton dynamics are understood (Prepas and Rigler 1978), but still usually ignored.

The body size, swimming ability and diel vertical migration of zooplankton influence how they are re-distributed by wind-driven currents in lakes (Dirnerger and Threlkeld 1986; Zurek and Bucka 2004). The swimming speed of cyclopoids increases with body size (Saunders and Lewis 1988); therefore, large animals should be able to maintain their position in currents better than smaller conspecifics. It is expected that organisms inhabiting the surface waters of lakes will be more affected by wind-induced currents than those organisms found in the meta- and hypolimnion (Naithani et al. 2003). Zooplankton that are strong swimmers, such as *Leptodiptomus minutus* (0.340 cm/s, Muirhead and Sprules 2003) can swim against and out of turbulent layers of the water and remain in a specific location (Woodson et al. 2005). Epilimnetic zooplankton require greater swimming abilities to maintain their position in the more turbulent surface layers. Those zooplankton found in deeper waters inhabit denser and less turbulent water than epilimnetic species, and therefore, require less effort to maintain their position in the water column (Woodson et al. 2005). Therefore, we need to understand wind-driven water movements and density gradients in lakes as well as the behaviour and swimming abilities of zooplankton to understand the distribution of animals. It starts with the wind.

What generates wind? Wind is the product of Newton's Second Law of Motion (force = mass*acceleration) and the friction between air masses and surfaces (Ahrens 2000). When a low-pressure air mass (generally warm air) comes in contact with a high-pressure air mass (generally cooler air), an intervening pressure gradient is generated

(Ahrens 2000). A high-pressure air mass will always move towards a low-pressure air mass (Butz 2004). Newton's 2nd law implies that the acceleration and change in pressure within the pressure gradient causes force on an object, e.g., wind is the result of the forces operating between air masses with different pressures (Ahrens 2000). The pressure gradient determines the strength of the wind, e.g., its speed, moving over a surface (Ahrens 2000).

Wind speeds at surfaces are influenced by the roughness of that surface. Optimal laminar flow is consistent with smoothly gliding air masses over a smooth, stationary medium (Ahrens 2007). Surface roughness caused by trees and buildings increases eddy viscosity, which then generates friction among eddies and an irregular production of whirling winds (Ahrens 2007). For example, Tanentzap et al. (2007) found a 34% decrease in annual average wind speeds at Sudbury Airport over the preceding 3 decades attributing this to an increase in surface roughness, caused by forest growth in a previously barren, industrial landscape. It is important to note that the airflow over rough land versus smooth water has a dramatic effect on wind dynamics (Ahrens 2007). Since water is smoother than land, there is less friction and therefore wind speeds are faster over large water bodies compared to adjacent, normally "rougher" land (Ahrens 2007). Aside from wind speed, wind direction itself can have interesting effects on the climate and weather systems surrounding bodies of water. Changes in wind direction can cause changes in the climate especially since lakes are not commonly circular. The direction of wind can bring in cooler air masses to a particular area and cause storms and windy behaviour.

The interplay of wind dynamics with water masses, and the swimming ability and diel behaviour of zooplankton all influence zooplankton distribution. The topography and cover of the watershed and the shape and size of the lake basin influence water movement within the lake (Ahrens 2007). Winds mix and move water masses thus altering the distribution of zooplankton populations in the water column (George and Edwards 1976; Cloern et al. 1992; Naithani et al. 2003; Vanschoenwinkel et al. 2008). Wind-induced currents begin in the epilimnion where water is pushed downwind, the direction away from the origin of the blowing wind (Zurek and Bucka 2004) (Figure 1.1). Plankton that prefer epilimnetic waters will be concentrated downwind if they are able to swim faster than the speed of the downwelling water at the downwind end of the lake. If animals are not able to swim faster than the downwelling current, they will be moved, conveyor-like, downward with the downwelling current, then upwind with the deeper water return current (George 1981, Blukacz et al. 2009). In this case, animals will be concentrated into lower strata (Naithani et al. 2003). In contrast, plankton that prefer lower strata (e.g., metalimnion or hypolimnion) are upwelled by internal waves (seiches) and may become concentrated upwind in warmer surface waters (Naithani et al. 2003). Of course, wind speed and direction change frequently, thus actual distributions of animals are a product of recent wind forcing, and a legacy of preceding wind fields, where the influence of past winds decreases with year.

Changes in zooplankton distribution that are induced by changes in the wind may confound our ability to detect the influence of many drivers on zooplankton abundance, especially if we sample at only one site. Few studies have explored the long-term noise

that can be generated from wind-induced currents and the impact it may have on their results (Owens 1989; Blukacz et al. 2009; Mackenzie and Leggett 1991). For example, Mackenzie and Leggett (1991) found that weak wind-induced currents caused zooplankton to be patchily distributed on a vertical scale of 5-10 m. Although they focused on tracking predator-prey contact rates, that study provides an example of how the wind may affect zooplankton distributions.

Here, I focus on Harp Lake, a small (71.4 ha), single-basin, Canadian Shield lake that has been monitored by personnel of the Ontario Ministry of the Environment's (MOE's) Dorset Environmental Science Centre (DESC) for over 30 years (Yan and Strus 1980; Yan and Pawson 1997; Paterson et al. 2008; Yan et al. 2008; Young et al. 2009). Zooplankton are collected from Harp Lake at a single permanent station at the deepest portion of the lake (Yan et al. 2008). Harp Lake is changing in many ways. NaCl levels are increasing because of the maintenance of winter roads (Molot and Dillon 2008), and DOC levels are increasing likely because of slight reductions in acidity (Monteith et al. 2007), and climatic changes (Keller et al. 2008). Phosphorus and Ca levels are declining (Yan et al. 2008).

In the early 1990s, Harp Lake was invaded by a nonindigenous zooplanktivore, *Bythotrephes longimanus*, which has reduced zooplankton richness and affected the structure of the zooplankton community (Yan et al. 2002). Dumitru et al. (2001) found that *Bythotrephes* consumption has reduced or eliminated several zooplankton species despite their high production (Yan and Pawson 1997). Zooplankton species that remain in Harp Lake are those that are too large for *Bythotrephes* to consume (e.g., *Holopedium*),

too fast for *Bythotrephes* to catch (e.g., *Daphnia mendotae*) (Dumitru et al. 2001), or reside in layers *Bythotrephes* does not frequent (e.g. *L. sicilis*). Petruniak (2009) found that *Bythotrephes* had an aggregated spatial distribution in Harp Lake in 2007, both across the whole lake and in the region of the lake outflow, and her model runs suggested there were predictable changes in the horizontal position of *Bythotrephes* in the lake from day to night. Therefore, Harp Lake is ideal for my study because the native zooplankton species may exhibit the same wind-induced patterns that have been observed for *Bythotrephes*.

I also chose Harp Lake because of its sampling frequency (fortnightly in all years, Yan et al. 2008), its predator-simplified zooplankton assemblage, its probable lack of water quality or habitat control of its zooplankton assemblage, its well oxygenated hypolimnion (unlike several of the other dimictic lakes), the fact that it never acidified, that Ca^{2+} levels were always above damaging thresholds (Ashforth and Yan 2008), that it had a strong mid-record signal from the invasion of *Bythotrephes*, and, because the vertical distribution of zooplankton in the lake had been assessed. Studies of zooplankton species in temperate lakes like Harp Lake (e.g., *D. mendotae*) have found that animals migrate to different water depths, depending on factors such as predator presence and food availability (Pinel-Alloul 1995; Folt and Burns 1999). Young and Yan (2008) discovered that *Daphnia*, *Bosmina*, and copepod populations migrated vertically at night in Harp Lake. In particular, *Daphnia mendotae* occupied the epilimnion during the night and migrated to the hypolimnion during the day (Young and Yan 2008).

Despite research on the influence of wind on zooplankton distributions, no one has determined if long-term changes in the wind contribute to the variability in zooplankton abundance. Such a study would be justified because wind speed does have a significant effect on estimates of zooplankton biomass (Frank and Leggett 1982), and also alters zooplankton distributions. Here my overall goal was to examine the long-term trends of zooplankton abundance in Harp Lake, and to determine if these trends are correlated with changes in the wind field (speed and direction) examined at annual steps. My objectives were: (1) to determine if there were significant long-term trends in the regional wind field from 1980-2004, (2) to extract the annual residuals of zooplankton abundance from regression models based on *Bythotrephes* P/A, average surface temperature, and days since spring ice break-up, and (3) to examine the correlation between the residual abundance from these models and the regional wind field patterns.

I predict that zooplankton species inhabiting the surface waters are affected by wind-induced currents, that the residual abundance of epilimnetic species will not correlate with the wind field, because their distribution in the surface waters will be homogenized by the wind. Those species typically found in the lower depth strata will be less affected by the wind field, and will be able to hold their position in the water column at lower wind speeds. As wind speeds fall to a point where these animals can resist advection by wind-induced currents, they will become more patchy as well as being able to hold their position in the water column. Thus residual abundance will increase for these species as wind speed falls. For example, Visser et al. (2009) found that large, strong swimming copepods could hold their position in the water despite the turbulent

mixing. The relatively high swimming speed of copepods versus cladocerans is well documented, thus copepods are expected to withstand the wind-induced current (Link 1996; Woodson et al. 2005; Visser et al. 2009). Smaller and slower zooplankton species will be easily re-distributed in the water column and will not exhibit any predictable changes in residual abundance. In other words, any reduction in wind speeds should not be enough to let patches form and thus allow a change in the distributional patterns that would lead to a correlation with the residual abundance and the wind. Larger and quicker zooplankton species will not be so easily re-distributed in the water column and will be able to maintain their distribution pattern.

Methods

Harp Lake (45°23'N, 79°07'W) is a small (71.4 ha), stratified, dimictic lake with a maximum depth of 37.5 m (Paterson et al. 2008; Young et al. 2009) (Figure 1.2). It is one of 8 Canadian Shield lakes in south-central Ontario that has been the subject of long-term biological and chemical monitoring by the Ontario Ministry of the Environment's Dorset Environmental Science Centre (DESC) (e.g., Yan and Strus 1980; Yan et al. 2008). Crustacean zooplankton are collected biweekly in vertical net tows (from 6, 6, 13, 21 and 30m to the surface) at the deepest portion of lake during the ice-free season using a conical zooplankton net with a length of 138.43 cm, a diameter of 12.4 cm, and a mesh size of 76 µm (Girard et al. 2007). Sample volumes are calculated from net haul lengths and the measured net filtration efficiency (Girard et al. 2007).

Over the last 30 years, many limnological changes have been documented in south-central, Ontario lakes, and Harp Lake is no exception. It has experienced increased concentrations of Na, Cl, Mg and dissolved organic carbon (DOC) and decreases in pH, Ca and total phosphorus (TP), for reasons discussed by Paterson et al. (2008), Molot and Dillon (2008), and Yan et al. (2008). In the early 1990s, Harp Lake was invaded by a predatory Eurasian cladoceran species, *Bythotrephes longimanus*, which has reduced zooplankton species richness and affected the zooplankton community structure of the lake (Yan et al. 2002). Yan and Pawson (1997) found that prior to the invasion of *Bythotrephes* in 1993, the total biomass and diversity of the zooplankton community was relatively stable. After the invasion, two larger cladocerans (*D. mendotae* and *H. glacialis*) became more abundant while many species declined or completely disappeared including *D. birgei*, *B. tubicen* and *T. extensus* (Yan and Pawson 1997).

I used zooplankton data from 1980-2004 for my study. Yan et al. (2008) have reported the general changes in the composition, body size and species richness of the zooplankton community of the lake over this study period, but have not considered possible effects of the wind field on the lake zooplankton. N. D. Yan provided me with the raw zooplankton data.

Bythotrephes in Harp Lake have been found to respond to the wind field (Petruniak 2009), and I saw no reason why other zooplankton should not also respond. In addition, given the fortnightly sampling for multiple decades, the abundance of data was vast. Zooplankton characteristics that might influence their vulnerability to the wind, excluding abundance and body size (which came from the Harp Lake data) were

identified from a review of literature. I selected species for this study based on their body size, their swimming ability, pelagic habitat, and their frequency of occurrence in the database (common and abundant taxa). I modelled the relationship between annual zooplankton abundance and *Bythotrephes* P/A, the average surface temperature, and average number of days of sampling since ice off, then determined if there were any significant correlations between the residual variation in abundance and the wind field. As independent variables I first used *Bythotrephes* P/A to control for the long-term effects of the *Bythotrephes* invasion. As the first correction of the temporal sequence for interannual differences in heating season, I used Days since ice-free, e.g., the average number of days since spring ice break of all the sample dates in the year. This measure was used to explain changes in zooplankton abundance that may be due to the length of the ice-free season. Finally, I used the rate of surface heating to control for any changes the surface and bottom water temperatures (average surface temperature). These models were run using simple multiple linear regression, and then I examined the correlation of their residuals with the wind field (speed and direction, separately). Volumetric abundances of zooplankton species were available from 291 dates from 1980 to 2004 in Harp Lake. Missing values, indicating that animals were not detected in the count, were replaced with zeroes. Abundance values of the species were sorted by date, averaged by year, and compiled into tables along with the additional heating season and *Bythotrephes* P/A variables (Yan et al. 2008). I expected that *Bythotrephes* P/A would account for previously observed changes in abundances of several species associated with the arrival of this invader in 1993 (Yan et al. 2008; Young et al. 2009). My second predictor

variable, “Days since ice-free date” was designed to reflect the fact that the date of spring ice-breakup varies substantially among years. I took ice break-up dates from the MOE, calculated the days of ice break-up from that date to each sampling date, and the average of these differences between sampling and ice break-up up formed my second annual integrator – average number of days since ice break-up. Then I took the average of all these values for each year as my average days since ice break-up. My average surface temperature variable was a measure of the water temperatures in the surface waters in each year, as changes that occur in the heating of the surface waters over the study period may affect abundance. In other words, the annual average surface temperature using the heating rates over baselines of the hypolimnion on the days of sampling. To calculate the average surface temperature (AST) metric I used the water temperature at 1 m depth from the surface and took the average of all those measured values for the year. Days since ice-free and the average surface temperature were used in addition to *Bythotrephes* P/A to better explain the variation in abundance that may be attributable to a potentially warming climate (denoted by longer ice-free seasons or warmer the surface water heating with year)

The following zooplankton species were used (Table 1.1): *Daphnia mendotae*, *Holopedium glacialis* (formerly *Holopedium gibberum*), *Bosmina tubicen*, *Diaphanosoma birgei*, *Leptodiptomus sicilis*, *Leptodiptomus minutus*, *Diacyclops bicuspidatus thomasi* and *Tropocyclops extensus* (formerly *Tropocyclops prasinus mexicanus*) based mainly on their frequency of occurrence in the database, but also to provide a range of swimming speed, body size, order/class and preferred temperature

stratum. Abundance and body size were taken from the MOE's Harp Lake data. A literature search was done using ISI's Web of Science using the keywords: zooplankton, distribut*, body size, swim* speed, diel migrat*, feed*, vertical depth and the scientific names of each zooplankton species. This search provided the information needed to compile the physical and behavioural characteristics of the selected species.

As dependent variables for each species, I considered: abundance, LOGabundance, SQRTabundance. The later two variables were used to transform the averaged abundance data and the use of one instead of the other depended on the residuals that resulted from these regression models. As independent variables, I considered the dummy variable *Bythtrophes* P/A (Bytho), Days since ice-break (or the average Julian date since ice-free of all the samples in the year) (Free), the average surface temperature in Julian date at the last sample date (AST), Free², AST², Bytho x Free, (Bytho x Free)², Bytho x AST, (Bytho x AST)², Free x AST, and (Free x AST)². All species had abundance log-transformed (LogAbundance) to reduce heterogeneity and to reduce outliers observed in regression plots.

Wind Characteristics

Wind direction (recorded in degrees) and wind speed (recorded in km/h) were taken from the online National Climate Data and Information Archives through Environment Canada (http://climate.weatheroffice.ec.gc.ca/climateData/canada_e.html) as hourly data from 1980-2004 on the zooplankton sample dates. All wind directions report the direction the wind is blowing from. The MOE's DESC maintains a

meteorological station in the Harp Lake watershed, however forest growth around the MET station has reduced the accuracy of, and introduced substantial bias to, the wind data. Therefore, I used the data from the next closest, well-maintained, meteorological recording station at the Muskoka Airport near Bracebridge, Ontario, Canada (44°58'29N, 79°18'12W, approximately 60 km from Harp Lake). The forest height around the Muskoka Airport is maintained for aircraft safety (personal communication, Mark Stirling, Manager). The nearest tree is 75 m from the anemometer. This anemometer was upgraded and moved a couple of yards in 2009, but otherwise it has not been changed or its use interrupted during the period of my study, e.g., 1980 to 2004 (personal communication, Mark Stirling, Manager, Muskoka Airport).

How does the wind speed compare between Muskoka Airport and Harp Lake?

The wind field at the Muskoka Airport may not accurately reflect the wind field over Harp Lake. I checked this in 2 ways: (1) by comparing the 2003-2004 wind speed measurements from Harp Lake and the Muskoka Airport, and (2) by comparing the wind data the DESC generates at Paint Lake, which is closer to Harp Lake, with those from the Muskoka Airport from 1990-2004. Both methods determined that Harp Lake wind speeds were much lower than Muskoka Airport and Paint Lake wind speeds. Harp Lake winds are less strong because of the forest growth over the study period.

We could not use the wind data from Harp Lake because its speeds were artefactually low compared to other wind speeds in the area and missed potentially important trends (Figure 1.3). The simplest explanation is that afforestation at the site

has swamped the anemometer, artefactually lowering wind speeds. Hence, I could not use the Harp Lake MET data. The range of wind speeds from Muskoka Airport was 0-9.734 m/s, whereas the range from Harp Lake was 0.291-3.172 m/s. The average wind speed for Muskoka Airport for 2003-2004 was 2.610 m/s, while the average was 1.210 m/s for Harp Lake. There was a significantly increasing wind speed for Muskoka Airport ($r=0.13$, $p=0.0013$) from 2003-2004 while Harp Lake wind speed did not significantly change ($r=-0.05$, $p=0.2267$).

Comparisons of data from Paint Lake and the Muskoka Airport indicate that wind speeds are fairly constant in Muskoka over the scale of tens of km. The DESC maintains a MET station at Paint Lake located 40 km from Harp Lake and 60 km from the Muskoka airport. The Paint Lake anemometer has not been absorbed by the growing forest as has happened at Harp Lake. The long-term forestation in Harp Lake may have affected the anemometer, therefore using Paint Lake, we can better prove that the wind field over Harp Lake is being obscured by the forestation. Since Paint Lake wind speeds resemble those over Muskoka Airport, we can apply the airport data to Harp Lake.

Similar to Muskoka Airport, the wind speed over Paint Lake is significantly decreasing ($r^2=0.012$, $p<0.0001$) with the same ups and downs, despite it being lower in elevation (Figure 1.4). However, the wind speed over Muskoka Airport is 1/2 the strength of the wind speed at Paint Lake (wind speed ranges: 1.87-1.45 m/s, 3.51-3.38 m/s, respectively).

Statistical Analyses

Objective 1: Has the wind field in Muskoka changed?

Because forest growth at the Harp Lake MET site has rendered its wind speed and direction data unsuitable, I employed the wind data from the Muskoka airport. I determined if the regional wind speed or direction had changed at monthly, seasonal and annual steps from 1980 to 2004. I used November to March as the winter (ice-cover) period and April to October as the ice-free period. To determine if the annual trends were significant, I employed the squared Pearson correlation of wind speed vs. year, using the Analyze-it add-on for Excel (Analyze-it Software, Ltd 2011), and linear-circular associations for wind direction, using Oriana 3.21 (Kovach Computing Services 2010). The associations provided by Oriana were given as the unsquared r-value of the Pearson correlation. If wind speed or direction was changing, then there might be some effect on zooplankton distribution in the lake, and thus some developing bias in our 1 sampling station data.

Objective 2: Does the annual trend in the wind field correlate with the changes in zooplankton abundance over Harp Lake between 1980-2004?

I calculated the residual variation in zooplankton in linear, multiple or polynomial regression models that predicted the annual average of zooplankton abundance. Then I examined the part correlations of the residuals with two components of the wind field: speed and direction. In addition to generating these residuals, I also calculated the partial correlation coefficients to explicitly determine the relationship between abundance and the wind field (speed and direction) after partialling out the effect of the various

annual steps used in the respective models for each species separately. I did this by choosing my final regression model (using the criteria below) and adding wind speed into the model and ran the new model in PAST (Hammer et al. 2010) to calculate the partial correlation coefficient for just abundance and wind speed with the other predictors in the model being partialled out. Those correlations for wind direction were not performed because Oriana 4 (Kovach Computing Services 2010) could not compute these values.

To select my final regression model I examined many regression diagnostics, i.e. correlation coefficient (r), t-statistic, and F-statistic to assess the significance of the entire model, and I examined the residuals aiming for low skewness and low kurtosis, independence, and normal distribution (Kleinbaum et al. 1988, Birkes and Dodge 1993).

Objective 3: Do the residual abundances correlate with the wind field over Harp Lake between 1980-2004?

After choosing a model to describe the long-term changes in each zooplankton species, I determined if the residual abundance might be attributable to changes in the wind field at annual steps. For all species, the abundance was non-normal (Shapiro-Wilk test, Analyse-it add-on for Excel) and I transformed the data prior to computing the residuals.

The annual residual abundances for each species obtained from the regression models were correlated with the wind field from that year using part correlations with $p=0.05$. I ran the correlations with the wind speed using Analyse-it add-on for Excel (Analyse-it Software, Ltd 2011). The correlations (r) between the residual abundance

and wind direction were performed using Oriana 3.21 (Kovach Computing Services 2010) as bivariate linear-circular associations as follows:

$$r^2 = \frac{r_{xc}^2 + r_{xs}^2 - 2r_{xc}r_{xs}r_{cs}}{1 - r_{cs}^2} \quad (\text{Mardia 2000}) \quad \text{Equation 1.2}$$

where r_{xc} is the correlation between x and $\cos \alpha$, r_{xs} is the correlation between x and $\sin \alpha$, and r_{cs} is the correlation between $\cos \alpha$ and $\sin \alpha$. The α denotes a circular value (wind direction) and x denotes a linear value (residual abundance) (refer to Appendix B1 for how to identify an association between residual abundance and wind direction). I compared and confirmed the part correlation coefficients generated with those calculated from the partial correlation coefficients. The part correlation coefficients were very similar or equal to those calculated using the partial method.

Results

Objective 1: Has the wind field changed in Muskoka?

On average, the wind speed has decreased from 1980 to 2004 from about 4.0 to 3.0 m/s ($r^2=0.82$, $p<0.0001$) (Figure 1.6). For the winter season, the wind speed has decreased by 0.8 m/s over 25 years from 4.0 to 3.2 m/s ($r^2=0.75$, $p<0.0001$) (Figure 1.7) and for the ice-free season, the wind speed has decreased by 1.1 m/s from 4.0 to 2.9 m/s ($r^2=0.79$, $p<0.0001$) (Figure 1.8). The monthly wind speeds from 1980-2004 decreased with the same long-term patterns as the annually averaged data (Figure 1.6, Figure 1.9ab).

On average, wind direction has shifted from 33 degrees to 12 degrees (more to the north, $r^2=0.63$, $p<0.0001$) (Figure 1.10). For the winter season, the wind direction shifted

from 35.1 degrees to 15.3 degrees ($r^2=0.58$, $p=0.0004$) (Figure 1.7). For the ice-free season, the wind direction shifted from 30.2 degrees to 8.3 degrees ($r^2=0.60$, $p=0.0002$) (Figure 1.8) The wind directions had monthly, seasonal and annual patterns that shifted more towards the north from the northeast or coming from the south/southwest (Figure 1.10, Figure 1.11ab).

Objective 2: Was the annual trend in the wind field correlated with the changes in zooplankton abundance over Harp Lake between 1980-2004?

To start, most of the zooplankton species had abundance that changed with year (Figure 1.12). The smaller species (*B. tubicen*, *D. birgei* and *T. extensus*) decreased with year beginning in 1993 while the larger species (*D. mendotae*, *H. glacialis* and *L. sicilis*) increased with year also beginning at 1993. Only 2 of the 8 species remained relatively stable throughout the study period (*L. minutus* and *D. thomasi*).

The majority of the species had abundance that was influenced by *Bythotrephes* P/A (Table 1.2). *Bythotrephes* appeared in 1993 and was found in Harp Lake for the remainder of the study (Figure 1.13). All cladoceran abundances significantly changed with the presence of *Bythotrephes*. *L. sicilis* was the only copepod that had abundance significantly affected by the presence of the invader.

The average surface temperature influenced zooplankton abundance (Figure 1.14). In fact, the average surface temperature varied by almost two fold between years from 10.82 to 18.33 degrees (Figure 1.15). The annual average surface temperature is getting warmer in recent years. The larger cladoceran, *D. mendotae*, had abundances that increased with the average surface temperature ($r^2=0.45$, $p=0.0003$). Three of the 8

species have abundances that decreased with the average surface temperature (*B. tubicen* $r^2=0.68$ with $p<0.0001$, *D. birgei* $r^2=0.75$ with $p<0.0001$ and *L. minutus* $r^2=0.16$ with $p=0.0455$). The remaining species had abundance that did not have any particular trend with the average surface temperature (*L. sicilis*, *D. thomasi* and *T. extensus*). *L. minutus* was the only copepod that had abundance that changed with the average surface temperature. Seven of the 8 species had abundances that could be significantly explained by using only the average surface temperature in regression models (Figure 1.16a,b). Only 3 species had polynomial fitted models (*B. tubicen*, *D. thomasi* and *T. extensus*). Average abundance of the majority of the species was best explained by a linear relationship with average surface water heating.

Ice-free season length for the sample dates that generally influenced average zooplankton abundance, even though it varied by only 35 days among all years (with averaged annual values ranging from 84 to 119 days) (Figure 1.17). Four of the 8 species had an abundance peak between 90 and 95 days (or 3 months) after the ice break-up (*D. mendotae*, *H. glacialis*, *L. sicilis*, and *L. minutus*). These species have abundances that increased after 3 months of ice-free waters and declined after this point. Of the remaining species, 3 of the 4 species have abundances that increased after 95 days after the first ice-break and had a larger range of days where their abundance was high (*B. tubicen*, *D. birgei* and *T. extensus*). In other words, the abundance of these species increases when the water has had a chance to warm up for over 3 months (or 95 days+ since ice-break) on average. *D. thomasi* abundance could not be explained by days since ice off. *T. extensus* was the only species with abundances that increased with more days

since ice-free ($r^2=0.42$, $p=0.0004$) (Figure 1.18b). All species abundance had a linear relationship with days since ice-free (Figure 1.18ab).

Each selected zooplankton species had abundance patterns that could be explained by some combination of *Bythotrephes* P/A, days since ice-break up and/or the average surface temperature (Table 1.3, Figure 1.19ab). *D. thomasi* was the only species that required a polynomial fit with the average surface temperature (Figure 1.19b). Five of the 8 species had abundance that was significantly explained by *Bythotrephes* P/A either alone or with another annual predictor (e.g., average surface temperature). *D. mendotae*, *H. glacialis* and *L. sicilis* had abundances that could be explained by *Bythotrephes* alone in a linear model (Figure 1.19ab). *L. minutus* and *D. thomasi* had abundance that was significantly explained by the average surface temperature ($r^2=0.2138$, $p=0.0199$; $r^2=0.4781$, $p=0.0030$, respectively) (Figure 1.19b). These species were less abundant in years with cooler epilimnia. *T. extensus* was the only species that had abundance that was explained by days since ice-break up in a linear regression model ($r^2=0.3400$, $p=0.0024$) (Figure 1.19b).

Objective 3: Does residual abundance correlate with the wind field over Harp Lake between 1980-2004?

With one exception, the residual abundance of the above regression models for the selected species was not correlated with wind speed or direction from 1980-2004 (Table 1.4, Figure 1.20). The exception was *D. mendotae*. For *D. mendotae*, there was a significant association between the residual abundance and the wind direction ($r^2=0.2330$, $p=0.005$) (Figure 1.21, refer to Appendix B1 for a further explanation of this

relationship between residual abundance and wind direction). When the residual abundances were lower for this species, the wind generally originated in a different range of directions than when positive residuals were observed. All correlations between the residual abundance and wind speed and direction can be found in Appendix C.

Discussion

All species had abundance that could be explained by *Bythotrephes* P/A, by annual averaged average surface temperature and/or by the dates of ice breakup each year. Those species whose long-term average abundance patterns were best explained by *Bythotrephes* alone (*D. mendotae*, *H. glacialis* and *L. sicilis*) were probably responding to the invasion by *Bythotrephes*. In 1993, *Bythotrephes* appeared in Harp Lake and affected the abundance of large and small cladocerans (Yan and Pawson 1997). Therefore, species that were affected by the invasion demonstrated a change (increase or decrease) in abundance between pre- and post-1993.

A polynomial fit for the annual regression models was appropriate for *D. thomasi*, perhaps likely because of the sensitivity of its phenology to summer heating. The average surface temperature was particularly important in this polynomial model. First, abundance could be anticipated based on the warming conditions. Second, the relationship between warming conditions and the abundance of this species was non-linear. An increase in temperature can lead to extra generations in a year by stimulating the early hatching of resting eggs (Chen and Folt 1996).

Despite the obvious effects of *Bythotrephes* P/A, the abundance of *L. minutus*, *D. thomasi* and *T. extensus* were only significantly correlated with average surface

temperature or days since ice-free. This suggests that these species were not influenced by *Bythotrephes* invasion in Harp Lake, as has also been observed in spatial surveys (Boudreau and Yan 2003). The long-term warming of Harp Lake is the predictor that best correlates with the abundance of these species. This may be because all these species are below the mixing layer. An increase in warmer waters would affect the long-term changes in lake physics denoted by earlier ice break-up, warmer epilimnia and life history stages.

Based on annual averages, predictions of zooplankton abundance were not improved significantly by considering the wind field in this lake. This result did not support with my predictions that some species would be significantly correlated with the wind field depending on their physical and behavioural characteristics (e.g., body size, strata location, and swim speed). According to Waife and Frid (1996), zooplankton are best viewed as ‘passive drifters’ that cannot swim against the wind-induced water current and are transported within the flow field. The animals can clearly swim, but not as fast or as strongly as the wind-induced current. Similarly, Sollberger and Paulson (1991) found that wind-induced currents could easily homogenize zooplankton distributions under turbulent mixing and aid in the transportation of zooplankton. However, it is possible that large, fast swimming animals such as *D. mendotae*, could out-swim the weaker currents when the wind speeds are slow and be concentrated downwind (Huber et al. 2011). With the exception of *D. mendotae*, all 7 species had residual abundance that could not be predicted by the wind field. *D. mendotae* is a large cladoceran that inhabits the hypolimnion during the daytime and returns to the surface during the night (Young

and Yan 2008). A possible reason why *D. mendotae* may have been the only species to show a significant association with wind direction may be due to thermocline tilting, which can cause animals in the hypolimnion to be distributed upward or concentrated downwind. However, this is unlikely since other species chosen in this study that inhabit the hypolimnion that are larger and faster than *D. mendotae* did not have a significant association with the wind direction (e.g., *L. sicilis*). This study has indicated that the wind field overpowers the swimming strength of the animals, even at low wind speeds (3-4 m/s, Zurek and Bucka 2004) but there may be chance occurrences where animals can actually withstand the hydrodynamics present in the lake.

The physical and behavioural characteristics of each species did not play a role in predicting abundance under the influence of the wind field. Surface water current speed is ~1.5 percent of the wind speed moving over the water (Haines and Bryson 1961). To hold a fixed position in the water against its movement, the animals would need to be able to swim at least 3.47 cm/s (corresponding with 2.32 m/s of wind speed), the slowest daily wind speeds observed over the study period. According to Zurek and Bucka (2004), weak winds are characterized as 3-4 m/s and the mobility of animals would depend on their swimming behaviour, physiology and anatomy. Almost 30% of the wind speeds on the sample date over Muskoka Airport were between 3-4 m/s during the study period. In fact, 77% of the wind speeds were <4 m/s, therefore the possibility that animals may be able to hold their position in the water is likely. However, based on the lack of pattern between the residual abundance and the wind field, the sustained swimming speed of the animals (average swim speed=0.199 cm/s) in this study must

have been lower than the current speed (even though the long-term wind speed was decreasing), and thus animals were downwelled if found in downwelling surface waters or upwelled to upper strata if found in the hypolimnion (Sollberger and Paulson 1991). It is also possible that the animals may become concentrated at the ends of the lake in the direction of the wind if the wind speed was very strong (Sollberger and Paulson 1991) but this does not seem to have influenced the data.

Wind speed was less important for predicting abundance compared to wind direction. The mean of all variance in residual abundance that could be explained by wind speed was 2.75%, less than the 5.25% that could be attributed to wind direction. The majority of 5.25% of the variance in residual abundance that could be attributed to wind direction was due to *D. mendotae*. The variance in residual *D. thomasi* abundance attributable to wind direction was 2.88%, much greater than that attributable to wind speed (0.88%). While not statistically significant, the relationship between the residual abundance and the wind direction suggests that zooplankton in Harp Lake may have changed their spatial distribution somewhat over time, at annual scales. They may have moved in a direction that better suits their preference for a particular depth (such as, resisting the water currents in the hypolimnion during the daytime to avoid predators, Herzig 1994).

In summary, two aspects of the annual overwater wind field (speed and direction) did not improve the prediction of long-term changes in zooplankton abundance at annual scales, when these data were generated fortnightly at a single, mid-lake station. Data from one station at the deepest portion of the lake was sufficient to indicate that the long-term

zooplankton abundance patterns vary annually, as previously shown (Yan et al. 2008). Yan et al. (2001) found that the zooplankton species in Harp Lake have indeed varied between 1978-1997, however, the present study documented long-term patterns beyond 1997 to 2004. Of the 8 species chosen in this study, only half had abundance that continued to follow the yearly trends observed from Yan et al. (2001). For instance, *D. mendotae* abundance continued to increase between 1997-2004, while *B. tubicen* and *D. birgei* abundance continued to decrease. However half of the species, *H. glacialis*, *L. sicilis* and *D. thomasi* abundance started decreasing. At the same time, *T. extensus* abundance began to increase. This is particularly surprising since *T. extensus* abundance declined in 1993 when *Bythotrephes* appeared (Yan and Pawson 1997). The reason for this could be that *T. extensus* populations have had the chance to replenish their numbers from the drastic decrease in 1993. *Bythotrephes* P/A did significantly correlate with the abundance of 5 of the 8 species chosen in the annual regression models (excluding *L. minutus*, *D. thomasi* and *T. extensus*). The presence of this invader in 1993 continued to affect the abundance of these 5 species beyond the time frame observed in Yan et al. (2001).

What has not been shown is that the species chosen in this study have abundances that can also be predicted based on the duration and heating of the ice-free season. The average surface temperature proved to be a significant predictor for 7 of the 8 species chosen (excluding *T. extensus*). This is not a surprise since many life stages are dependent on water temperature (Balcer et al. 1984). For example, *D. mendotae* abundance had a significant positive linear relationship with the average surface

temperature ($r^2=0.50$, $p<0.0001$), which indicates that this species is more abundant at warmer temperatures. However, *D. thomasi* abundance had a significant polynomial relationship with the average surface temperature ($r^2=0.48$, $p=0.0030$). In contrast to the average surface temperature, days since ice-free alone was not a significant predictor of abundance, with the exception of *T. extensus*. This lack of significance may arise because the overall range of days since ice-free (83.58-147) may not be large enough to notice a change in abundance. Therefore, using the average surface temperature alone as a measure to predict zooplankton abundance in Harp Lake may be useful for future analyses.

I chose to work on common species of zooplankton in Harp Lake that vary in size, swimming ability and depth preferences. My work suggests that these species can be used to quantify long-term changes in zooplankton at annual scales without consideration of the bias caused by changing wind fields. It is clear that the wind speed decreased over the study period and the wind direction shifted towards the north. Yet, zooplankton have not responded to these changes observed in the wind field at an annual average scale. Therefore, changing wind fields do not appear to have compromised our ability to detect the influence of other drivers such as *Bythotrephes* P/A (Yan et al. 2008) at annual scales. The greater interpretability of phytoplankton, fish, and benthos data requires an alternative explanation, at least at annually averaged scales (Arnott et al. 1998, Allen et al. 1999).

D. mendotae residual abundance was correlated with the wind direction using annual averages, but the other zooplankton species commonly found in the hypolimnion

during the day, *D. thomasi* and *L. siclis*, had no such association. In chapter 2, I examine whether a detailed inspection of seasonal changes in residual abundance patterns can clarify this result. Further insight may also be gathered by a more careful examination of the effect of the wind field on the thermocline, for animals that migrated between thermal layers. The wind effect within the thermocline is rather small and the turbulence level is diminished (Bengtsson 1973; Gorham and Boyce 1989; Elci 2008). The current speeds are thus low enough that directed animal movements might create patchiness within the metalimnion. Although wind effects on the long-term zooplankton data did not appear at annual scales, it remains to be seen if the same pattern is true at daily scales.

References

- Ahrens, C. D. 2000. Essentials of Meteorology: an invitation to the atmosphere. Brooks/Cole, Cengage Learning USA.
- Ahrens, C. D. 2007. Meteorology today: an introduction to weather, climate and the environment. Thomson Brooks/Cole USA.
- Allen, A. P., Whittier, T. R., Larsen, D. P., Kaufmann, P. R., O'Connor, R. J., Hughes, R. M., Stemberger, R. S., Dixit, S. S., Brinkhurst, R. O., Herlihy, A. T. and S. G. Paulsen. 1999. Concordance of taxonomic composition patterns across multiple lake assemblages: effects of scale, body size, and land use. Canadian Journal of Fisheries and Aquatic Sciences 56:2029-40.
- Analyse-it Software, Ltd. 2011. Analyse-it Add-on for Excel. Retrieved 2011. <http://www.analyse-it.com>.
- Arnott, S. E., Magnuson, J. J. and N. D. Yan. 1998. Crustacean zooplankton species richness: single- and multiple-year estimates. Canadian Journal of Fisheries and Aquatic Sciences 55:1573-82.
- Arnott, S. E., Yan, N. D., Keller, W. B. and K. Nicholls. 2001. The influence of drought-induced acidification on the recovery of plankton in Swan Lake (Canada). Ecological Applications 11:747-63.

Ashforth, D. and N. D. Yan. 2008. The interactive effects of calcium concentration and temperature on the survival and reproduction of *Daphnia pulex* at high and low food concentrations. *Limnology and Oceanography* 53:420-32.

Balcer, M. D., Korda, N. L. and S. I. Dodson. 1984. Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species. The University of Wisconsin Press, Wisconsin.

Barbiero, R. P., Schacht, L. L., Little, R. E. and M. L. Tuchman. 2005. Crustacean zooplankton communities in Lake Michigan. *In* The Lake Michigan ecosystem: ecology, health and management Edsall, T. and M. Munawar, editors, eds., pp. 237-67. Ecovision World Monograph Series. Amsterdam, The Netherlands SBP Academic Publishing.

Barnett, A. J., Finlay, K. and B. E. Beisner. 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* 52:796-813.

Bengtsson, L. 1973. Mathematical models of wind induced circulation in a lake. *In*: Hydrology of Lakes, International Association of Hydrological Sciences Publication No.109.

Birkes, D. and Y. Dodge. 1993. Alternative methods of regression. John Wiley and Sons, Inc. Canada

Blukacz, E. A., Shuter, B. J. and W. G. Sprules. 2009. Towards understanding the relationship between wind conditions and plankton patchiness. *Limnology and Oceanography*. 54:1530-40.

Boudreau, S.A. and N.D. Yan 2003. The differing crustacean zooplankton communities of Canadian Shield lakes with and without the nonindigenous zooplanktivore *Bythotrephes longimanus*. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1307-1313

Burkes, R. L., Lodge, D. M., Jeppessen, E. and T. L. Lauridsen. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater Biology* 47:343-65.

Butz, S. D. 2004. Science of Earth systems. Delmar Learning New York

Chen, C. Y. and C. L. Folt. 1996. Consequences of fall warming for zooplankton overwintering success. *Limnology and Oceanography* 41:1077-86.

- Cloern, J. E., Alpine, A. E., Cole, B. E. and T. Heller. 1992. Seasonal changes in the spatial distribution of phytoplankton in small, temperate-zone lakes. *Journal of Plankton Research* 14:1017-24.
- Cooke, S. L., Williamson, C. E., Leech, D. M., Boeing, W. J. and L. Torres. 2008. Effects of temperature and ultraviolet radiation on diel vertical migration of freshwater crustacean zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 65:1144-52.
- Dieguez, A. C. and J. J. Gilbert. 2002. Suppression of the rotifer *Polyarthra remata* by the omnivorous copepod *Tropocyclops extensus*: predation or competition. *Journal of Plankton Research* 24:359-69.
- Dirnberger, J. M. and S. T. Threlkeld. 1986. Advective effects of a reservoir flood on zooplankton abundance and dispersion. *Freshwater Biology* 16:387-96.
- Dodson, S. I., R. Tollrian and W. Lampert. 1997. *Daphnia* swimming behavior during vertical migration. *Journal of Plankton Research* 19:969-978.
- Doulka, E. and G. Kehayias. 2008. Spatial and temporal distribution of zooplankton in lake Trichonis (Greece). *Journal of Natural History* 42:575-95.
- Dumitru, C., Sprules, W. G. and N. D. Yan. 2001. Impact of *Bythotrephes longimanus* on zooplankton assemblages of Harp Lake, Canada: an assessment based on predator consumption and prey production. *Freshwater Biology* 46:241-51.
- Elci, S. 2008. Effects of thermal stratification and mixing on reservoir water quality. *Limnology* 9:135-42.
- Environmental Canada (EC). 2010. National environmental effects monitoring office. Retrieved April 24, 2010. <http://www.ec.gc.ca/eseem/default.asp?lang=En&n=453D78FC-1>.
- Folt, C. L. and C. W. Burns. 1999. Biological drivers of zooplankton patchiness. *Trends in Ecology and Evolution*. 14:300-5.
- Frank, K. T. and W. C. Leggett. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 39:991-1003.
- George, D. G. 1981. Wind-induced water movements in the South Basin of Windermere. *Freshwater Biology* 11:37-60.

George, D. G. and R. W. Edwards. 1976. The effect of wind on the distribution of chlorophyll a and crustacean plankton in a shallow eutrophic reservoir. *Journal of Applied Ecology* 13:667-90.

Girard, R. E., Clark, B. J., Yan, N. D., Reid, R. A., David, S. M., Ingram, R. G. and J. G. Findels. 2007. History of chemical, physical and biological methods, sample locations and lake morphometry for the Dorset Environmental Science Centre (1973-2006) Ontario Ministry of Environment Technical Report 2007.

Glizicz, Z. M. and A. Rykowska. 1992. 'Shore avoidance' in zooplankton: a predator-induced behavior or predator-induced mortality? *Journal of Plankton Research* 14:1331-42.

Gorham, E. and F. M. Boyce. 1989. Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. *Journal of Great Lakes Research* 15:233-45.

Haines, D. A. and R. A. Bryson. 1961. An empirical study of wind factor in lake Mendota. *Limnology and Oceanography* 6:356-64.

Hammer, O., Harper, D. A. T. and P. D. Ryan. 2010. PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1):9pp.

Herzig, A. 1994. Predator-prey relationships within the pelagic community of Neusiedler See. *Hydrobiologia* 275/6:81-96.

Huber, A. M. R., Peeters, F. and A. Larke. 2011. Active and passive vertical motion of zooplankton in a lake. *Limnology and Oceanography*. 56:695-706.

Jeppesen, E., P. Nöges, T.A. Davidson, J. Haberman, T. Nöges, K. Blank, T.L. Lauridsen, M. Dondergaard, C. Sayer, R. Laugaste, L.s. Jahansson, R. Bjerring, and S.L. Amsinck. 2011. Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). *Hydrobiologia* 676: 279-297.

Keller, W., Paterson, A. M., Somers, K. M., Dillon, P. J., Heneberry, J. and A. Ford. 2008. Relationships between dissolved organic carbon concentrations, weather, and acidification in small Boreal Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 65:786-95.

Kleinbaum, D. G., Kupper, L. L. and K. E. Muller. 1988. Applied regression analysis and other multivariate methods. PWS-KENT Publishing Company, Boston

- Kovach Computing Services. 2010. Oriana 3.21. Retrieved 2009.
<http://www.kovcomp.com/>
- Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* 3:21-27.
- Lampert, W., McCauley, E. and B. F. J. Manly. 2003. Trade-offs in the vertical distribution of zooplankton: ideal free distribution with costs? *Proceedings: Biological Sciences* 270:765-73.
- Lagergren, R., Hellsten, M. and J. A. E. Manly. 2003. Trade-offs in the vertical distribution of zooplankton: ideal free distribution with costs? *Proceedings: Biological Sciences* 270:765-73.
- Larsson, P. and W. Lampert. 2011. Experimental evidence of a low-oxygen refuge for large zooplankton. *Limnology and Oceanography*. 56:1682-1688.
- Leech, D. M. and C. E. Williamson. 2001. In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. *Limnology and Oceanography* 46:416-420.
- Link, J. 1996. Capture probabilities of Lake Superior zooplankton by an obligate planktivorous fish-the Lake Herring. *Transactions of the American Fisheries Society* 125:139-42.
- MacKenzie, B. R. and W. C. Leggett. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and zooplankton prey effects of wind and tide. *Marine Ecology Progress Series*. 73:149-60.
- Mardia, K. V. 2000. *Statistics of directional data*. Academic Press Inc., London
- Marmorek, D. R. and J. Korman. 1993. The use of zooplankton in a biomonitoring program to detect lake acidification and recovery. *Water, Air, and Soil Pollution* 69:223-41.
- Molot, L. A. and P. J. Dillon. 2008. Long-term trends in catchment export and lake concentrations of base cations in the Dorset study area, central Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 65:809-20.
- Monteith, D. T., Stoddard, J. L., Evans, C. D., de Wit, H. A., Forsius, M., Hogasen, T., Wilander, A., Skjelkvale, B. L., Jeffries, D. S., Vuorenmaa, J., Keller, B., Kopacek, J. and J. Vesely. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* 450:537-41.

- Muirhead, J. and W. G. Sprules. 2003. Reaction distance of *Bythotrephes longimanus*, encounter rate and index of prey risk for Harp Lake, Ontario. *Freshwater Biology* 48:135-46.
- Naithani, J., Deleersnijder, E. and P. Plisnier. 2003. Analysis of wind-induced thermocline oscillations of Lake Tanganyika. *Environmental Fluid Mechanics* 3:23-39.
- O'Connor, R. J., Walls, T. E. and R. M. Hughes. 2000. Using multiple taxonomic groups to index the ecological condition of lakes. *Environmental Monitoring and Assessment* 61:207-228.
- Owens, R. W. 1989. Microscale and finescale variations of small plankton in coastal and pelagic environments *Journal of Marine Research* 47:197-240.
- Paterson, A. M., Winter, J. G., Nicholls, K. H., Clark, B. J., Ramcharan, C. W., Yan, N. D. and K. M. Somers. 2008. Long-term changes in phytoplankton composition in seven Canadian Shield lakes in response to multiple anthropogenic stressors. *Canadian Journal of Fisheries and Aquatic Science* 65:846-61.
- Petruniak, J. 2009. Analysis of *Bythotrephes longimanus* spatial dynamics in Harp Lake, Ontario. M.Sc. thesis, York University, Toronto, Ontario.
- Pinel-Alloul, B. 1995. Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia* 300/301:17-42.
- Pinel-Alloul, B. and A. Ghadouani. 2007. The spatial distribution of microbes in the environment. Springer Netherlands.
- Prepas, E. and F. H. Rigler. 1978. The enigma of *Daphnia* death rates. *Limnological Oceanography* 23:970-88.
- Ramcharan, C. W. and W. G. Sprules. 1978. The enigma of *Daphnia* death rates. *Limnology and Oceanography* 23:970-88.
- Saunders, J. F. III and W. M. Jr. Lewis. 1988. Composition and seasonality of the zooplankton community of Lake Valencia, Venezuela. *Journal of Plankton Research* 10:957-85.
- Semyalo, R., Nattabi, J. K. and P. Larsson. 2009. Diel vertical migration of zooplankton in a eutrophic bay of Lake Victoria. *Hydrobiologia* 635:383-94.
- Sollberger, P. J. and L. J. Paulson. 1991. Littoral and limnetic zooplankton communities in Lake Mead, Nevada-Arizona, USA. *Hydrobiologia* 0:1-11.

- Strecker, A. L. and S. E. Arnott. 2008. Invasive predator, *Bythotrephes*, has varied effects on ecosystem function in freshwater lake. *Canadian Journal of Fisheries and Aquatic Sciences* 11:490-503.
- Tanentzap, A. J., Taylor, P. A., Yan, N. D. and J. R. Salmon. 2007. On Sudbury-area wind speeds – a tale of forest regeneration. *Journal of Applied Meteorology and Climatology*. 46:1645-1654.
- Tessier, A. J. 1983. Coherence and horizontal movements of patches of *Holopedium gibberum* (Cladocera). *Oecologia* 60:71-75.
- Vanschoenwinkel, B., Gielen, S., Seaman, M. and L. Brendonck. 2008. Any way the wind blows-frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* 117:125-34.
- Visser, A. W., Mariani, P. and S. Pigolotti. 2009. Swimming in turbulence zooplankton fitness in terms of foraging efficiency and predation risk. *Journal of Plankton Research* 31:121-133.
- Waervagen, S. B. and J. P. Nilssen. 2011. Seasonal dynamics and life histories of pelagic cladocerans (Crustacea: Cladocera) in an acid boreal lake. *Journal of Limnology* 70:83-101.
- Waife, G. and C. L. J. Frid. 1996. Short-term temporal variation in coastal zooplankton communities: the relative importance of physical and biological mechanisms. *Journal of Plankton Research* 18:1485-1501.
- Woodson, C. B., Webster, D. R., Weissburg, M. J. and J. Yen. 2005. Response of copepods to physical gradients associated with structure in the ocean. *Limnology and Oceanography* 50:1552-64.
- Yan, N. D. and T. W. Pawson. 1997. Changes in the crustacean zooplankton community of Harp Lake, Canada, following invasion by *Bythotrephes cederstroemi*. *Freshwater Biology* 37:409-25.
- Yan, N. D. and R. Strus. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lake near Sudbury, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 37:2282-2293.
- Yan, N. D., Blukacz, A., Sprules, W. G., Kindy, P. K., Hackett, D., Girard, R. E. and B. J. Clark. 2001. Changes in zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Ontario, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2341-50.

Yan, N. D., Girard, R. and S. Boudreau. 2002. An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. *Ecology Letters* 5:481-85.

Yan, N. D., Paterson, A. M., Somers, K. M. and W. A. Scheider. 2008. An introduction to the Dorset special issue: transforming understanding of factors that regulate aquatic ecosystems on the southern Canadian Shield. *Canadian Journal of Fisheries and Aquatic Sciences* 65:781-85.

Young, J. D. and N. D. Yan. 2008. Modification of the diel vertical migration of *Bythotrephes longimanus* by the cold-water planktivore, *Coregonus artedii*. *Freshwater Biology* 53:981-95.

Young, J. D., Loew, E. R. and N. D. Yan. 2009. Examination of direct daytime predation by *Coregonus artedii* on *Bythotrephes longimanus* in Harp Lake, Ontario, Canada: no evidence for the refuge hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 66:449-59.

Zurek, R. and H. Bucka. 2004. Horizontal distribution of phytoplankton and zooplankton from the littoral towards open waters under wind stress. *Oceanological and Hydrobiological Studies* 33:69-81.

Table 1.1: Physical and behavioural characteristics of the selected freshwater crustacean zooplankton from Harp Lake, Ontario. Blanks indicate unknown information.

Species	Mean body length (cm)	Swim speed (cm/s)	Vertical Migratory Behaviour (e.g., day/night, strata)	Food Size Range (μm)	Feeding method
Cladocerans					
<i>Daphnia galeata mendotae</i>	0.092	0.120 ¹	Day (Hypolimnion) ³ Night (Epilimnion) ³	1.1-20 ²	Filtration ²
<i>Holopedium glacialis</i>	0.068	Very slow ⁴	Day (Epilimnion/Metalimnion) ¹⁰ Night (Hypolimnion) ¹⁰	4.0-25 ²	Filtration ²
<i>Bosmina tubicen</i>	0.038	0.408 ⁶	Day (Epilimnion) ³ Night (Metalimnion) ³		
<i>Diaphanosoma birgei</i>	0.059	0.150 ¹³	Day (Epilimnion/Metalimnion) ¹¹ Night (Epilimnion/Metalimnion) ¹¹		Filtration ²
Copepods, Calanoids					
<i>Leptodiaptomus sicilis</i>	0.132	0.168 ¹	Day (Hypolimnion) ³ Night (All depths) ³	5-50 ²	Stationary suspension ²
<i>Leptodiaptomus minutus</i>	0.089	0.340 ¹	Day (Epilimnion/Metalimnion) ⁹ Night (Epilimnion/Metalimnion) ⁹		Stationary suspension ²
Copepods, Cyclopoids					
<i>Diacyclops bicuspidatus thomasi</i>	0.087	0.170 ¹	Day (Hypolimnion) ¹² Night (Epilimnion/Metalimnion) ¹²	15-100 ²	Omnivore carnivore ²
<i>Tropocyclops extensus</i>	0.050	0.035 ⁸	Day (Hypolimnion) ¹² Night (Epilimnion/Metalimnion) ¹²	6.5-80 ²	Omnivore carnivore ²

¹Muirhead and Sprules 2003; ²Barnett et al. 2007; ³Young and Yan 2008; ⁴Link 1996; ⁵Young et al. 2009; ⁶Lagergren et al. 1997; ⁷Strecker and Arnott 2008; ⁸Dieguez and Gilbert 2002; ⁹Cooke et al. 2008; ¹⁰Tessier 1983 and Warvagen and Nilssen 2011; ¹¹Doulka and Kebayias 2008; ¹²Barbiero et al. 2005; ¹³Ramcharan and Sprules 198.

Table 1.2: Regression models using the average abundance of zooplankton species and *Bythotrephes* P/A (Bytho).

Species	Model	r ²	p-value
<i>D. mendotae</i>	LogAbundance = 2.315 + 0.5708*Bytho	0.62	<0.0001
<i>H. glacialis</i>	LogAbundance = 2.121 + 0.4199*Bytho	0.27	0.0076
<i>B. tubicen</i>	LogAbundance = 2.527 - 1.276*Bytho	0.55	<0.0001
<i>D. birgei</i>	LogAbundance = 2.781 - 1.801*Bytho	0.64	<0.0001
<i>L. sicilis</i>	LogAbundance = 1.314 + 0.7874*Bytho	0.54	<0.0001
<i>L. minutus</i>	A significant model could not be generated using <i>Bythotrephes</i> P/A	---	---
<i>D. thomasi</i>	A significant model could not be generated using <i>Bythotrephes</i> P/A	---	---
<i>T. extensus</i>	LogAbundance = 2.65 - 0.2821*Bytho	0.16	0.0457

Table 1.3: Models using the average abundance of zooplankton species using stepwise multiple regressions with an annual predictor: *Bythotrephes* P/A (Bytho), days since ice-free (Free), and average surface temperature (AST).

Species	Model	r ²	p-value
<i>D. mendotae</i>	LogAbundance = 2.315 + 0.5708*Bytho	0.62	<0.0001
<i>H. glacialis</i>	LogAbundance = 2.121 + 0.4199*Bytho	0.27	0.0076
<i>B. tubicen</i>	LogAbundance = 4.561 - 0.8354*Bytho - 0.1578*AST	0.65	<0.0001
<i>D. birgei</i>	LogAbundance = 6.82 - 0.937*Bytho - 0.3133*AST	0.90	<0.0001
<i>L. sicilis</i>	LogAbundance = 1.314 + 0.7874*Bytho	0.54	<0.0001
<i>L. minutus</i>	LogAbundance = 3.479 - 0.0487*AST	0.21	0.0199
<i>D. thomasi</i>	LogAbundance = -46.82 + 10.46*AST - 0.7323*AST ² + 0.01684*AST ³	0.48	0.0030
<i>T. extensus</i>	LogAbundance = 0.8918 + 0.01555* Free	0.34	0.0024

Table 1.4: Squared part/parital correlation coefficients between the residual abundance of zooplankton from the models in Table 1.3 and the wind field. Significance denoted by a p-value<0.05 and an asterisk. The top number is the part correlation and the bottom number is the partial correlation coefficients.

Zooplankton Species	Wind Speed ^a (m/s)		Wind Direction ^b (degrees)	
	Squared Coefficient of Determination (r ²)	p-value	Squared Coefficient of Determination (r ²)	p-value
<i>D. mendotae</i>	0.0441 0.0733	0.3137 0.2006	0.2330	0.005*
<i>H. glacialis</i>	0.0064 0.0061	0.7039 0.7161	0.0010	0.977
<i>B. tubicen</i>	0.0345 0.0207	0.4080 0.5449	0.0188	0.700
<i>D. birgei</i>	0.0265 0.0787	0.4807 0.2446	0.0041	0.928
<i>L. sicilis</i>	0.0223 0.0127	0.4859 0.6176	0.0213	0.640
<i>L. minutus</i>	0.0002 0.0003	0.9510 0.9413	0.0055	0.885
<i>D. thomasi</i>	0.0056 0.0088	0.7219 0.6781	0.1005	0.108
<i>T. extensus</i>	0.0162 0.0169	0.5445 0.5451	0.0357	0.457

^aPart/partial Pearson correlation coefficients (presented as the coefficient of determination, squared correlation coefficient) using Analyse-it add on for Excel

^bBivariate linear-circular association coefficients squared using Oriana 3.0

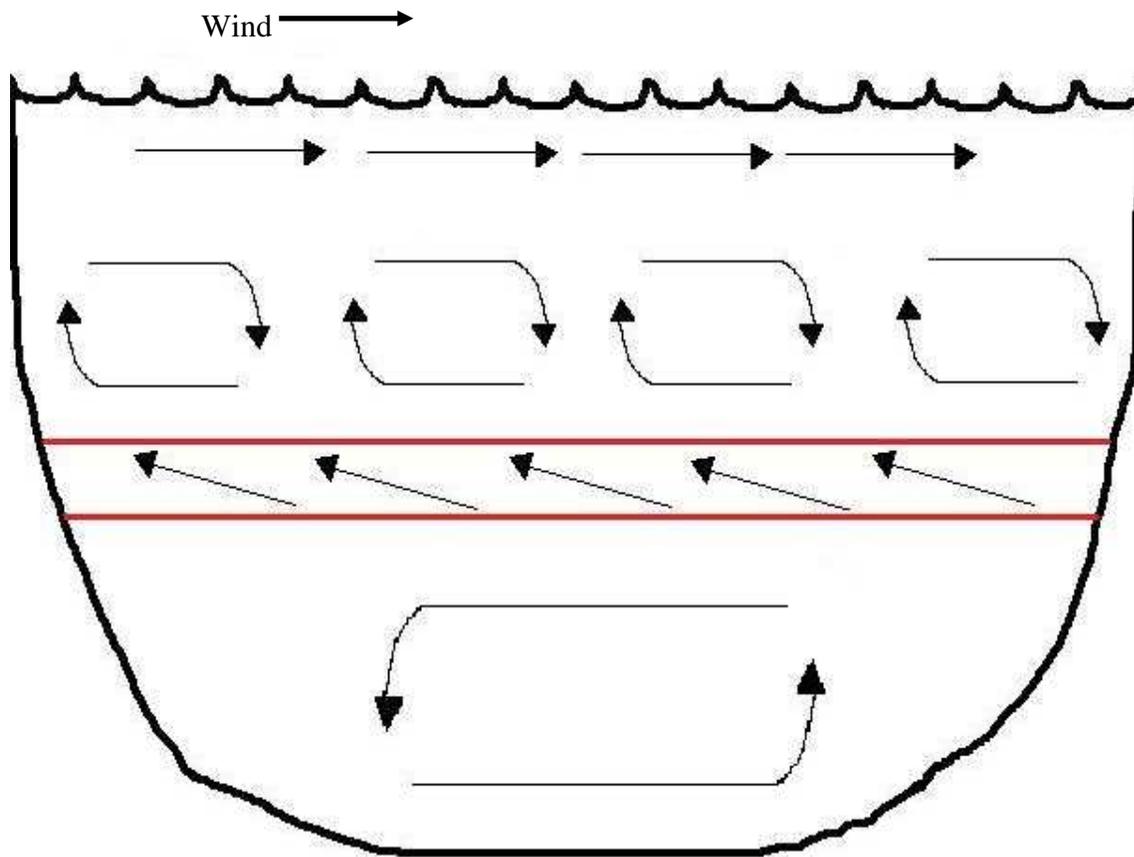


Figure 1.1: A simplified schematic representation of the water movement in a stratified lake. There are 3 distinct strata indicated: above the upper gray line, the epilimnion; within the gray lines, the metalimnion/thermocline; and below the lower gray line, the hypolimnion.

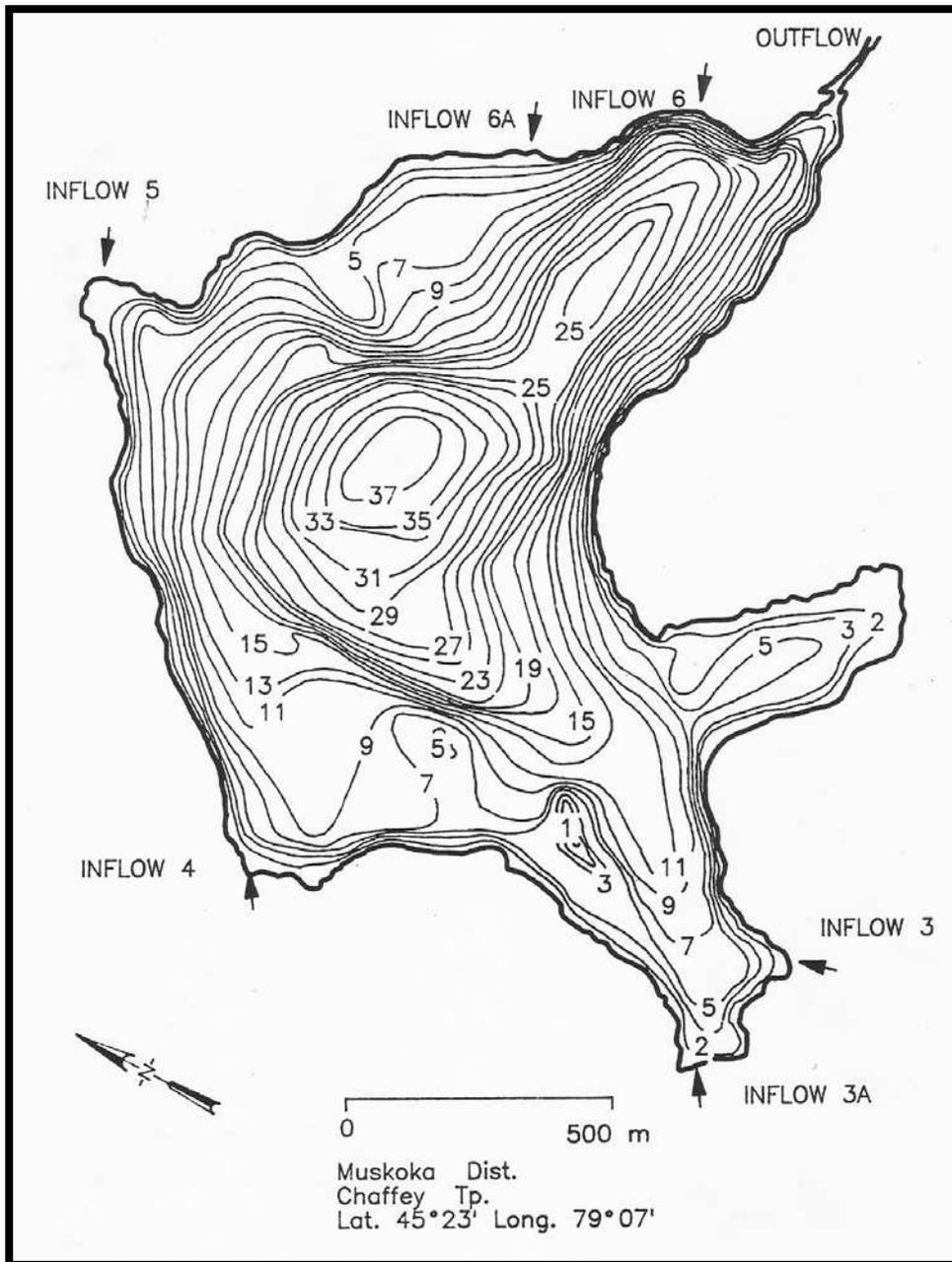


Figure 1.2: Bathymetric map of Harp Lake, Ontario. Contours are shown in meters.

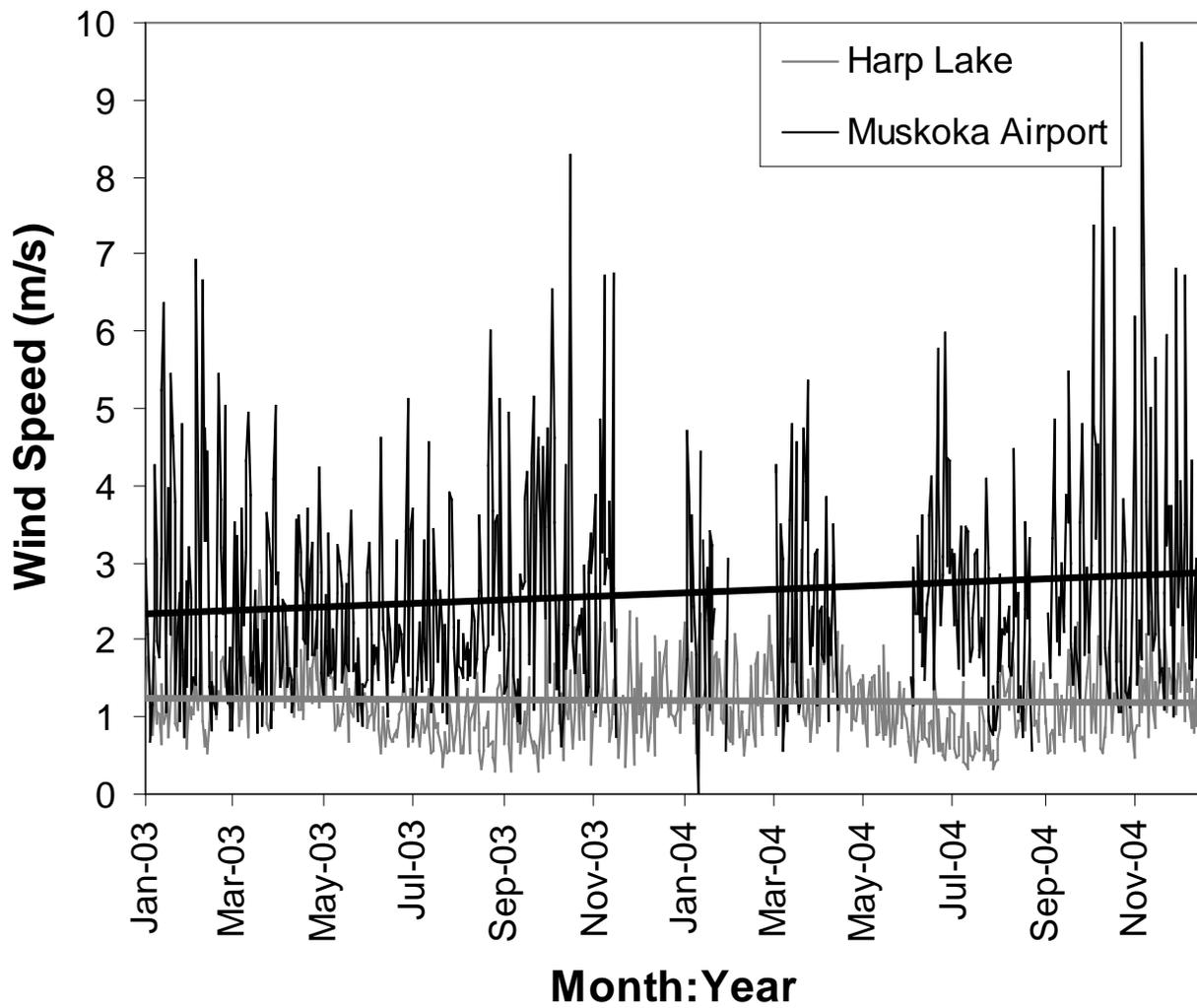


Figure 1.3: The daily wind speeds from Harp Lake and Muskoka Airport between 2003-2004. The thick gray line indicates the regression line for Muskoka Airport ($r^2=0.0139$). The black thick line indicates the regression line for Harp Lake ($r^2=0.0020$).

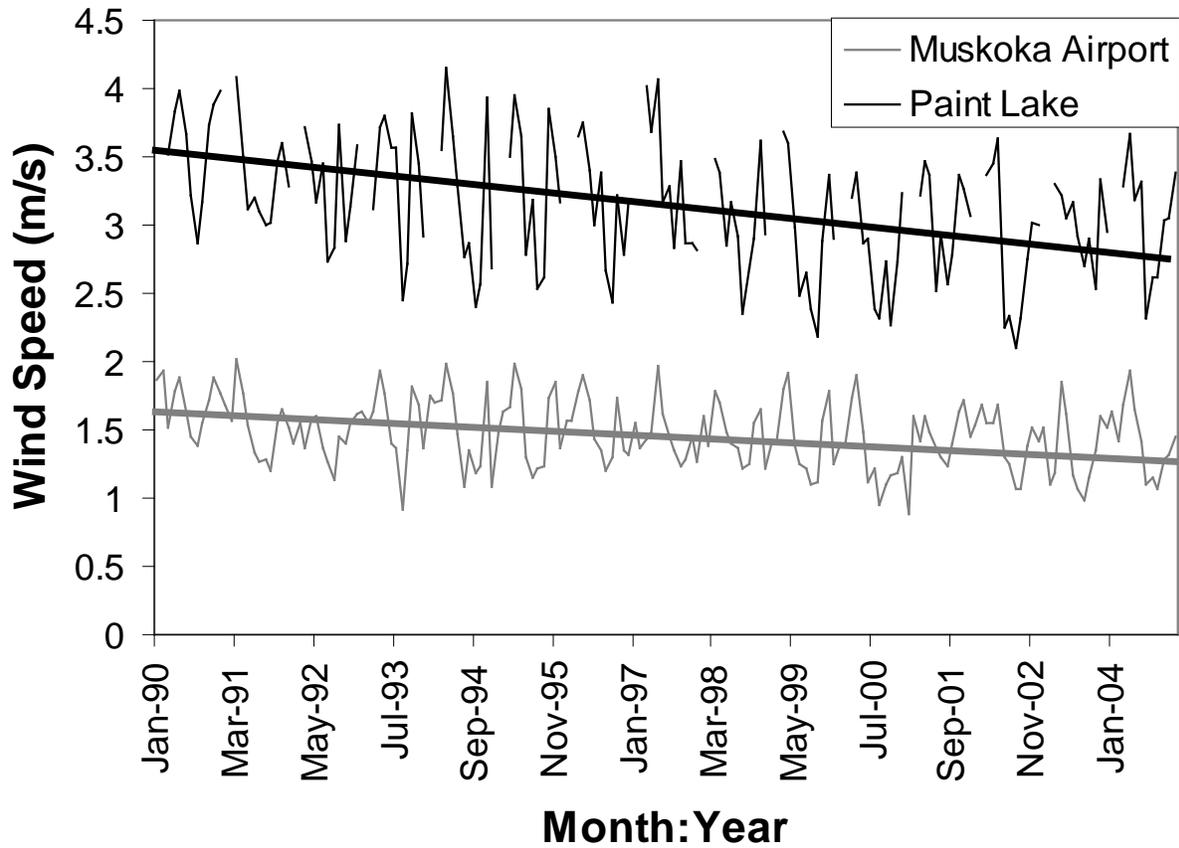


Figure 1.4: The monthly wind speeds from Paint Lake and Muskoka Airport between 1990-2004. The thick gray line indicates the regression line for Muskoka Airport ($r^2=0.0861$). The black thick line indicates the regression line for Paint Lake ($r^2=0.1447$).

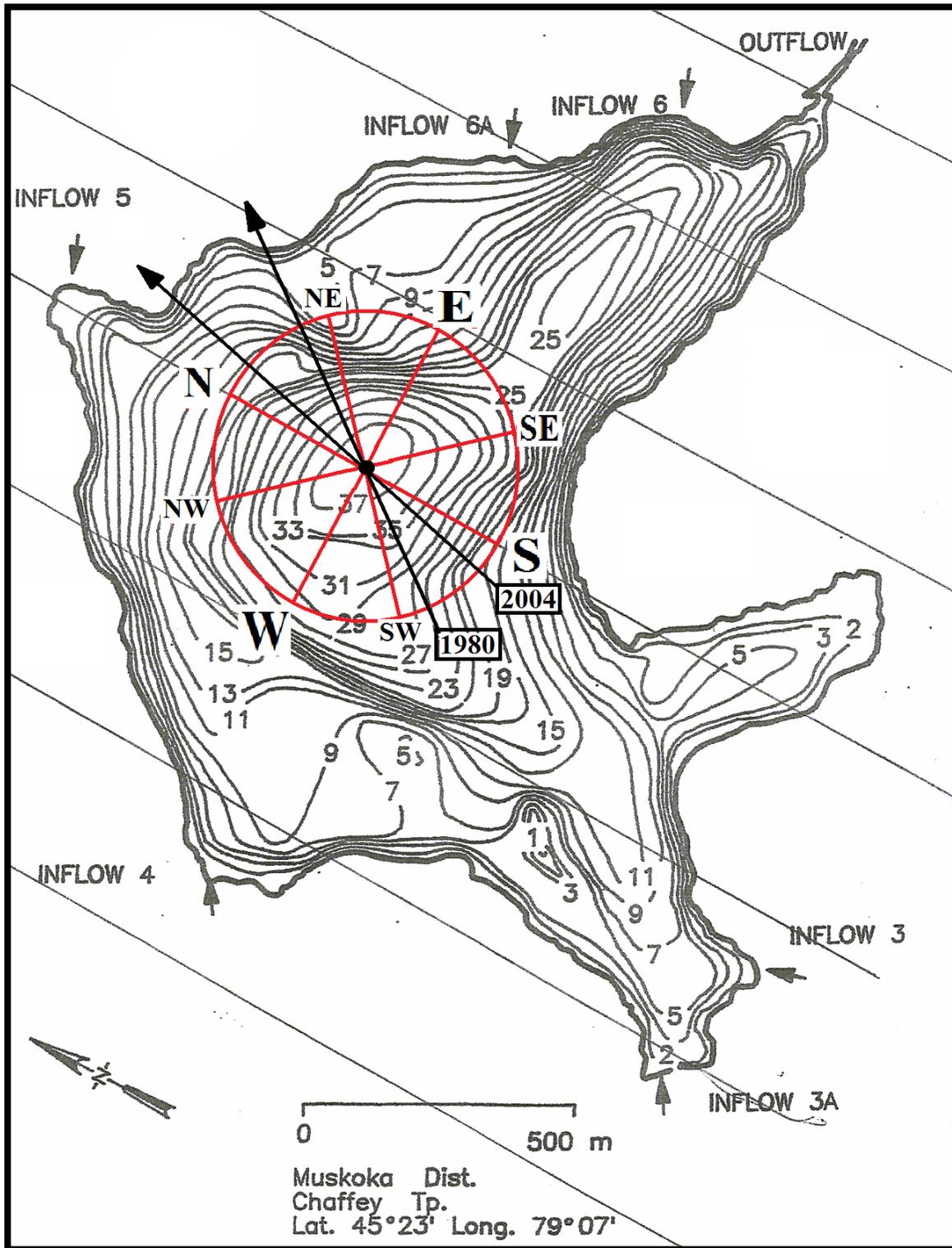


Figure 1.5: Bathymetric map of Harp Lake, Ontario with an overlay of a standard compass rose diagram in the direction of true North. The sampling station is indicated by a black circle at the deepest portion of the lake. The wind directions are shown separately for 1980 and 2004.

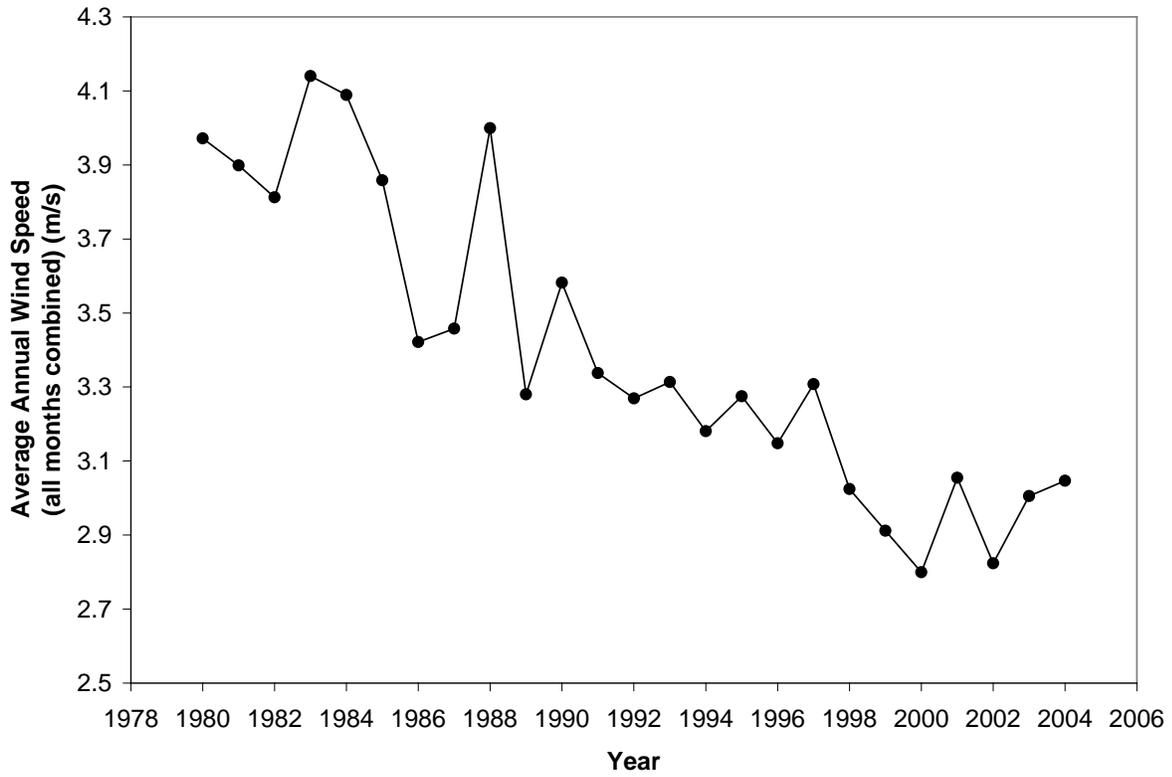
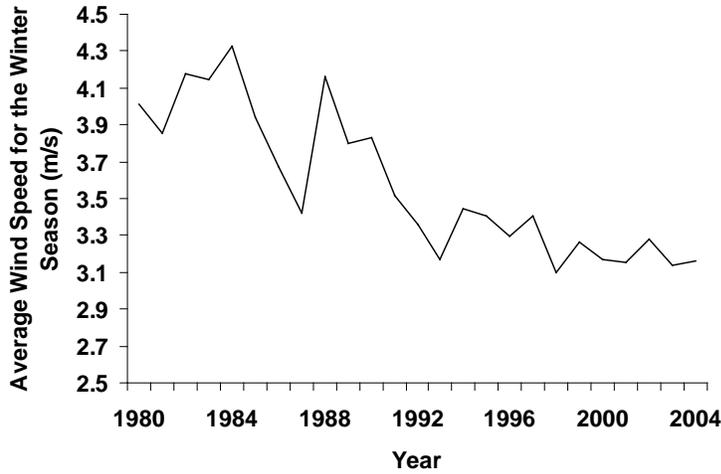


Figure 1.6: Long-term trends in average annual wind speed for all months combined from 1980-2004 at the Muskoka Airport, Ontario, Canada.

A)



B)

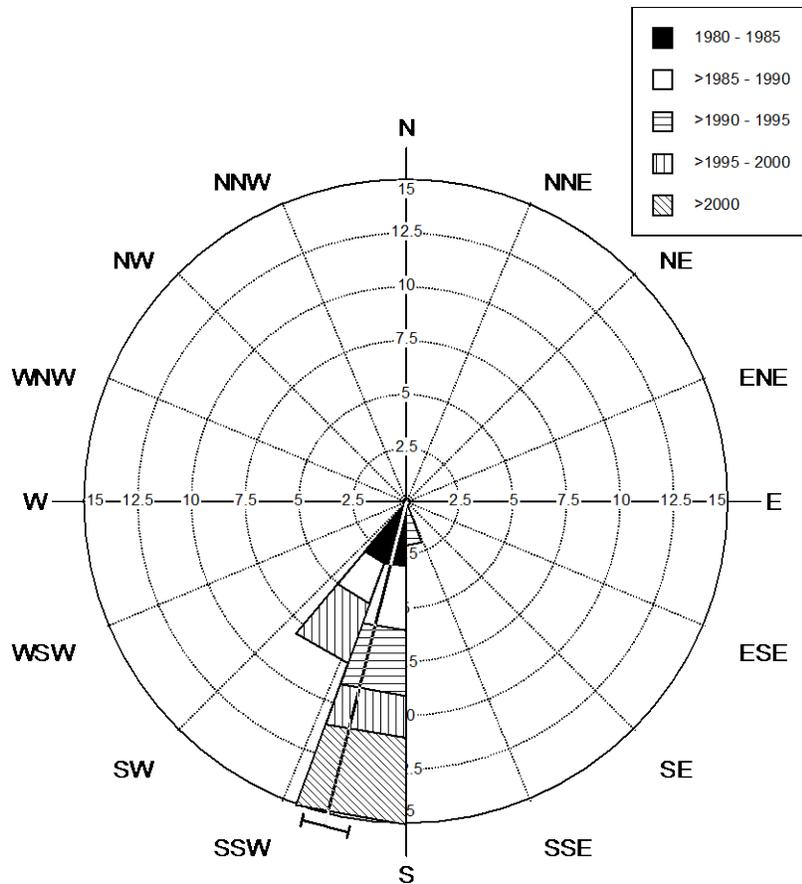
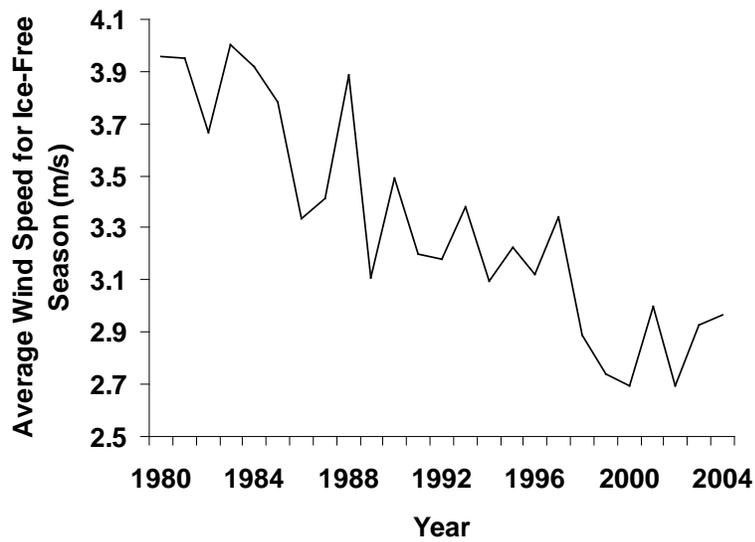


Figure 1.7: Summary of winter wind fields (November to March) from 1980-2004 over Muskoka Airport. A) Linear plot depicting the average yearly wind speed for the winter season. B) Two-variable rose histogram depicting the average yearly wind direction (compass direction) for the winter season where the single vertical arrow is the mean wind direction (generated using Oriana 3.0).

A)



B)

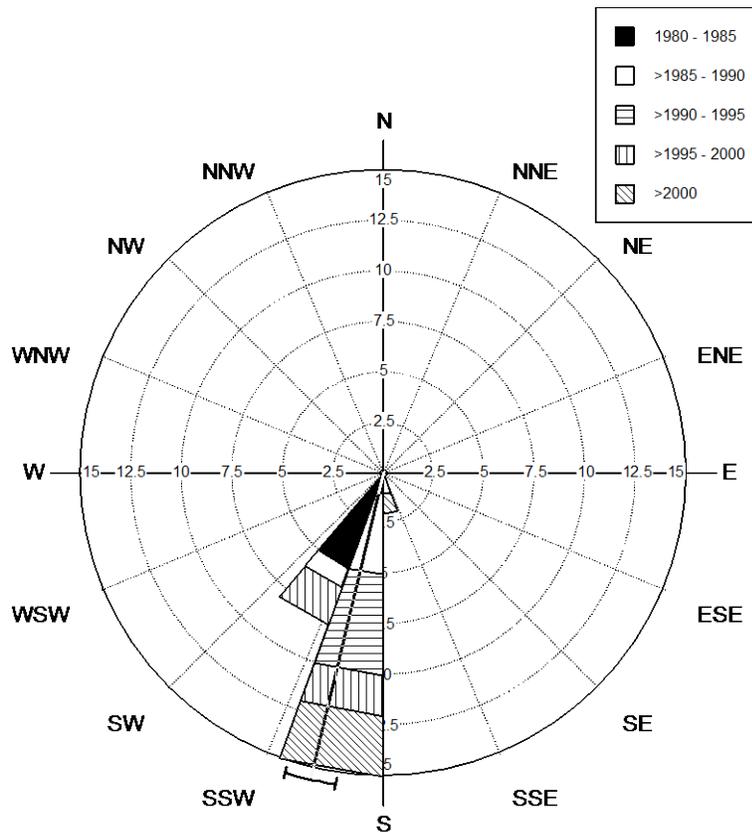


Figure 1.8: Summary of ice-free wind fields (April to October) from 1980-2004 over Muskoka Airport. A) Linear plot depicting the average yearly wind speed for the ice-free season. B) Two-variable rose histogram depicting the average yearly wind direction (compass direction) for the ice-free season where the single vertical arrow is the mean wind direction (generated using Oriana 3.0).

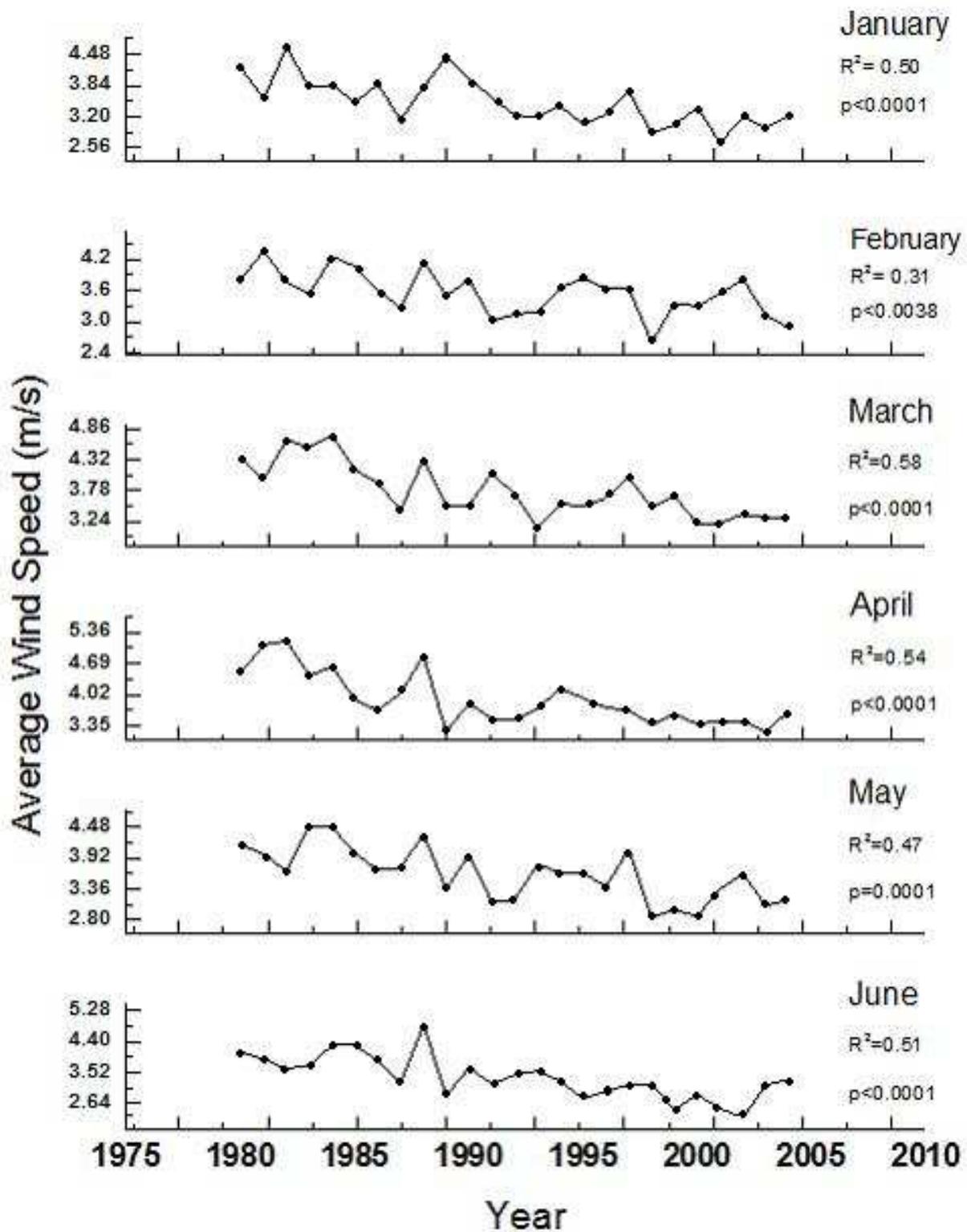


Figure 1.9a: Long-term trends in average monthly wind speed from 1980-2004 at the Muskoka Airport, Ontario, Canada.

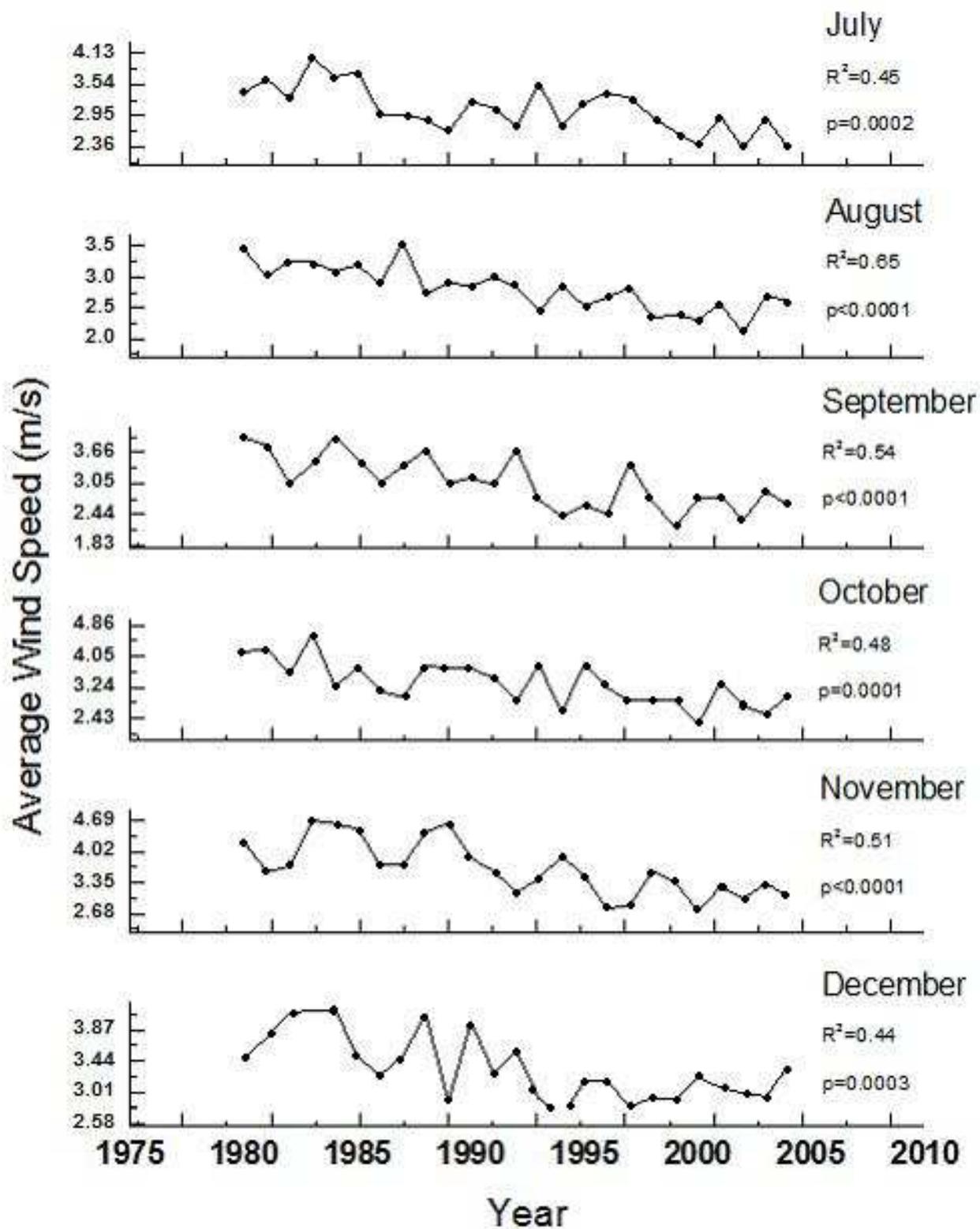


Figure 1.9b: Long-term trends in average monthly wind speed from 1980-2004 at the Muskoka Airport, Ontario, Canada.

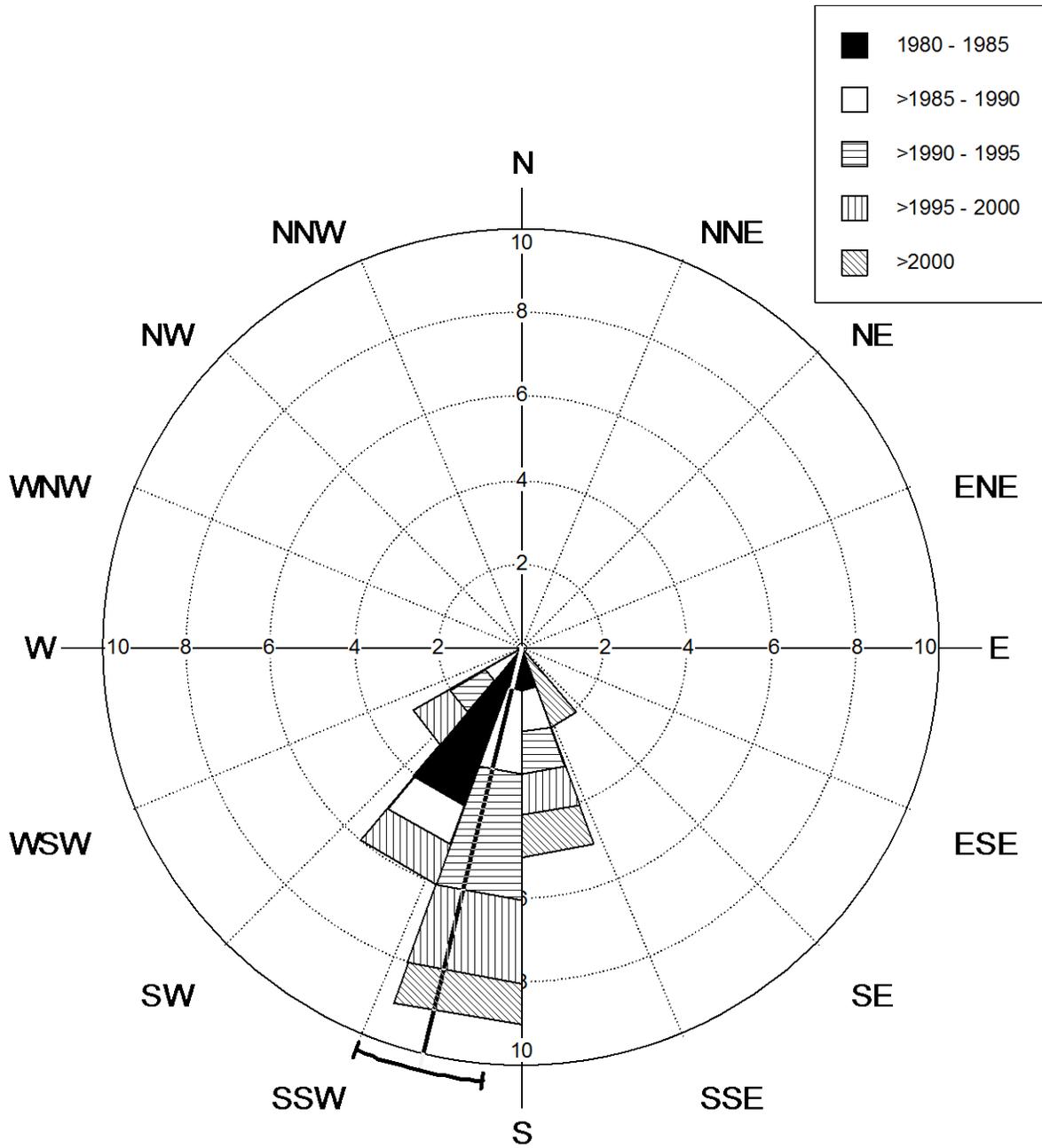


Figure 1.10: Two-variable rose histogram depicting the average yearly wind direction (compass directions) for all months combined from 1980-2004 at the Muskoka Airport, Ontario, Canada. The plots were generated using Oriana 3.0.

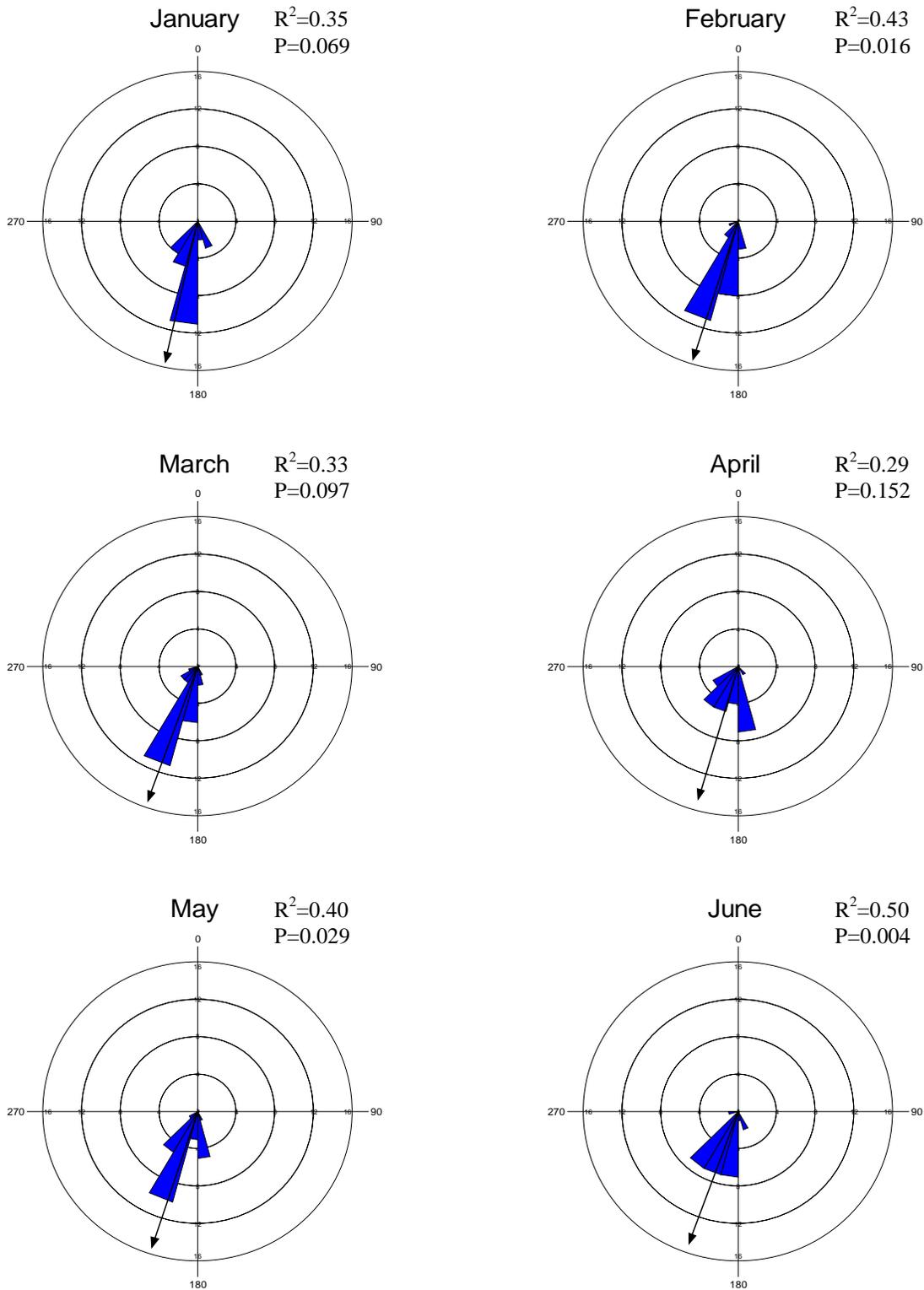


Figure 1.11a: Rose plots depicting the average yearly wind direction (degrees) for each month from 1980-2004 at the Muskoka Airport, Ontario, Canada. The single vertical arrow is the mean wind direction. The wedges depict the frequency of wind directions during the time span from that particular wind direction. The rose plots were generated using Oriana 3.0.

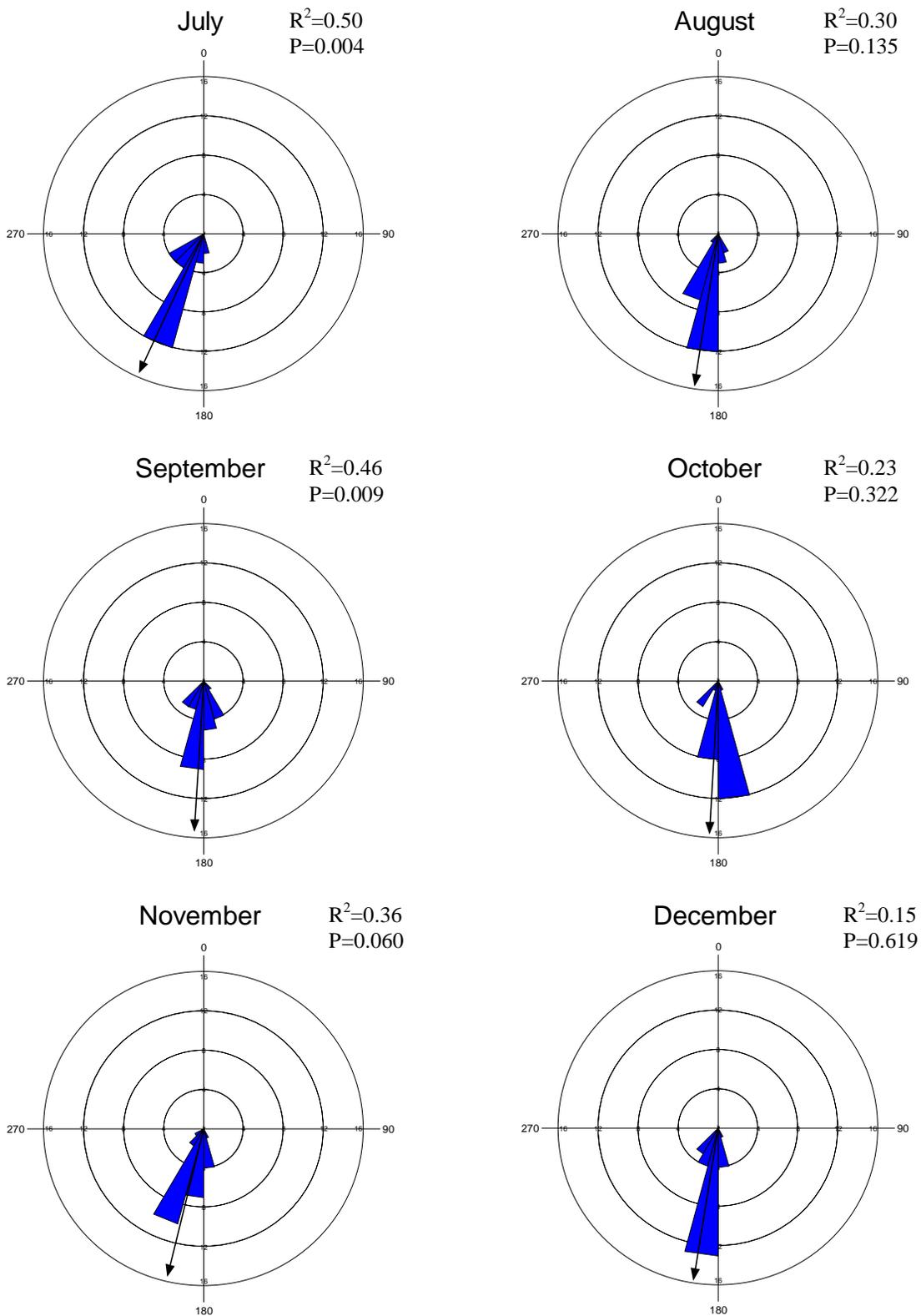


Figure 1.11b: Rose plots depicting the average yearly wind direction (degrees) for each month from 1980-2004 at the Muskoka Airport, Ontario, Canada. The single vertical arrow is the mean wind direction. The wedges depict the frequency of wind directions during the time span from that particular wind direction. The rose plots were generated using Oriana 3.0.

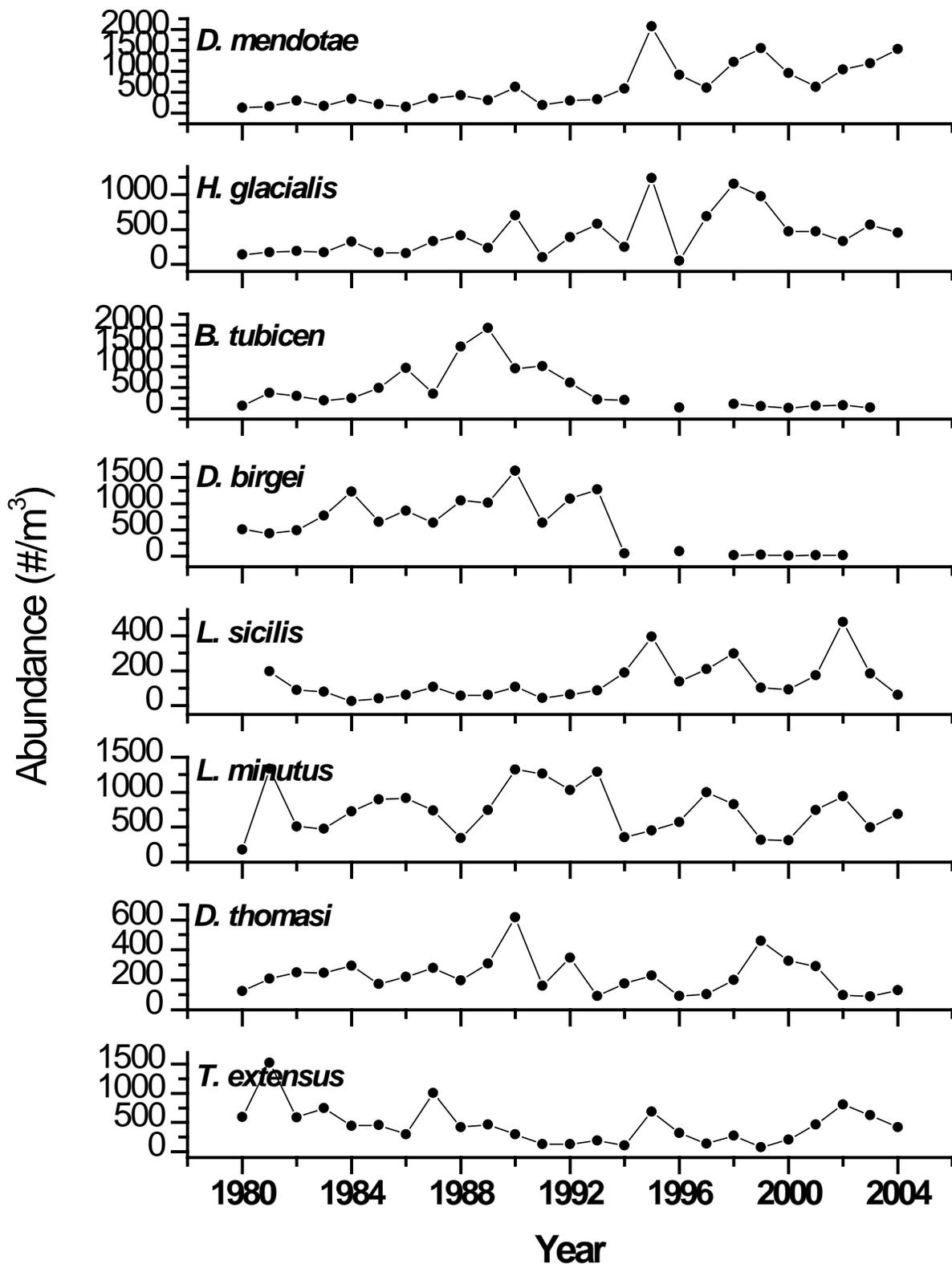


Figure 1.12: The long-term trends in average annual abundance of the selected zooplankton species in Harp Lake, Ontario.

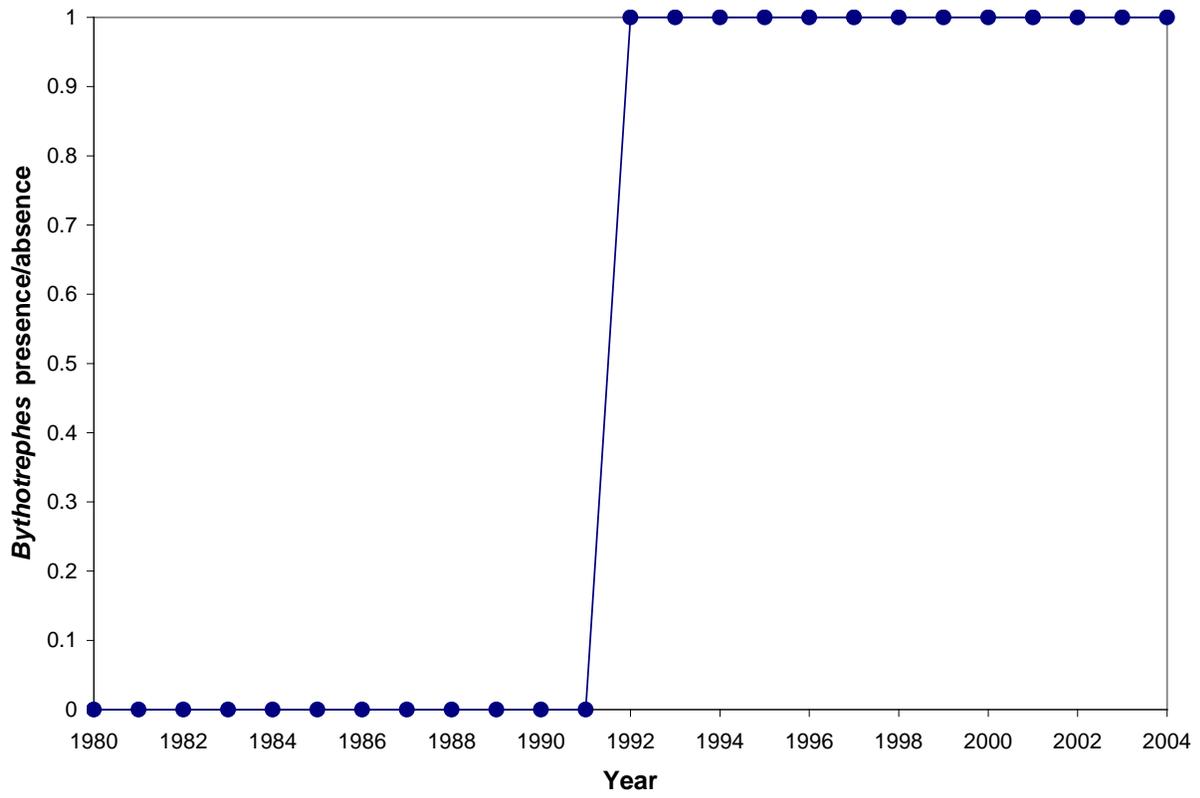


Figure 1.13: The presence/absence of *Bythotrephes* in Harp Lake, Ontario between 1980-2004.

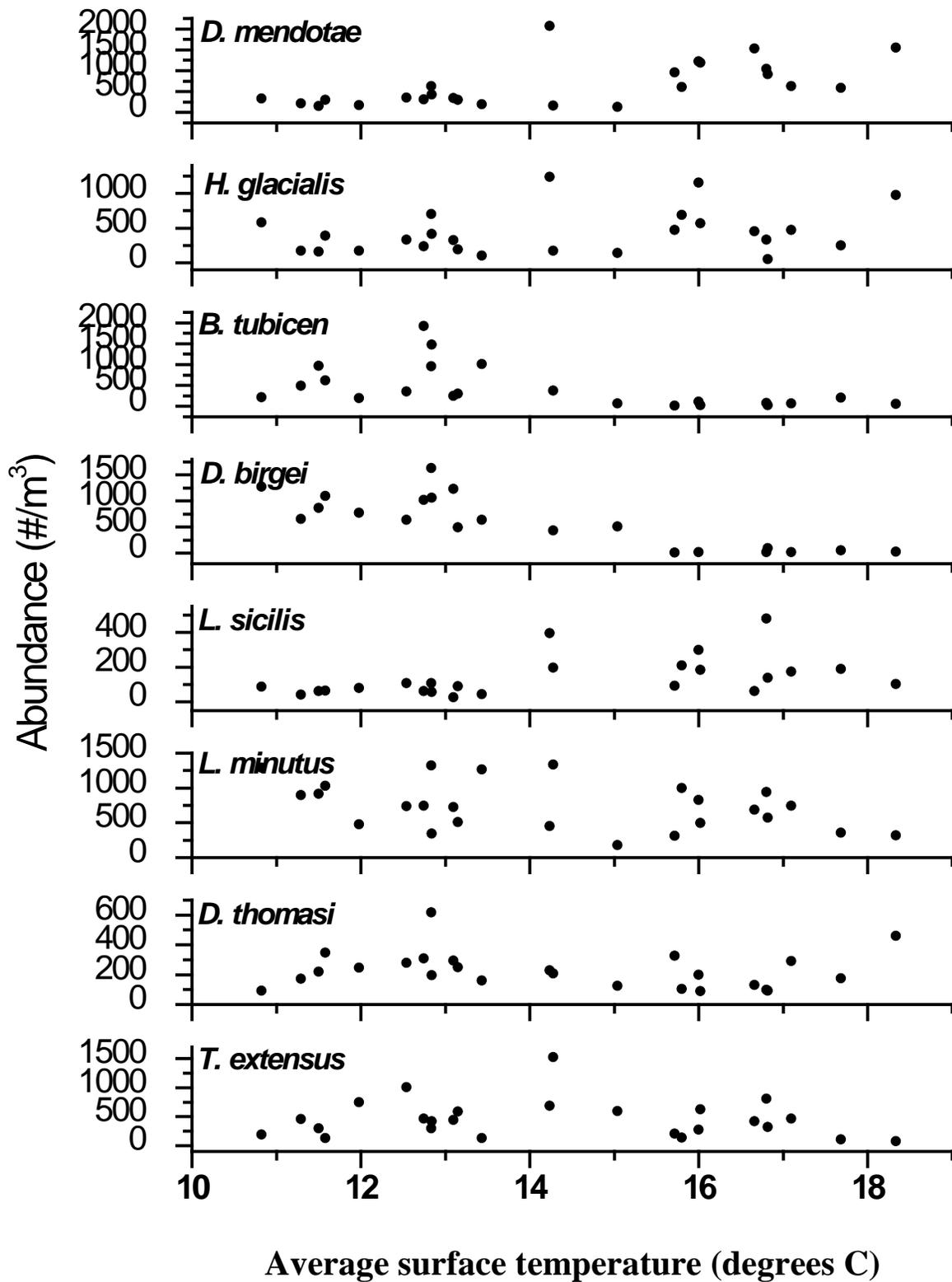


Figure 1.14: The long-term trends in average annual abundance versus average surface temperature of the selected zooplankton species in Harp Lake, Ontario.

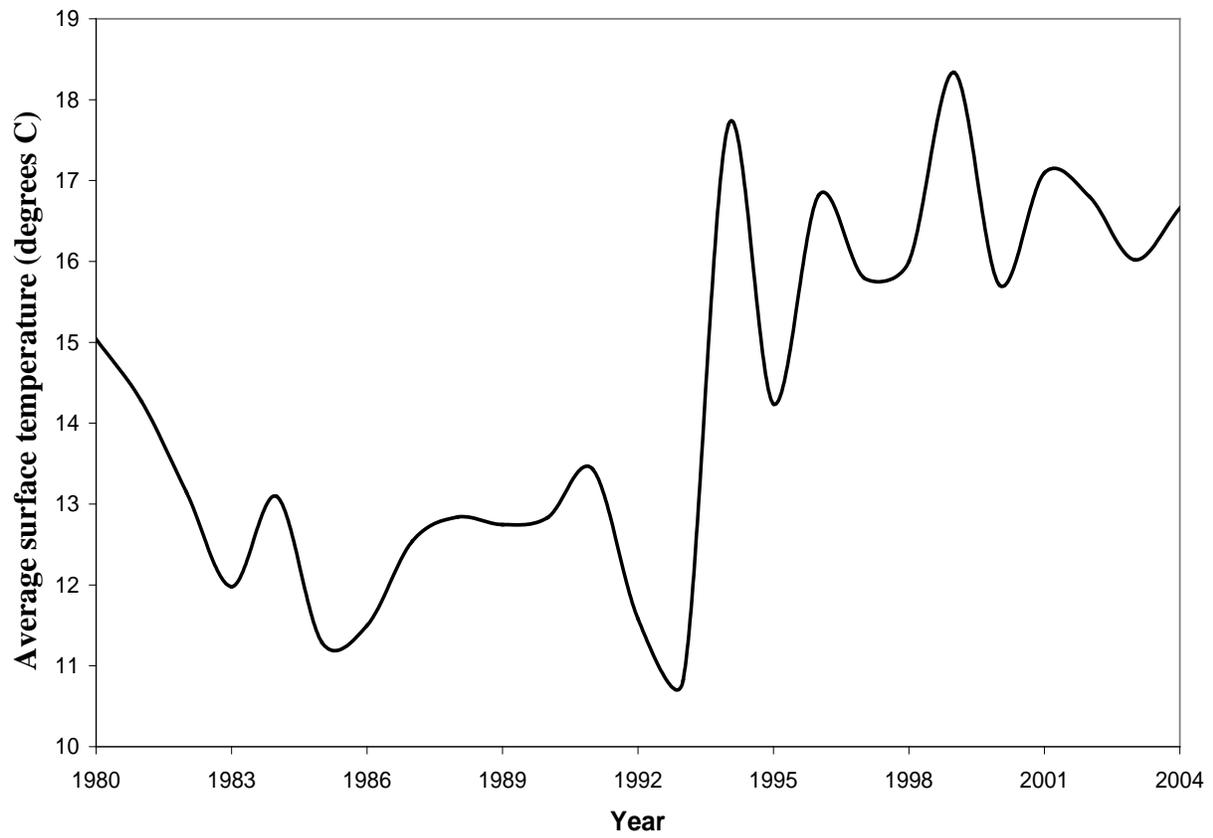


Figure 1.15: The average surface temperature in Harp Lake, Ontario from 1980-2004.

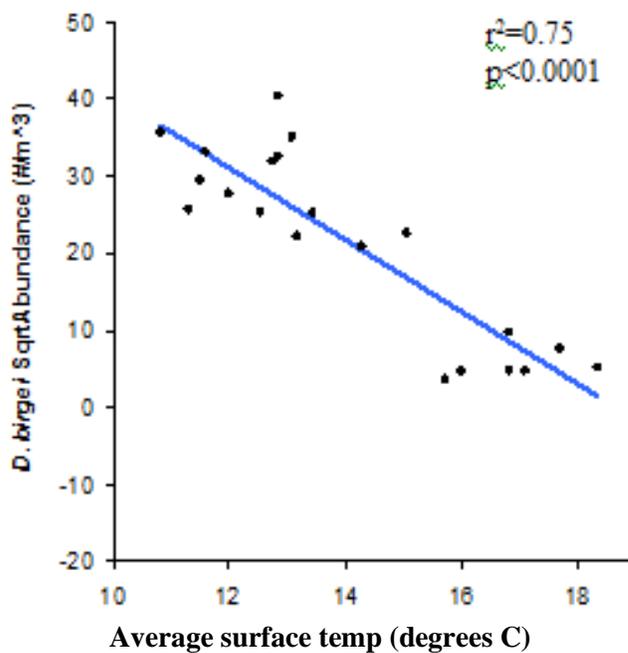
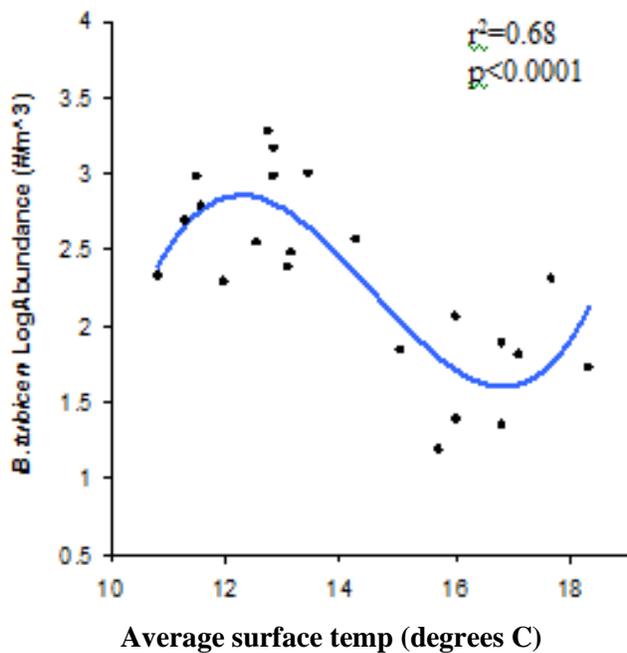
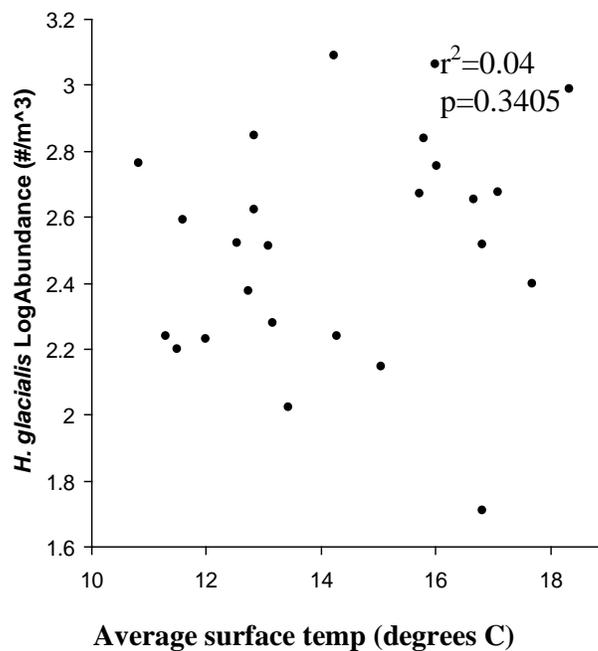
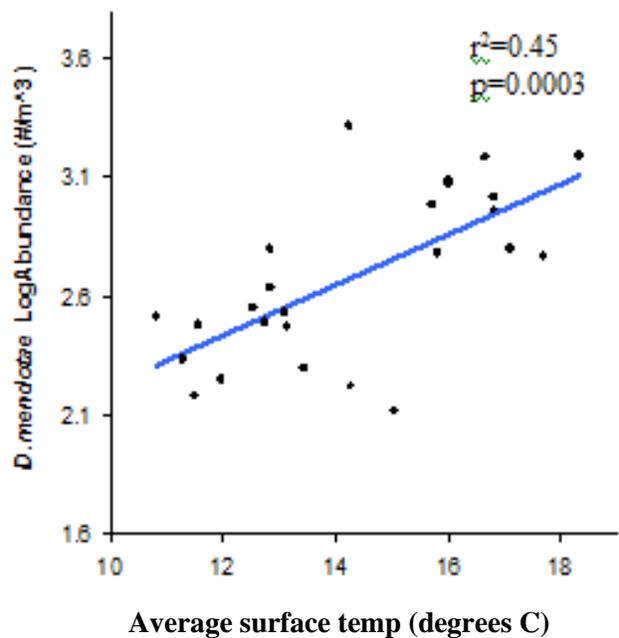


Figure 1.16a: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect to the average surface temperature in Harp Lake, Ontario.

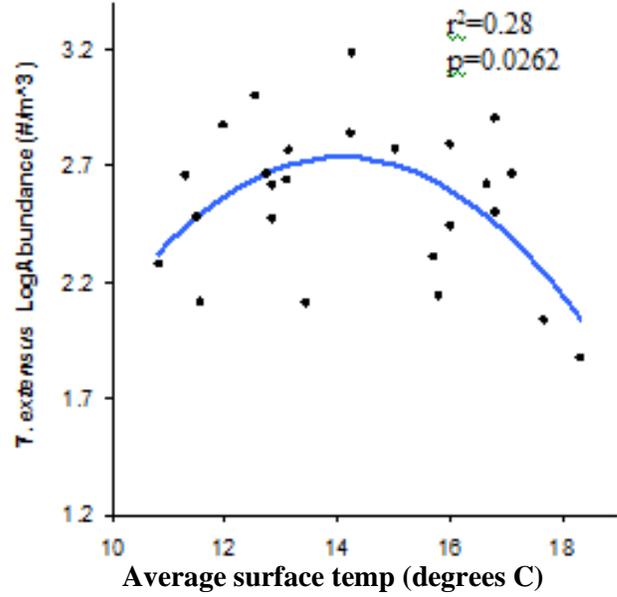
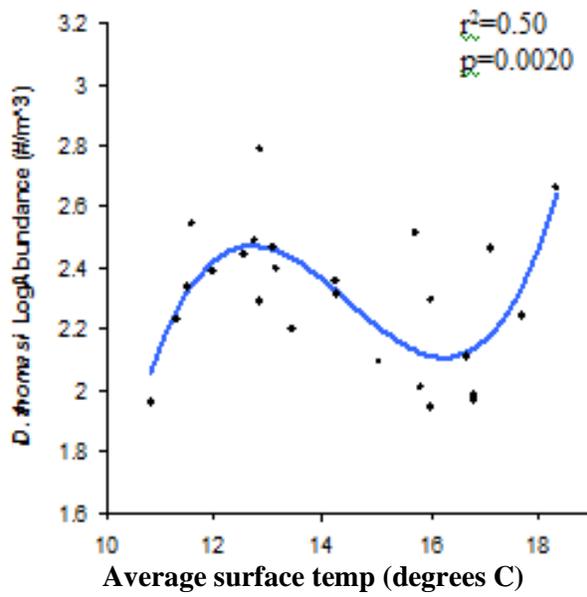
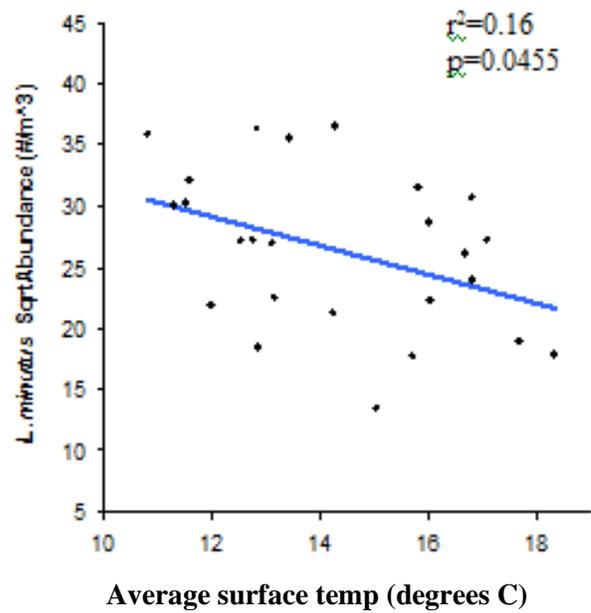
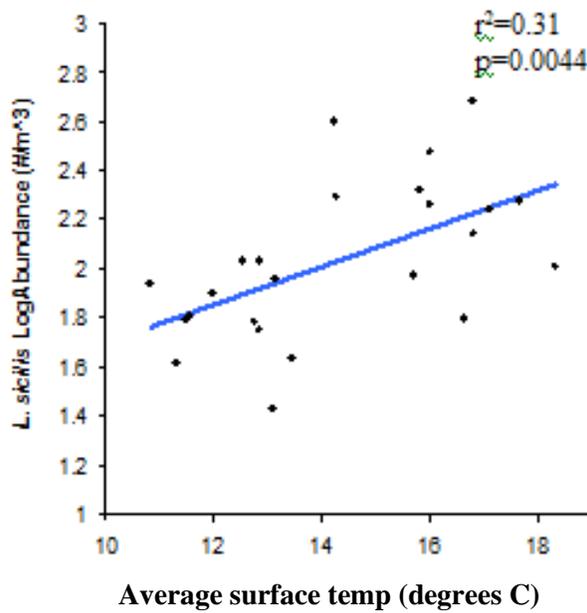


Figure 1.16b: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect to the average surface temperature in Harp Lake, Ontario.

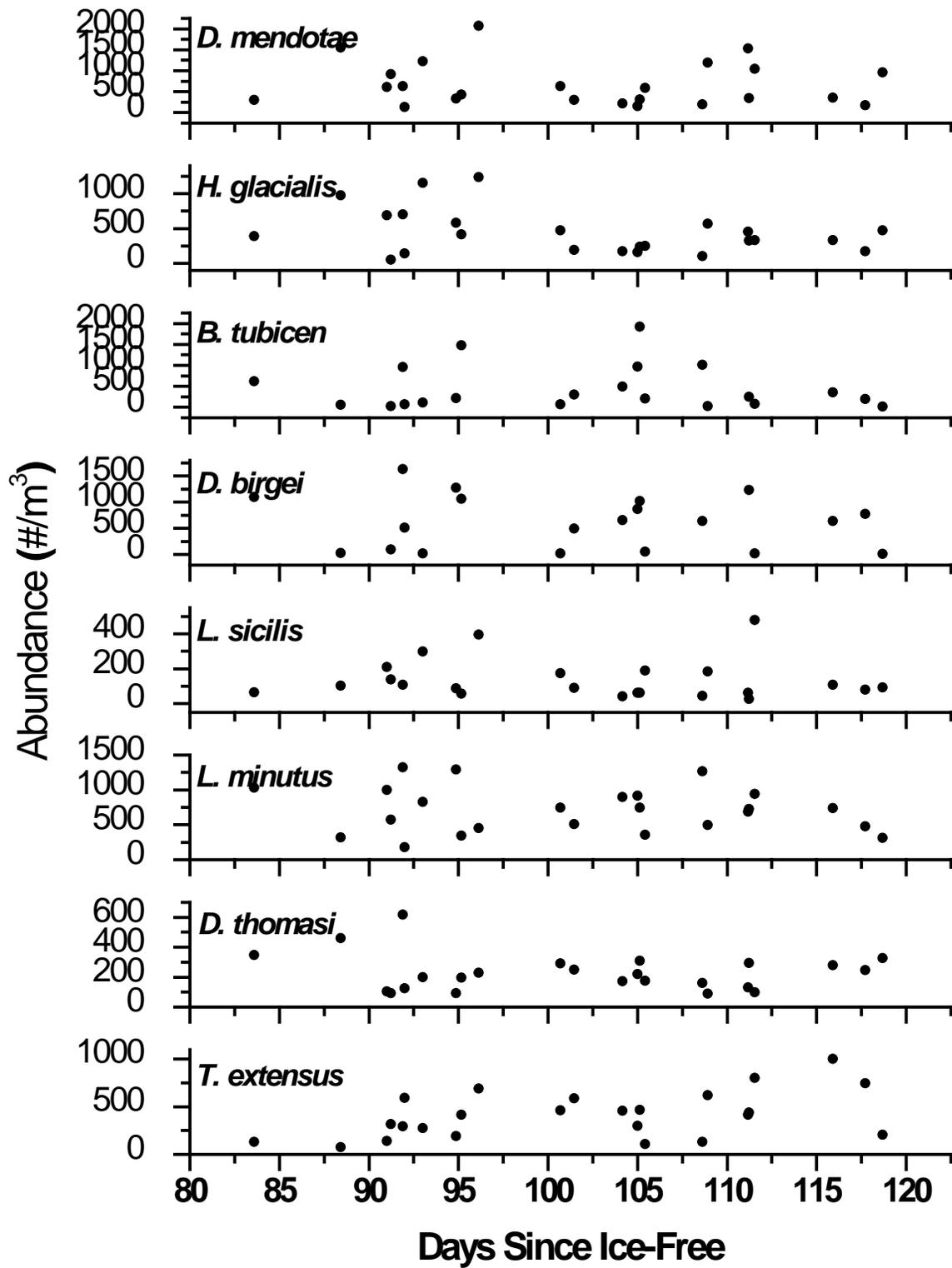


Figure 1.17: The long-term trends in abundance as a function of the annual average of days since ice free of the selected zooplankton species in Harp Lake, Ontario.

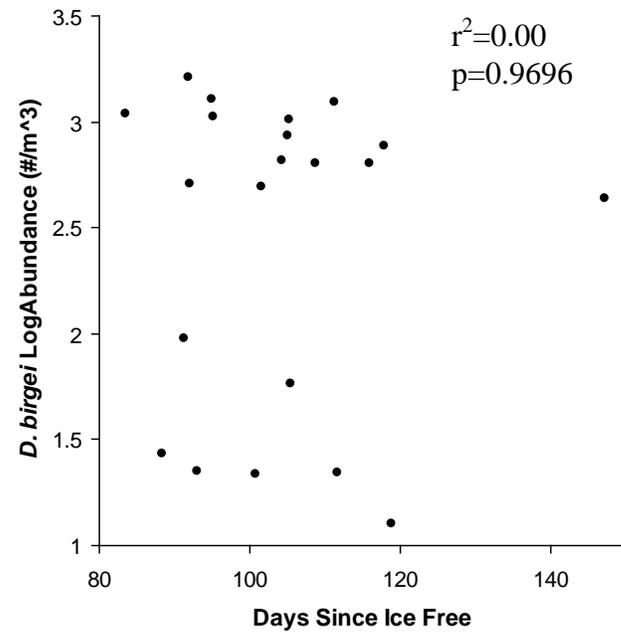
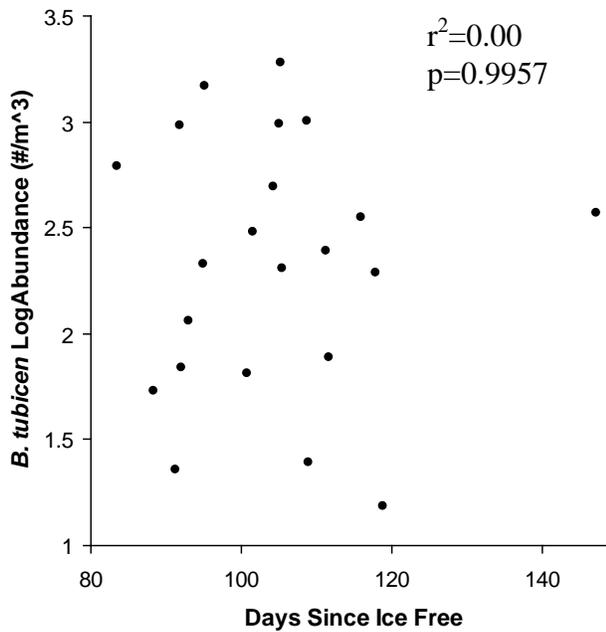
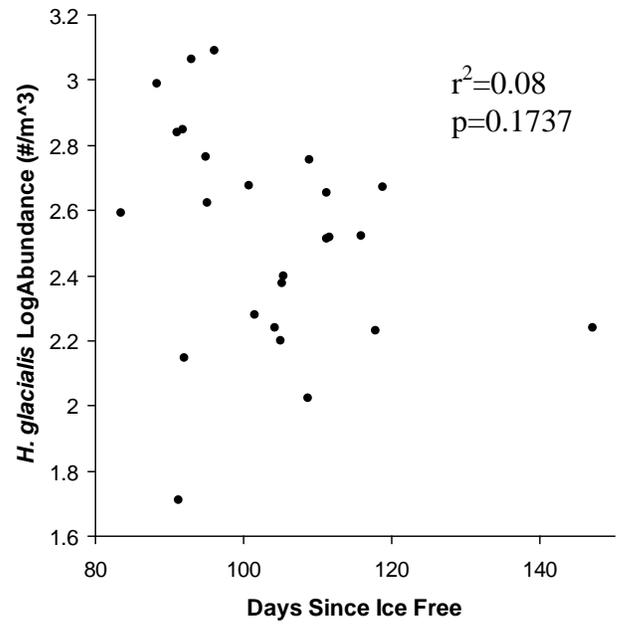
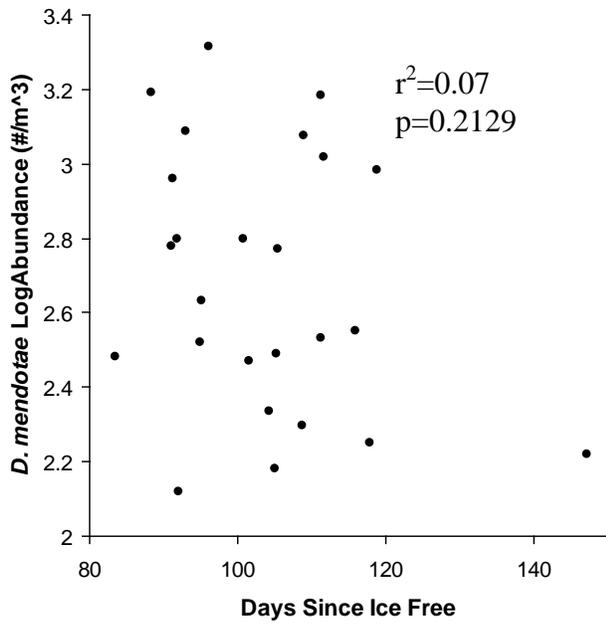


Figure 1.18a: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect days since ice-free.

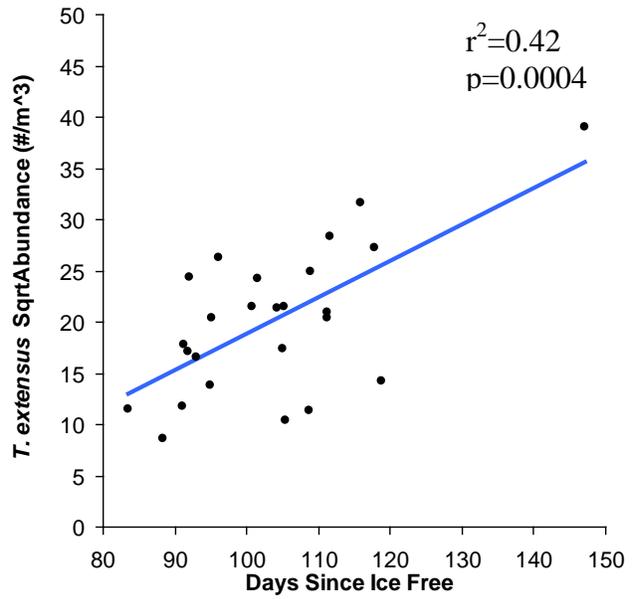
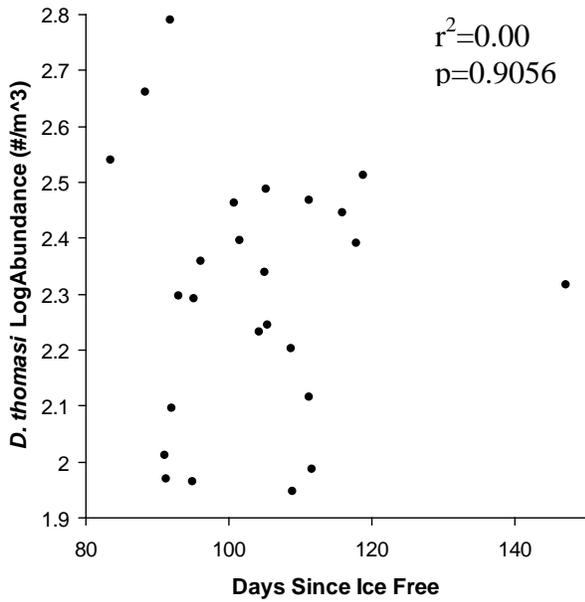
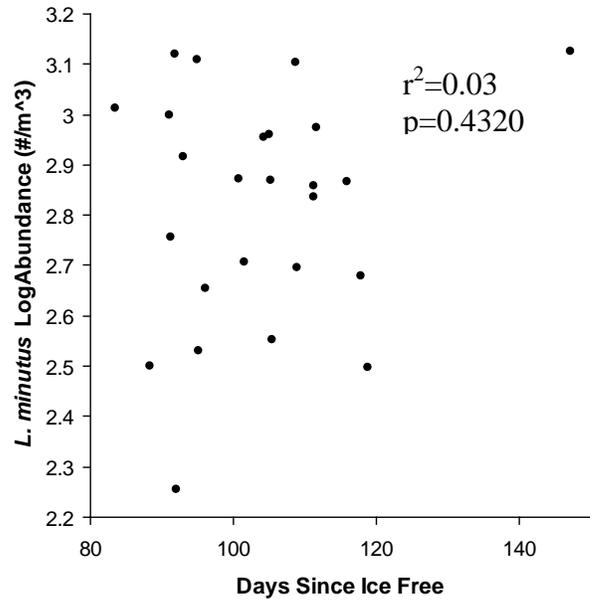
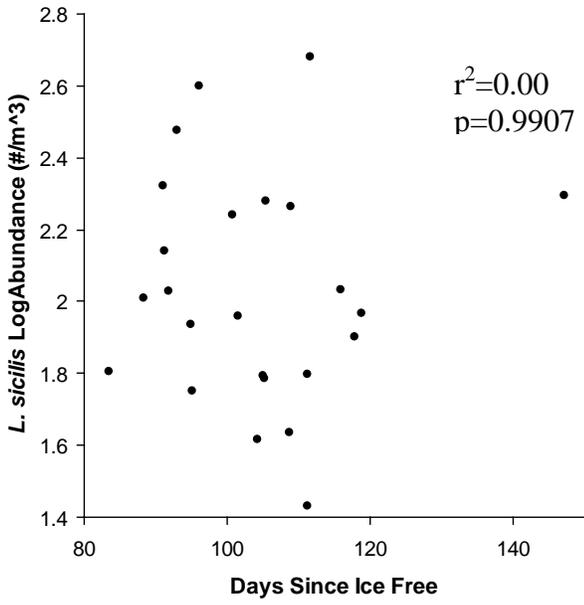


Figure 1.18b: Least squares regression models predicting the average annual abundance of the selected zooplankton species abundance with respect to days since ice-free.

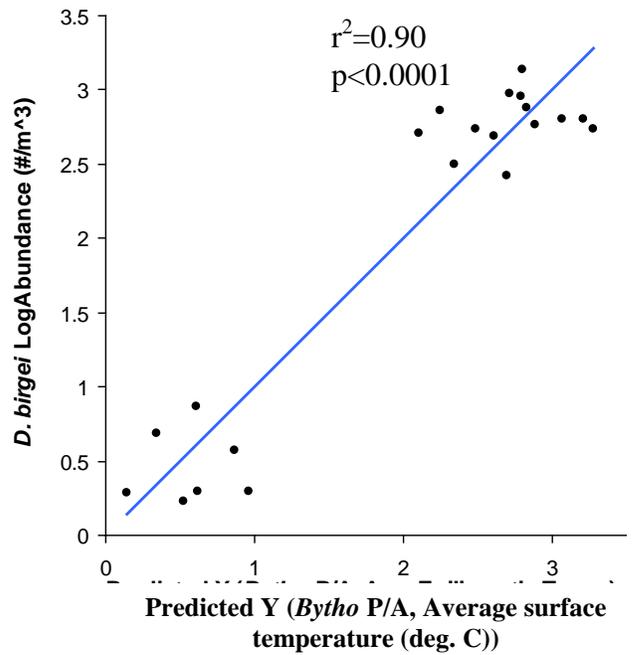
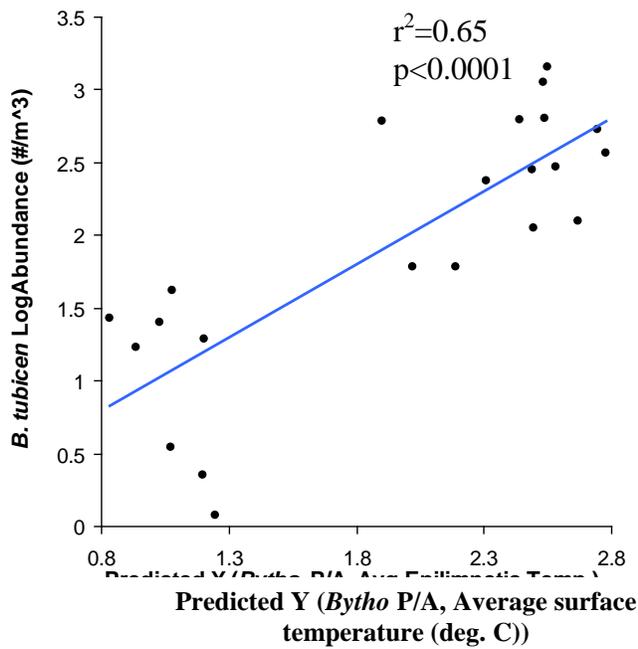
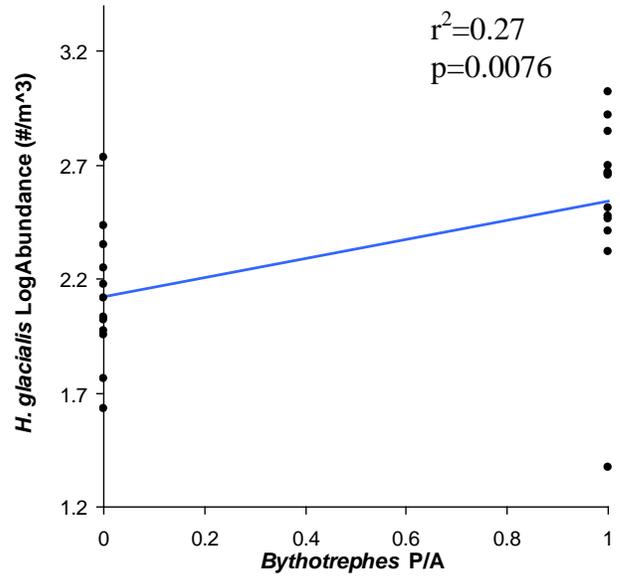
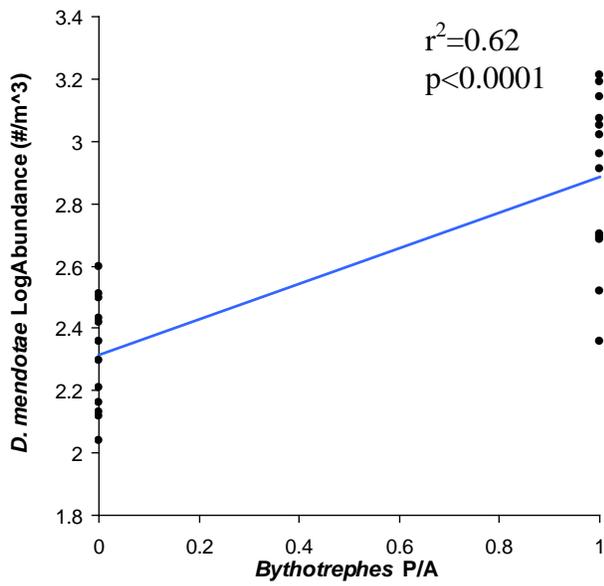


Figure 1.19a: Least squares regression models predicting the average annual abundance of the selected zooplankton species using various scales: *Bythotrephes* (presence/absence), average surface temperature, and days since ice-free.

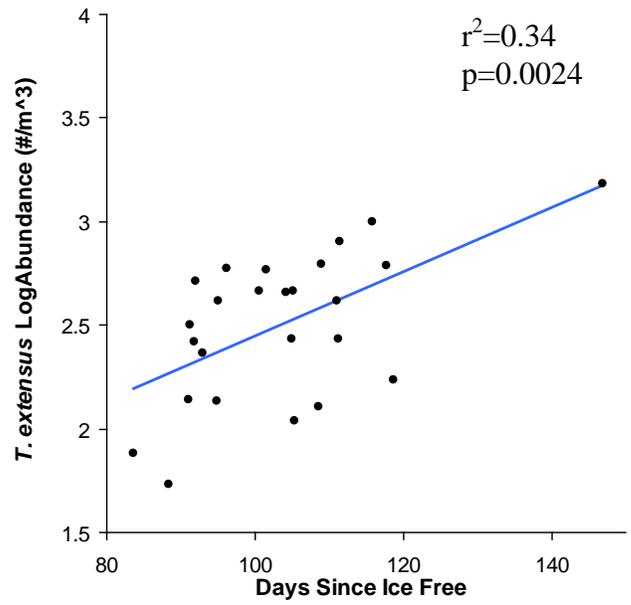
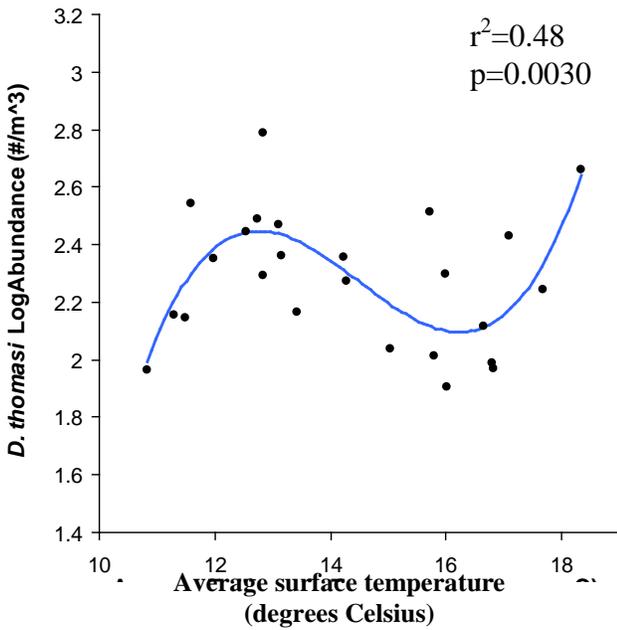
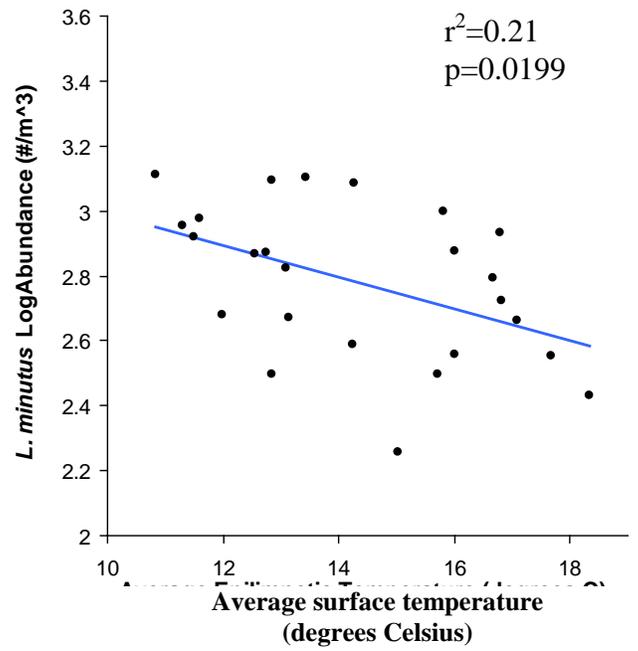
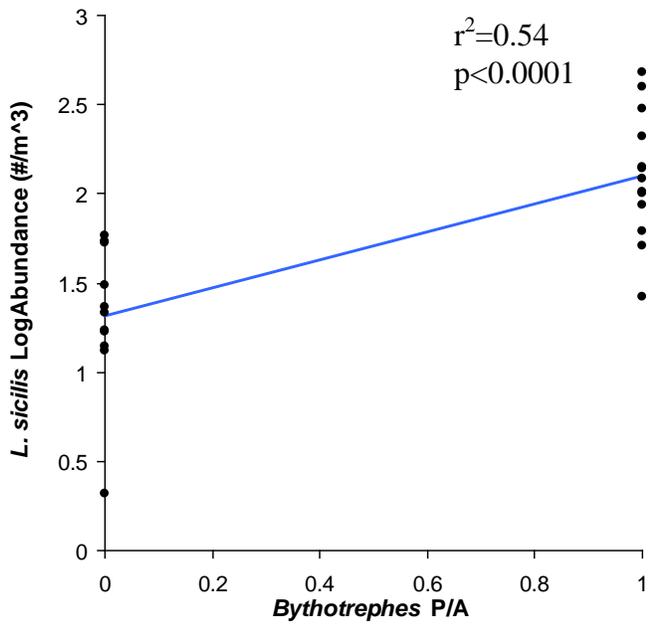


Figure 1.19b: Least squares regression models predicting the average annual abundance of the selected zooplankton species using various scales: *Bythotrephes* (presence/absence), average surface temperature, and days since ice-free.

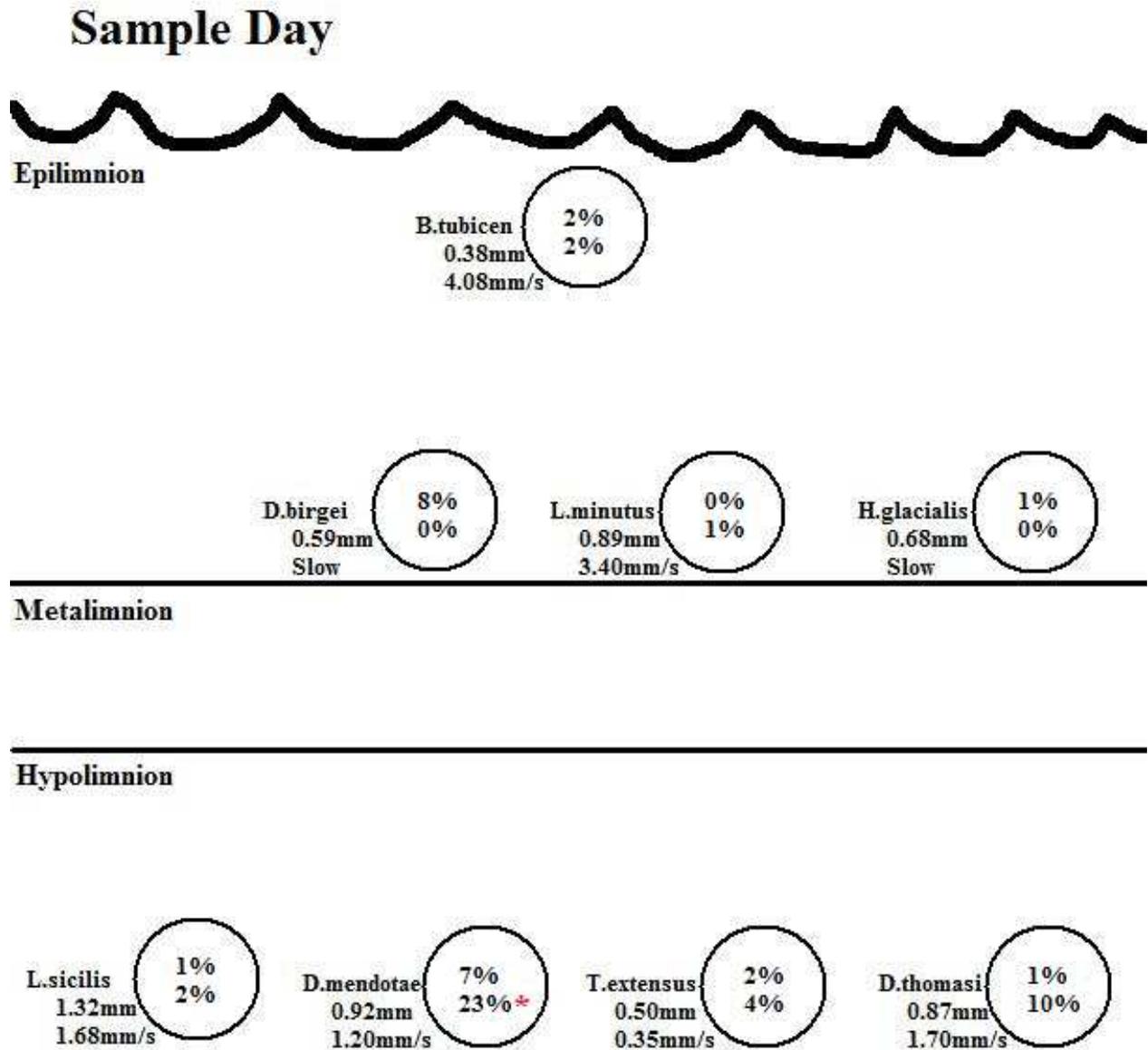


Figure 1.20: A schematic representation of the stratum locations of the selected zooplankton species in Harp Lake. Each circle indicates a specific zooplankton species with the name to the left with the body size and the speed below the name. The 2 values within the circle indicate where the residual abundance is explained by: the wind speed (m/s) (top); wind direction (degrees) (bottom). Asterisk percentage indicates significance ($p < 0.05$).

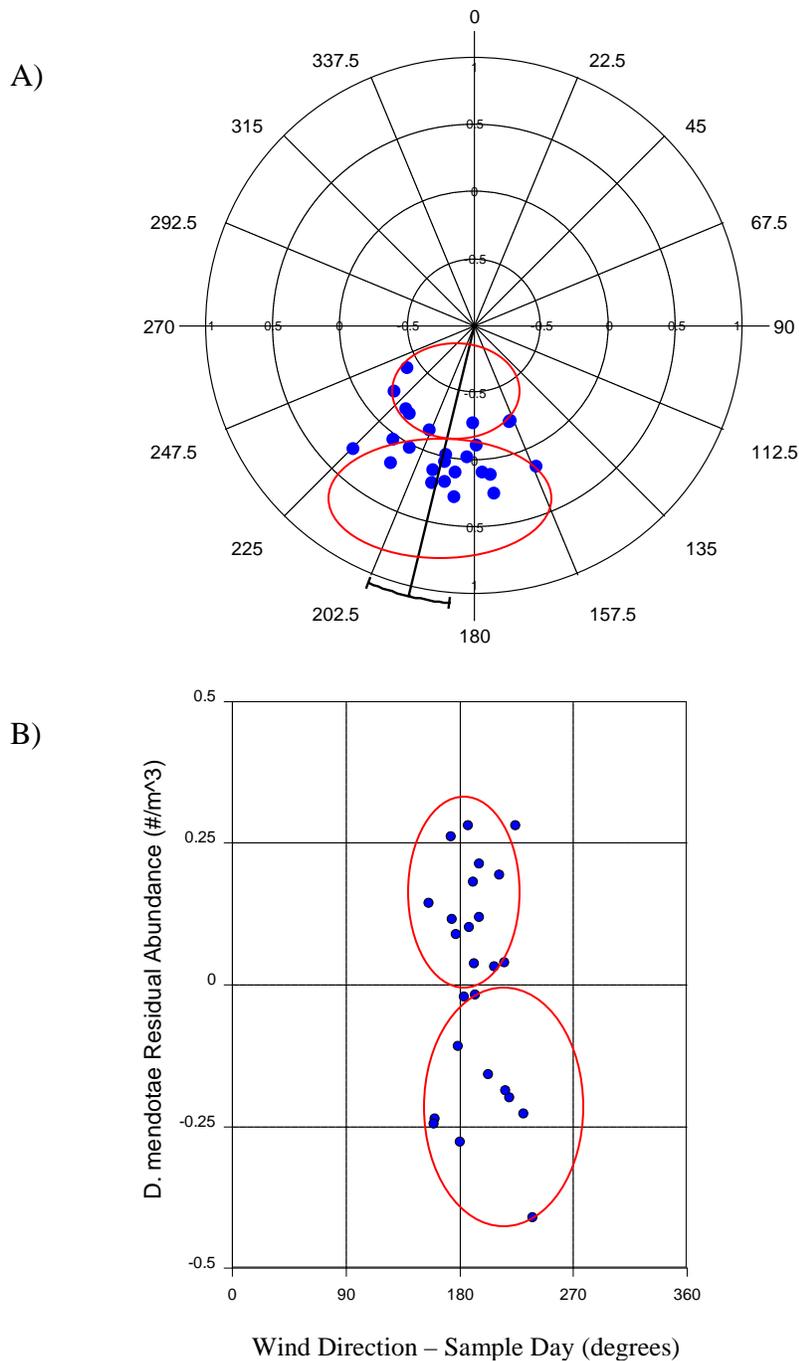


Figure 1.21: Plots demonstrating the association between the residual abundance of *D. thomasi* with wind direction from 1980-2004 over Muskoka Airport. A) Rose plot-scatterplot depiction with a single black arrow denoting the mean wind direction. The top circle indicates the area where the negative residuals complement the wind directions; whereas, the lower circle indicates the area where the positive residuals show a different range of wind directions. B) Two-sample linear-scatterplot. The positive residuals are denoted by the top circle and the negative residuals are denoted by the bottom circle. All plots were generated using Oriana 4.0.