WIND-DRIVEN HORIZONTAL DISTRIBUTIONS OF ZOOPLANKTON IN A SMALL MEROMICTIC LAKE

MELANIE B. GORAL

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Introduction

The study of zooplankton dispersal is important when trying to identify the causes of patchiness in lakes and for potentially determining major drivers responsible for heterogeneous distributions. Much of the research that examines zooplankton dispersal and distribution focuses on the multiple means of transport, such as: animal vectors (Allen 2007), shoreline avoidance behaviour (Dirnerger and Thredlkeld 1986; Zurek and Bucka 2004), diel vertical migration behaviour (Murtaugh 1985; Semyalo *et al.* 2009) and wind-induced mechanics (George and Edwards 1976; Cloern *et al.* 1992; Vanschoenwinkel *et al.* 2008).

A major problem associated with the study of zooplankton distributions often involves the use of minute spatial and temporal scales to measure the average dynamics of zooplankton. For example, by sampling only 1 or 2 stations over a short period, Dirnerger and Thredlkeld (1986) risked misidentifying the common drivers of spatial dynamics of zooplankton in a small lake. Similarly, Zurek and Bucka (2004) attempted to trace the horizontal distribution of phytoplankton and zooplankton movement toward open waters using only 2 littoral transects over 1 month. Comparatively, Malone and McQueen (1983) proved that horizontal distributions of zooplankton were indeed patchy and that multiple stations are necessary to characterize zooplankton patchiness, but the frequency of sampling has yet to be determined.

Among the multiple means of transport, wind-induced dispersal of zooplankton has been poorly studied and requires further exploration. The passive transport of zooplankton in surface waters is particularly influenced by wind-induced currents acting on the water surface; especially in thermally stratified lakes where there is a distinct surface mixing layer (George and Edwards 1976; Gorham and Boyce 1989; Rand and Hinch 1998; Ravens *et al.* 2000; Naithani *et al.* 2003). Several studies have indicated that the dispersal of zooplankton by passive transport has led to correlations between zooplankton heterogeneity and abundance where higher abundances are found at certain sampling stations (Dirnerger and Thredlkeld 1986; Primo *et al.* 2009). In particular, Vanschoenwinkel *et al.* (2008) suggests that horizontal aggregations of zooplankton found in 36 small-scale temporary rock pools from South Africa in 2006 were due to the vertical updrafts and short-term gusts that characterized the local wind fields during the summer. However, Zurek and Bucka (2004) report that winds as weak as 4-5 m/s have caused slight back currents on windward shores. All things considered, zooplankton dispersal and distribution is undeniably influenced by wind dynamics and requires further study.

The physical attributes of small versus large lakes influence the degree of wind-induced spatial distribution of zooplankton populations (Gorham and Boyce 1989; Naithani *et al.* 2003). The general distribution dispersal of plankton by wind is accomplished through surface water currents that are pushed windward by downwelling and are pulled below the surface waters (Naithani *et al.* 2003). Plankton are re-distributed in the water column by the upwelling of deeper water, which is fuelled by the surface water currents (Naithani *et al.* 2003). The movement of water masses, such as downwelling and upwelling is referred to as entrainment and can affect the horizontal and vertical spatial patterns of organisms in the water column (Naithani *et al.* 2003). Wind-induced entrainment transports plankton, nutrients and dissolved oxygen throughout the water column and causes the entire body of water to mix (Naithani *et al.* 2003). Larger bodies of water (10^4-10^6 ha) have a greater surface area for wind to blow, therefore small lakes (10-100 ha) will have a decreased sensitivity to blowing wind than compared to larger lakes (Mazumder *et al.* 1990; Naithani *et al.* 2003).

Lake Tanganyika, Africa is a large lake (325 ha, max. depth 1470 m) that routinely undergoes wind-induced mixing (Naithani *et al.* 2003). Naithani *et al.* (2003) reports that upwelled, nutrient-rich water from the direction of prevailing winds (southern end) takes roughly 2-3 weeks to reach the opposite end of the lake. However, relative to larger lakes, small lakes, such as Lake William, U.S.A (40 ha, max. depth 9.8 m) experience quicker plankton dispersal throughout the lake in response to wind-driven currents (Cloern *et al.* 1992). The development of these currents in Lake William led to the spatial distribution of plankton within a 1-10 day period (Cloern *et al.* 1992). Therefore, the complete cycling of water due to wind varies depending on the size and depth of the lake itself.

The natural environment surrounding bodies of water are also likely to affect the wind-induced dispersal of plankton communities (Dirnerger and Thredlkeld 1986; Rybak and Dickman 1988; Tanentzap *et al.* 2008). Forests increase watershed surface roughness, which causes a sheltering effect on smaller lakes, such as those reported from Crawford Lake and Clearwater Lake (Rybak and Dickman 1988; Tanentzap *et al.* 2008). A forestation surrounding Clearwater Lake has decreased wind speeds and thus reduced the velocity and mixing of wind-induced currents in surface waters (Tanentzap *et al.* 2008). River inflow and outflow areas connected to lakes can also influence the wind-induced distribution of plankton in the water column while also serving as an entrance or exit out of the lake (Dirnerger and Thredlkeld 1986). Heavy rainfall seasons can increase the amount of inflow or outflow of a lake and thereby weaken or encourage the effect of wind stress on the surface currents (Dirnerger and Thredlkeld 1986). All in all, changes in the physical attributes within and surrounding lakes can influence plankton distribution and could therefore cause adverse effects on spatial heterogeneity.

Lake types can vary from being warm and completely mixed to cold and never mixed, but north temperate lakes are most commonly dimictic, mixing in the spring and fall. The assessment of wind histories and overall climatic variability surrounding aquatic environments may help explain horizontal spatial heterogeneity in zooplankton communities (George and Edwards 1976). The main goal of this research is to combine *Daphnia* abundance data collected by Prepas and Rigler (1978) with the wind characteristics associated with Crawford Lake in order to better understand the wind-induced distributions of zooplankton and draw any particular correlations between wind field data and *Daphnia* abundance. The objectives of this study are: (1) to examine the relationships between wind direction, speed and surface temperatures at Crawford Lake during the study period; (2) to examine the correlation between *Daphnia* abundance distribution and either sampling station or date sampled; and (3) to examine the correlation between *Daphnia* abundance and wind dynamics.

This study will focus on a meromictic lake, which is anoxic below 14m in depth and is characterized by partial mixing properties where the upper layer (mixolimnion) is freely circulating and has a low density, while the bottom layer (monimolimnion) does not mix below 16 m, is very dense, highly saline and anoxic below 14 m (Prepas and Rigler 1978; Rybak and Dickam 1988; Mazumder *et al.* 1990). The examination of three sampling stations in this small 2.5 ha meromictic lake revealed patterns in the spatial heterogeneity of zooplankton abundance levels (Prepas and Rigler 1978). Prepas and Rigler (1978) documented this spatial heterogeneity among horizontal and vertical distributions in both *Daphnia rosea* and *Daphnia pulex* from Crawford Lake, Ontario. Apart from the useful spatial patterns observed in Prepas and Rigler (1978), zooplankton species such as *Daphnia* are highly reliable animal models used to study lake health and movement. Zooplankton populations can readily disperse using varying water connections and can colonize at varying depths of the water column (Vanschoenwinkel *et al.* 2008). Therefore, it is reasonable to assume that *D.rosea* and *D.pulex* will serve as beneficial model organisms for this particular study.

Method

Article Research

Journal articles were explored using the electronic database Web of Science in order to find studies that provided the necessary zooplankton abundance data taken at multiple stations while having accessible online wind records for areas in close proximity to the study location. The following terms were inputted into the search fields: zooplankton, patch*, multiple station*, climate, wind influence*, distribut*, upwelling, and downwelling. Many studies performed experiments using zooplankton abundance values; however, the studies were limited to either a single station (Gagnon and Lacroix 1981; Murtaugh 1985; Dirnerger and Threlkeld 1986; Stich and Maier 2007; Semyalo *et al.* 2009), multiple stations with no accessible wind data for the area around the study location (Siokou-Frangou *et al.* 1998; Chiba and Saino 2003; Queiroga *et al.* 2005; Pinel-Alloul *et al.* 2004; Primo *et al.* 2009) or single stations sampled between multiple lakes (Malone and McQueen 1983; Mazumder *et al.* 1990; Basu *et al.* 2000; Vanschoenwinkel *et al.* 2008).

In order to analyze zooplankton abundance and the possible influences of wind-induced distribution at multiple stations, an article was chosen that provided the necessary original zooplankton abundance data at multiple spatial scales. The peer-reviewed journal article, *The Enigma of Daphnia Death Rate* by E. Prepas and F. H. Rigler (1978) was chosen using the Web of Science database for supplementary data analysis. This article provided female adult abundance values for *Daphnia rosea* (between 29-May to 05-October 1975) and *Daphnia pulex* (between 10-April to 20-July 1976) at Crawford Lake, Ontario, Canada. Both species of *Daphnia* will be analyzed, however the abundance of *D.rosea* and *D.pulex* cannot be directly compared since they were sampled in different years. Only female adults were used in the data analysis as a result of the different vertical migratory behaviours (e.g., swimming speed) of the various immature *Daphnia* instars present in the water column (Prepas and Rigler 1978; Havel 2009).

Wind characteristics

Wind directions (recorded in degrees) and wind speeds (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) at varying time scales (hourly, daily and monthly) from 1975 and 1976 during the sampling events of the study in the Prepas and Rigler (1978) article. All wind directions are described as the direction the wind is blowing from. In addition to the wind characteristics, mean temperatures for all sampling events were also recorded for analysis. All meteorological environmental data was taken from the Toronto Lester B. Pearson International Airport recording station in Southern Ontario, Canada (43°40'N, 79°38'W) (approximately 69.8 km from Crawford Lake), as it was the nearest recording station that provided electronically accessible data for the study periods during 1975-76.

Site Description and *Daphnia* Collection

Crawford Lake (43°28'N, 79°57'W) is located in Southern Ontario, Canada near Campbellville (Figure 1) (Rybak and Dickman 1988). This meromictic lake is small (2.5 ha), deep (maximum depth 23.5 m) and surrounded by trees (primarily sugar maple and beech) and ridges of limestone equal or less than 6 m above lake surface (Prepas and Rigler 1978; Rybak and Dickman 1988). There is one inflow (northern end) and one outflow (southern end) stream connected to the lake (Rybak and Dickman 1988). The inflow stream in the northern region of the lake has an 85 ha drainage area that provides freshwater flow into the lake (Rybak and

Dickman 1988, Yu *et al.* 1997). Crawford Lake is stationary for the majority of the year and anoxic below 14 m depth (Prepas and Rigler 1978; Rybak and Dickman 1988).

Zooplankton samples were collected from May to October 1975 and April to July 1976 using vertical tows from directly above the bottom of the lake to the surface at three fixed stations (Figure 2). Three vertical hauls were taken on each sampling event (sampling date) at each sampling station and the zooplankton samples were pooled for that particular station. The zooplankton samples were preserved in 4% Formalin and 6% sucrose solution (Prepas and Rigler 1978). For a detailed outline of the procedure, refer to Prepas and Rigler (1978).

Statistical Analysis

Are there any relationships between environmental variables (atmospheric temperature, wind direction and wind speed) from Crawford Lake during the study periods?

Wind direction, wind speed and atmospheric temperature were documented for each sampling date of each study period (*D.rosea*: May to October 1975; *D.pulex*: April to July 1976) in order to assess any general interactions between these environmental variables during the study periods. The wind characteristics for each day were taken from the maximum wind gust. Since Crawford Lake is sheltered by trees and ridges, a stronger wind intensity measurement would increase the chances of documenting an interaction between environmental variables.

Wind direction data is circular and requires conversion into linear measurements as I did not have access to circular statistical software therefore, wind directions were categorized into 16 standard compass rose directions and the combined directions per month were tallied (see Appendix A, Table A1 for wind direction categories). The monthly tally is useful to observe any overall monthly changes in wind direction during the entire study period. Radar-type graphs (in Excel 2000) were used to compare monthly wind directions using the tallied amount of wind directions/category/day during the study periods for 1975 and 1976 separately. Pearson's correlation coefficient (in Excel+Analyse-it Add-in 2000) was used to assess the relationships between environmental variables for each study period using monthly values. Statistical significance is defined as values below p=0.05 (95% confidence).

Is there a significant difference in* Daphnia *abundance from sample station to station as well as sampling date at Crawford Lake?

The abundance of *D.rosea* and *D.pulex* cannot be directly compared since they were sampled in different years, however, such a comparison was not my purpose. *Daphnia* abundance collection was provided (by Prepas and Rigler 1978) as the number of female adults/10 cm^2 of lake surface.

One-Way and Two-Way Analysis of variance (ANOVA) tests were done to assess the significance of *Daphnia* abundance from station to station as well as sampling dates. The ANOVA test assumes that the samples are normally distributed, randomly selected and independent from all other groups being tested. In order to assess significant differences using the *Daphnia* abundance data, a test to check if the data are normally distributed is required. A Sharpio-Wilk normality test was performed in Excel+Analyse-it Add-in (2000) for each *Daphnia* species at each station. The abundance data for *D.rosea* at the North and South station were normally distributed (p=0.199 and p=0.391, respectively). However, the Central station was not normally distributed (p=0.005) and was log-transformed to normalize the data (p=0.356). The abundance data for *D.pulex* for all three stations were normally distributed (North, p=0.139; Central, p=0.899; South, p=0.574).

To determine if there is a significant difference between *Daphnia* abundance and either the sampled date and/or station sampled, a Two-Way ANOVA was performed using Excel (2000). If there is a significant difference between abundance values for both sampled date and station sampled, the next step was to assess by what means did the sampling dates differ with the abundance of *Daphnia* species and which stations were significantly different.

A One-Way ANOVA test (in Excel 2000) was used to test the null hypothesis that there is no significant difference between *Daphnia* abundance and each station sampled for each species using the combination of all sampled dates. This method provided insight to whether *Daphnia* abundance differed among sample stations. In order to assess the effect of sampling date on the abundance values, the sampling dates were broken down into seasons for each sample period. To determine if *Daphnia* abundance differs with season, a Two-Way ANOVA test was performed (in Excel 2000). For *D.rosea*, the study period was broken down into 3 different seasons in 1975: spring (29-May to 20-June), summer (25-June to 20-August) and fall (10-September to 5-October). For *D.pulex*, the study period was broken down into 2 different seasons in 1976: spring (10-April to 15-June) and summer (23-June to 20-July). The species abundance was combined for each season per station and the mean was taken.

Can the direction of wind (and wind speed) to a sampled station be used as a predictor of the abundance of* D.rosea *at that particular station as well as adjacent sampled stations?

To examine the hypothesis that *D.rosea* abundance can be predicted at a sample station by the direction of the wind blowing, the wind directions for the 24 hours up to the time of the sampling event were tallied according to the previously used 16 standard compass rose directions. The period of 24 hours was chosen to remain consistent with the daily wind speed values obtained from the National Climate Data and Information Archives through Environment Canada. These wind directions and the abundance values for that particular sampling event were plotted using the Radar-type graph (in Excel 2000). The sampling event was carried out at roughly noon on each sampling day.

To accept the hypothesis that *D.rosea* abundance can be predicted at a sample station from knowing the wind characteristics up to 24 hours prior to sampling, the following hypothetical analysis will be performed using a Radar-type graph (Figure 3). Since Crawford Lake is small and deep (small fetch), the effect of wind on the horizontal distribution of *D.rosea* will be evident in a shorter period of time rather than a larger lake (with a larger fetch).

If the results of this comparison provide evidence that *D.rosea* abundance cannot be predicted by wind direction, we can suppose that either wind influence is not strong enough to affect *Daphnia* distribution in the water column at Crawford Lake or that the distribution is a likely result of another force (e.g., river inflow, internal waves).

Is the horizontal distribution of* D.pulex *at each sampled station relatively similar over the entire study period, regardless of wind direction or wind speed?

D.pulex populations are typically tolerant of varying water conditions and can be found at depths up to 12 m (Prepas and Rigler 1978). Therefore, it is expected that *D.pulex* individuals occupying depths below the mixolimnion will be less susceptible to the effects of wind. The preference of vertical depths by *D.pulex* was not quantified for the entire study period at each sampling station in the Prepas and Rigler (1978) paper; however, the present study will assume that a relatively similar proportion of animals preferred depths below the mixolimnion at all sampling stations. This assumption is based on a June 1976 sample taken by Prepas and Rigler (1978) from the Central station at varying vertical depths. The observations by Prepas and Rigler (1978) suggested that *D.pulex* animals occupied variable depths from 1-2 m to 12 m below the surface with no consistent pattern through sample dates. To assess the hypothesis that *D.pulex* abundance will be distributed similarly across all sampling dates for each sampling station regardless of wind direction, the wind directions for the 24 hours up to the time of the sampling event were tallied according to the 16 standard compass rose directions. These wind directions and the abundance values for that particular sampling event were plotted using the Radar-type graph (in Excel 2000). The abundance samples were taken at roughly noon on each sampling day.

To accept the hypothesis that *D.pulex* abundance is distributed similarly across all sampling dates regardless of wind influence, changes in wind direction will not correspond to changes in abundance among stations (similar to Figure 3B).

Results

Are there any relationships between environmental variables (atmospheric temperature, wind direction and wind speed) from Crawford Lake during the study periods?

The wind directions during the study period from 1975 vary from month to month (Figure 4). There is no consistent wind direction throughout the entire study period using the combined daily tally of wind directions from Figure 4. However, using the total average of all wind directions per month (Table 1), the wind direction during the study period is quite similar from month to month (coming from the Southwest). In conjunction with the average southwest wind direction from Table 1, the wind speed appears to increase throughout the study period.

The wind directions during the study period from 1976 did not vary from month to month, unlike the study period from 1975 (Figure 5). There is a consistent wind coming from the West-northwest direction throughout the entire study period using the combined daily tally of wind directions from Figure 5. The total average of all wind directions per month (Table 2) also demonstrates this observation. However, the average wind speed does not appear to indicate any unidirectional trend from month to month.

The comparison of environmental variables during the study periods did not illustrate any particularly significant relationships. During the 1975 study period, neither atmospheric temperature and wind speed nor wind direction and wind speed revealed a relationship (r=0.17, p=0.5223; r=0.00, p=0.9885). However, atmospheric temperature and wind direction during the 1975 study period displayed a weak positive correlation with non-significance (r=0.42, p=0.0972, see Appendix B, Figure B1 for correlation plot). As monthly atmospheric temperature increased, the wind direction would originate more from the north and vice versa.

During the 1976 study period, neither atmospheric temperature and wind speed nor atmospheric temperature and wind direction demonstrated a correlation (r=-0.49, p=0.1084; r=0.22, p=0.4884). However, wind direction and wind speed during the 1976 study period illustrated a weak positive correlation with non-significance (r=0.56, p=0.0576, see Appendix B, Figure B2 for correlation plot). As wind directions originated from the north, the wind speed would also increase and vice versa.

Is there a significant difference in* Daphnia *abundance from sample station to station as well as sampling date at Crawford Lake?

The abundance of *D.rosea* at all three stations differed throughout the study period in 1975 at Crawford Lake. The abundance of *D.rosea* at the north station was greatest among all stations sampled between late July and late August (Figure 6). Thereafter, *D.rosea* abundance in the north station was least among all stations till late-September. The abundance of *D.rosea* at the north and central stations were inversely proportionate to each other. A high abundance of *D.rosea* at the north station led to a low abundance at the central station and vice versa.

By using a Two-Way ANOVA, the examination of *D.rosea* abundance data from each sampling date and station sampled was determined (Table 3). *D.rosea* abundance differed between sampling dates (p=0.02) as well as sampling stations (p<0.00). Therefore, the null hypothesis can be rejected, suggesting that at least two of the *D.rosea* sample means are different among the sampled dates for all stations combined. Also, at least two of the *D.rosea* sample means are different among the stations sampled for all dates combined. The R^2 value (0.344) for the sampling date factor suggests that 34.4% of the variation in the *D.rosea* abundance is explained by the sampling date. The R^2 value (0.374) for the stations sampled factor suggests that 37.4% of the variation in the *D.rosea* abundance is explained by the station sampled.

The abundance distribution of *D.pulex* rarely differed from station to station throughout the study period in 1976 at Crawford Lake. The greater abundance of *D.pulex* tended to disperse towards the north station, followed by the central station and finally the south station during the study period (Figure 7). An exception to this trend occurred during the 31-May sampling event where the abundance of *D.pulex* was roughly equal among all three stations.

The examination of *D.pulex* abundance data from each sampling date and station sampled is determined using a Two-Way ANOVA (Table 4). *D.pulex* abundance differed between sampling dates ($p<0.00$) as well as sampling stations ($p<0.00$). Therefore, the null hypothesis can be rejected, suggesting that at least two of the *D.pulex* sample means are different among the sampled dates for all stations combined. Also, at least two of the *D.pulex* sample means are different among the stations sampled for all dates combined. The R^2 value (0.521) for the sampling date factor suggests that 52.1% of the variation in the *D.pulex* abundance is explained by the sampling date. The R^2 value (0.339) for the stations sampled factor suggests that 33.9% of the variation in the *D.pulex* abundance is explained by the station sampled.

Given that *Daphnia* abundance differed for both sampling date and station, the next step assessed the abundance with both sampling season and specific stations sampled. The abundance of *D.rosea* differed between the North and Central stations (One-Way ANOVA, $p<0.00$) and the Central and South stations (One-Way ANOVA, $p<0.00$) (Table 5). As well, there was a significant difference in the abundance of *D.pulex* between the North and Central stations (p=0.009) and the North and South stations (p=0.002) (Table 5). However, both *D.rosea* and *D.pulex* abundance did not differ with seasonal period (p=0.17 and p=0.08, respectively).

Can the direction of wind (and wind speed) to a sampled station be used as a predictive measure to anticipate the abundance of* D.rosea *at that particular station as well as adjacent sampled stations?

D.rosea abundance distribution varied over the study period at each sampled station; however, the opposing wind direction and speed to a particular station were not useful as predictors to anticipate the abundance of *D.rosea* (Figure 8ab and Table 6). Only 47.1% of the sampling events demonstrated the hypothesized trend. Figure 8a (F) is an example of a sampling event that portrayed the hypothesized trend; however, Figure 8a (D) demonstrates the rejection of the hypothesis. The strength of wind speed with an opposing wind direction was not sufficient to prove the hypothesis.

Despite the rejection of the original hypothesis, distribution trends in *D.rosea* abundance among stations throughout the study period were observed. From 20-Jun to 23-Jul (includes 6 sampling events; Figure 8a(D-I)), the relative distribution of *D.rosea* was primarily found in the north station, while the south station carried few animals followed by very little in the central station. This observation was roughly seen throughout the 6 consecutive sampling events. The minute variations among these sampling dates at each sampling station for the most part corresponded to the particular wind direction and speed for that sampling event. For example on the sampling date 25-Jun, the major wind direction (North) with a wind speed of 39 km/h corresponded to the station with the highest abundance of *D.rosea* (North) (Table 6, E). However on the sampling date 16-Jul, the major wind direction (South) with a wind speed of 9 km/h did not correspond to the station with the highest abundance of *D.rosea* (North) (Table 6, H). Therefore, higher wind speeds increased the impact of wind directions on *D.rosea* accumulation at a particular station while lower speeds had little effect.

Referring to the sampling events on 20-Jun to 03-Jul (Figure 8a(D-F)), this trend is clearly evident. High wind speeds (39 km/h from Table 6, based on maximum daily wind gusts) on 25-Jun (E) coming from the northern direction increased the amount of *D.rosea* abundance in the south station, in comparison to the observed abundance on 20-Jun (D). However, the high wind speeds (34 km/h from Table 6) on 03-Jul (F) coming from the western direction decreased the amount of *D.rosea* abundance at the south station, in comparison to the abundance observed on 25-Jun (E). Similar distribution trends in *D.rosea* abundance were also found between the following sampling dates: 31-Jul to 20-Aug and 10-Sept to 28-Sept.

Is the horizontal distribution of* D.pulex *at each sampled station relatively similar over the entire study period, regardless of wind direction or wind speed?

D.pulex abundance distribution remained consistent over the study period at each sampled station, with the exception of 31-May. The distribution of *D.pulex* appeared unchanged with the influence of wind speed and direction (Figure 9ab and Table 7); therefore the hypothesis is accepted. In most cases, the North station contained the greatest accumulation of *D.pulex* while the Central and South stations held relatively fewer animals. The sampling event on 31-May (Figure 9a(E)) displayed a distribution different from all other sampling events during the study period in 1976 at Crawford Lake. This unusual distribution on 31-May may be the result of a sampling error. The lowest abundance of *D.pulex* on 31-May was documented from the north station while the south station occupied most of the abundance. The primary wind direction came from the east, which distributed *D.pulex* towards the south station rather than the north and central stations. However, excluding the unusual distribution on 31-May, the wind direction and speed appeared to have no effect on the distribution of all sampling events during the 1976 study period.

Discussion

Horizontal spatial heterogeneity was observed for both *Daphnia* species in Crawford Lake. The spatial dispersion of *Daphnia* did not exclusively depend on the direction or speed of wind present; however, the abundance of *D.rosea* tends to accumulate upwind (Figure 8). Many studies examining zooplankton distributions and wind influence can substantiate these findings (George and Edwards 1976; Dirnerger and Thredlkeld 1986; Vanschoenwinkel *et al.* 2008). While wind speed had little effect on dispersal, the yield of zooplankton numbers in temporary rock pools in South Africa corresponded to the dominant wind directions in the area, providing the vertical updrafts that encouraged dispersal (Vanschoenwinkel *et al.* 2008). The present study only focuses on one lake area rather than numerous rock pools, however the affect of wind direction on zooplankton abundance in both studies is apparent. Wind blowing towards a station in Crawford Lake yielded a greater abundance of *D.rosea*, particularly the north station, since this species is primarily found in the mixing layer (mixolimnion) and is subject to wind-induced blowing, and would resist downward translocation. This combination of circumstances should lead to wind- and behaviourally induced aggregation at the downwind end of a fetch. However, *D.pulex* abundance rarely fluctuated from station to station, as they were found closer to the chemocline (non-mixing layers) and at various vertical depths (Prepas and Rigler 1978). The preference of vertical depth by *D.pulex* was not determined in the study by Prepas and Rigler (1978) and the change in abundance at various vertical depths could not be accounted for.

The sheltered environmental landscape of Crawford Lake limits the effect of wind influence on the surface waters; therefore, it is logical to assume that an alternative force prior to any wind influences must initially establish the distribution of zooplankton (Mazumder *et al.* 1990). Stations closer to the lake inflow area, such as the north station, yielded greater *Daphnia* abundance for both species in Crawford Lake. Since wind direction and speed did not initially govern the distribution pattern of *Daphnia* (Figure 8 and 9), it is suggested that abundance and dispersal is primarily distributed in the direction of water inflow and subsequently intensified by wind influence. Primo *et al.* (2009) found that high river inflows transported zooplankton communities downstream by the influx of freshwater. Since Crawford Lake is meromictic and includes an inflow that drains an 80 ha catchment due to seepage (Yu *et al.* 1997), freshwater inflows would greatly affect the position of the chemocline and thereby change the distribution of zooplankton throughout the lake.

River inflow and water temperature change as a function of seasonality (Prepas and Rigler 1978; Bowling and Tyler 1986; Turton and McAndrews 2006). The inflow/outflow areas and water temperatures at Crawford Lake were not monitored; however, the abundance of *Daphnia* at the sampling stations can be used to infer the effect of temperature and inflowing freshwater on the distributions. *D.rosea* egg development greatly depends on the temperature of water and changes in the season can either increase or decrease the population numbers (Prepas and Rigler 1978). Warm temperatures in the spring (1975) facilitated egg development and an increase of *D.rosea* abundance from hatched resting eggs was found in the early summer at all stations (Prepas and Rigler 1978). As the summer progressed, the distribution of *D.rosea* abundance significantly shifted from the north to the central station ($p<0.00$) and continued to move downstream till the populations declined across all stations resulting in a complete absence by January 1976 (Prepas and Rigler 1978). *D.pulex* populations were consistently present all year (1976) and did not experience major changes in abundance as a function of seasonality

(Prepas and Rigler 1978). The high abundance of *D.pulex* in the north station was explained by greater fecundity in comparison to the remaining stations (Prepas and Rigler 1978). Greater fecundity is likely caused by inflowing nutrient-rich water that can lead to thriving population numbers (Murtaugh 1985; Naithani *et al.* 2003). The *D.pulex* populations are present all year since developing eggs are more tolerant of varying temperatures (24 - 5 °C) and can withstand any tilting of the chemocline (Prepas and Rigler 1978). Therefore, in a comparison between both *Daphnia* species, it is clear that the horizontal distributions of *D.rosea* communities are more susceptible to changes in climate (e.g., wind dynamics, temperature, and river inflow) and can adversely affect the aquatic food chains that involve these cladocerans.

The horizontal distributions of *Daphnia* observed in Crawford Lake have undeniable implications regarding the effect of wind influence on zooplankton. Despite the use of a small, moderately sheltered lake that may not necessarily demonstrate the full strength of wind influence on the water surface, wind-induced distributions are still evident. From the comparison of sampling stations, it appears that wind is somewhat influential on the movement of zooplankton inhabiting the mixing depths of stratified lakes. However, further study regarding the significant depth to which wind becomes influential would be of great value when considering any potential declines of zooplankton caused by wind stress. This study demonstrated that wind influence was a secondary factor affecting *Daphnia* distribution; therefore, potential minimization of wind effects may be possible to examine the effect of primary dispersal factors in the absence of wind (e.g., river inflows). Since small lakes have a decreased sensitivity to wind and sheltered lakes provide coverage against blowing winds, it would be ideal to monitor a series of small and extremely sheltered lakes in order to minimize or remove the effect (or noise) produced by wind influence.

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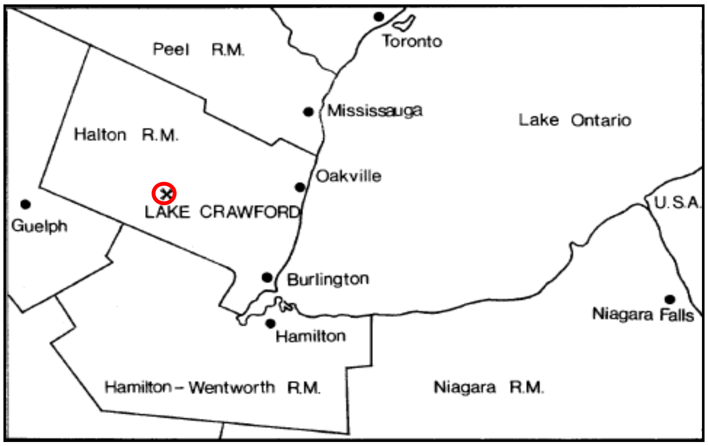

Figure 1. Crawford Lake location in Southern Ontario, Canada (Rybak and Dickman 1988).

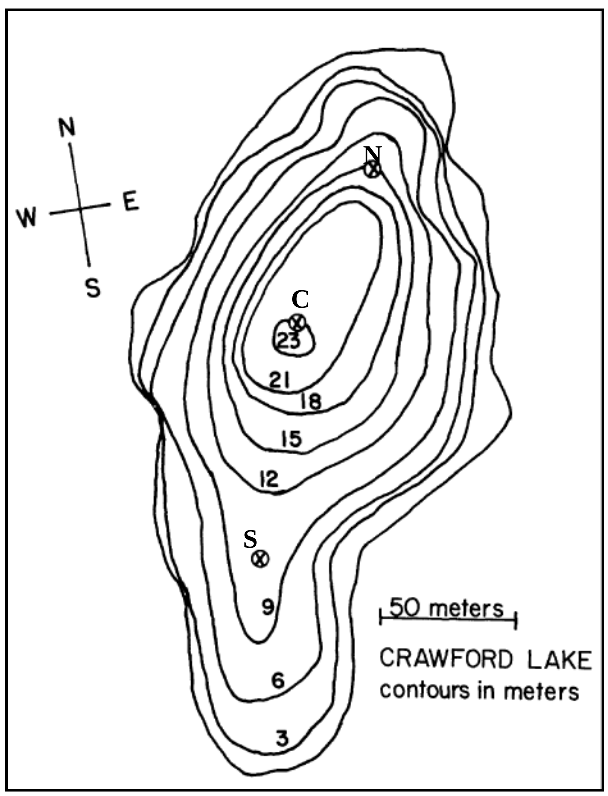

Figure 2. Bathymetric map of Crawford Lake. Three fixed sampling stations indicated: North (N), Central (C) and South (S) (Prepas and Rigler 1978).

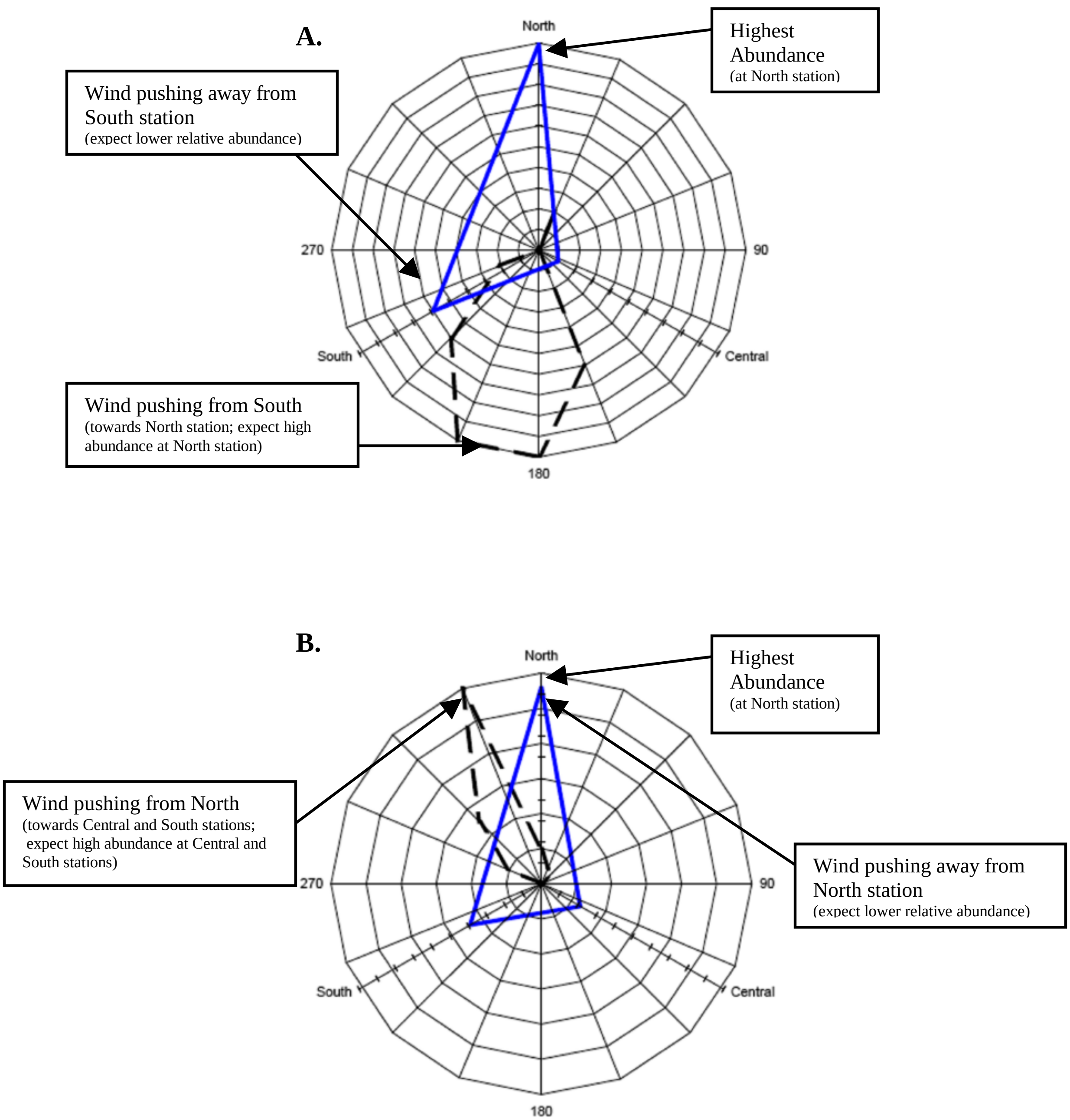

Figure 3. Hypothetical representations of the hypothesis that the relative abundance of *D.rosea* can be predicted at a sample station by the direction of wind blowing. (A) Accept hypothesis; (B) Reject hypothesis. Dashed black lines represent total tally of wind directions. Blue solid lines represent the relative orientarion of each sampling station on the lake, North, Central and South and the abundance of *D.rosea* (scale in relative number of individuals along the notched line) at each station from the epicentre of the graph and outward. Wind direction scale is in standard compass rose directions (degrees).

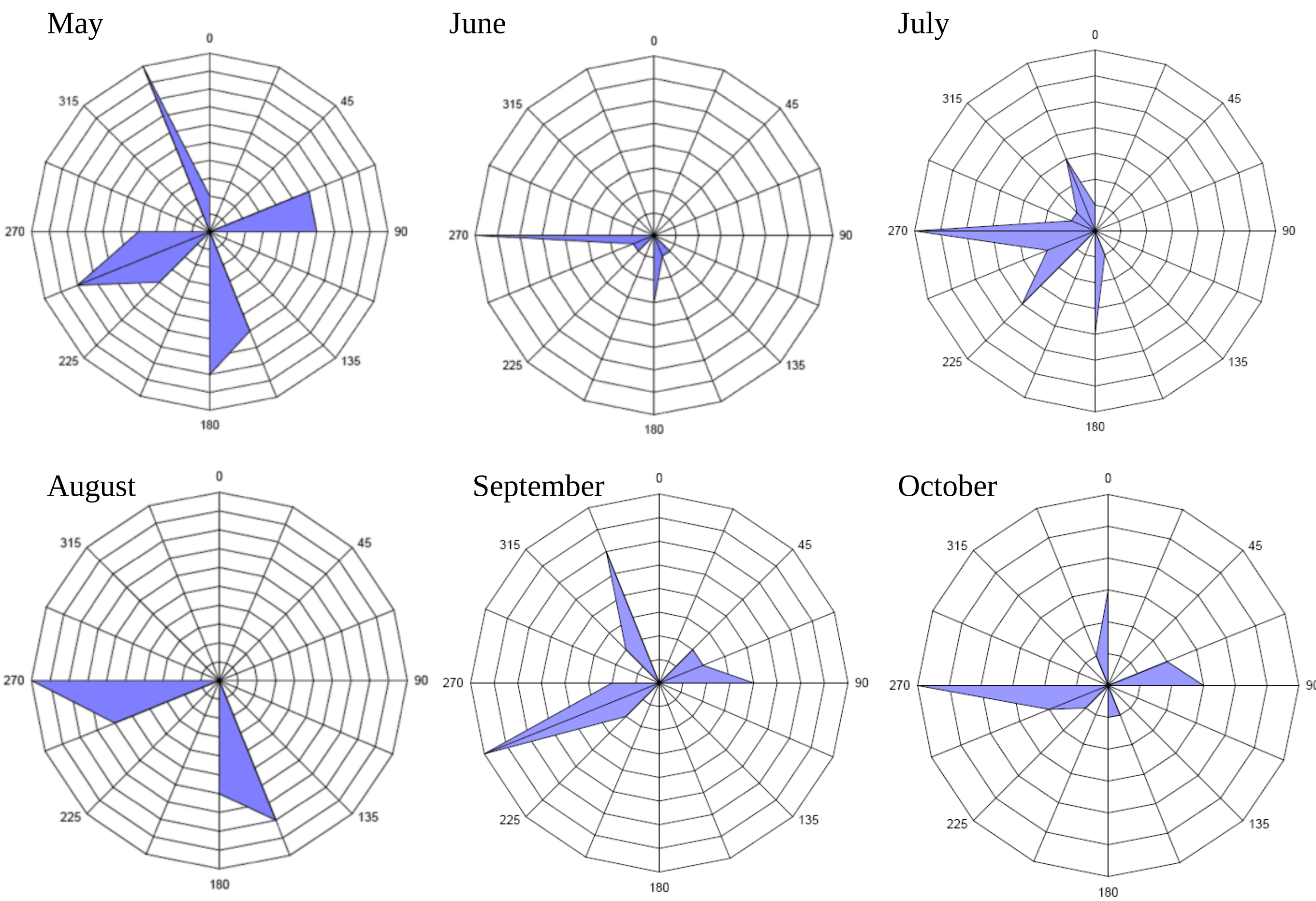

Figure 4. Monthly wind directions at Toronto Lester B. Pearson International Airport from 1975 (43°40'N, 79°38'W) (NCDIA 2008). Solid blue lines represent total tally of wind directions. Wind direction scale is in standard compass rose directions (degrees).

Table 1. Summary of the monthly wind direction, wind speed and atmospheric temperature for the study period at Crawford Lake in 1975. Data taken from Toronto Lester B. Pearson International Airport (43°40'N, 79°38'W) (NCDIA 2008).

Month	**Monthly Wind Direction (degrees)**	**Monthly Wind Speed (km/h)**	**Atmospheric Temperature (degrees Celsius)**
May	216	41	15.5
June	198	42	18.1
July	255	45.3	21.7
August	226	44.6	20
September	237	48.9	13.1
October	230	49.4	9.4
Average	**227**	**45.2**	**16.3**

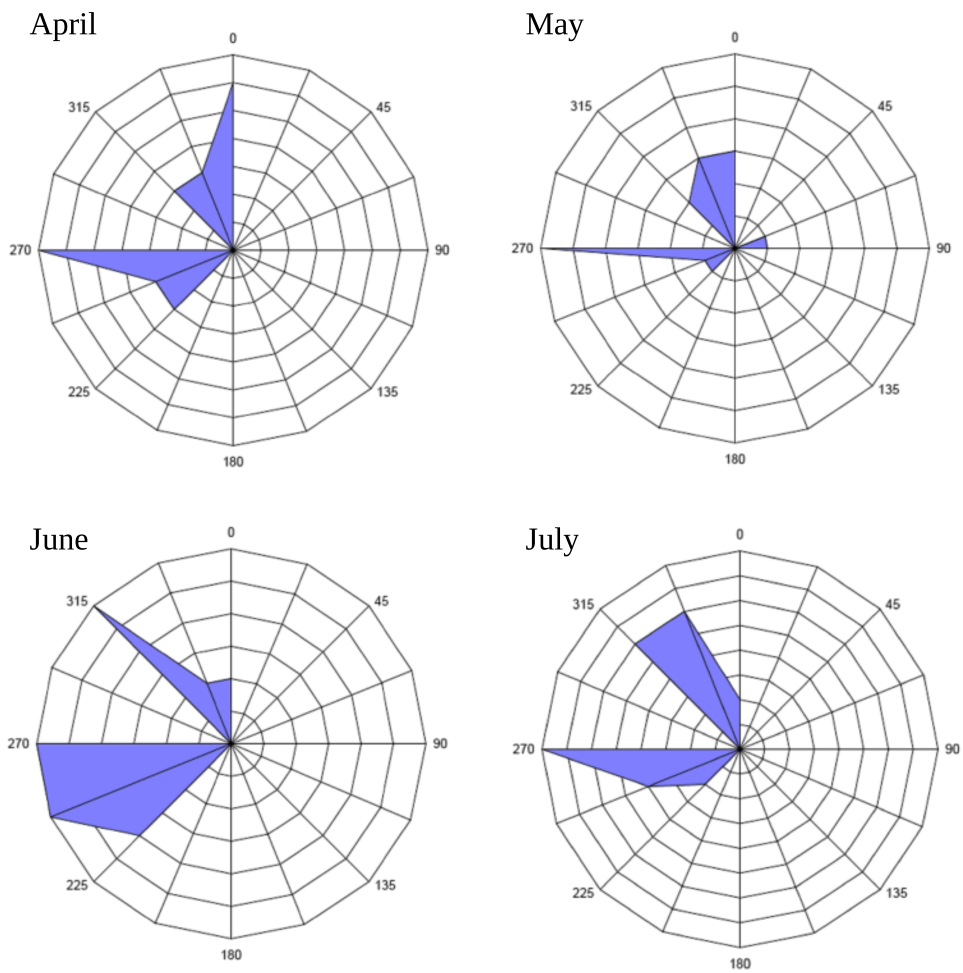

Figure 5. Monthly wind directions at Toronto Lester B. Pearson International Airport from 1976 (43°40'N, 79°38'W) (NCDIA 2008). Solid blue lines represent total tally of wind directions. Wind direction scale is in standard compass rose directions (degrees).

Table 2. Summary of the monthly wind direction, wind speed and atmospheric temperature for study period at Crawford Lake in 1976. Data taken from Toronto Lester B. Pearson International Airport (43°40'N, 79°38'W) (NCDIA 2008).

Month	**Monthly Wind Direction (degrees)**	**Monthly Wind Speed (km/h)**	**Atmospheric Temperature (degrees Celsius)**
April	276	48	7.6
May	268	51.1	10.6
June	253	43.7	18.6
July	280	43.1	18.6
Average	**269**	**46.5**	**13.9**

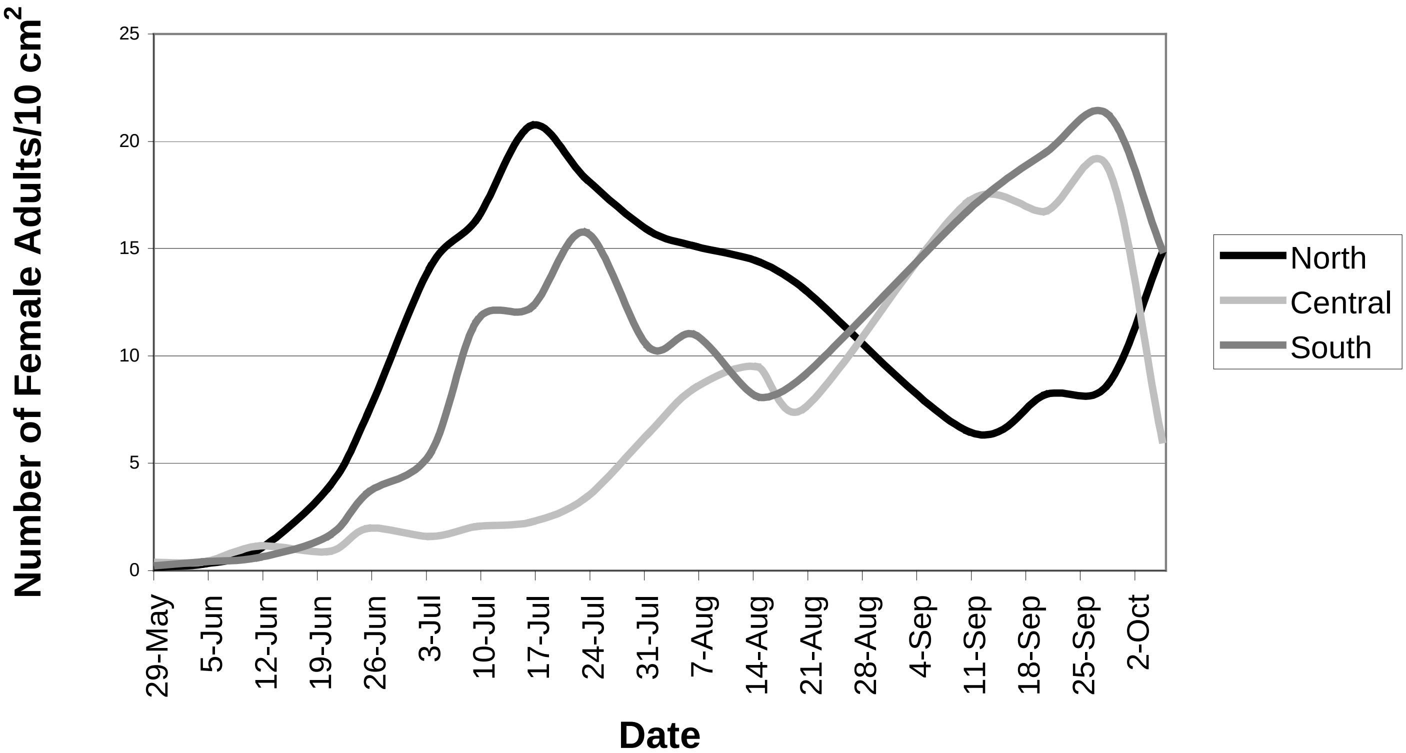

Figure 6. Abundance distributions of adult female *D.rosea* from 1975 at Crawford Lake at three sampling stations. *D.rosea* abundance data taken from Prepas and Rigler, 1978.

Table 3. Two-Way ANOVA for variation of *D.rosea* abundance regarding sampling dates and stations sampled using Excel (2000). The p-value for both factors (sampling date and station sampled) is significant and the null hypothesis can be rejected.

Source of Variation	SS	DF	MS	F	P-value
Sampled Date	773.04	16	48.31	2.38	0.02*
Station Sampled	1033.27	2	516.64	25.42	<0.00*
Error	650.47	32	20.33		
Total	2456.78	50			

***Significant difference**

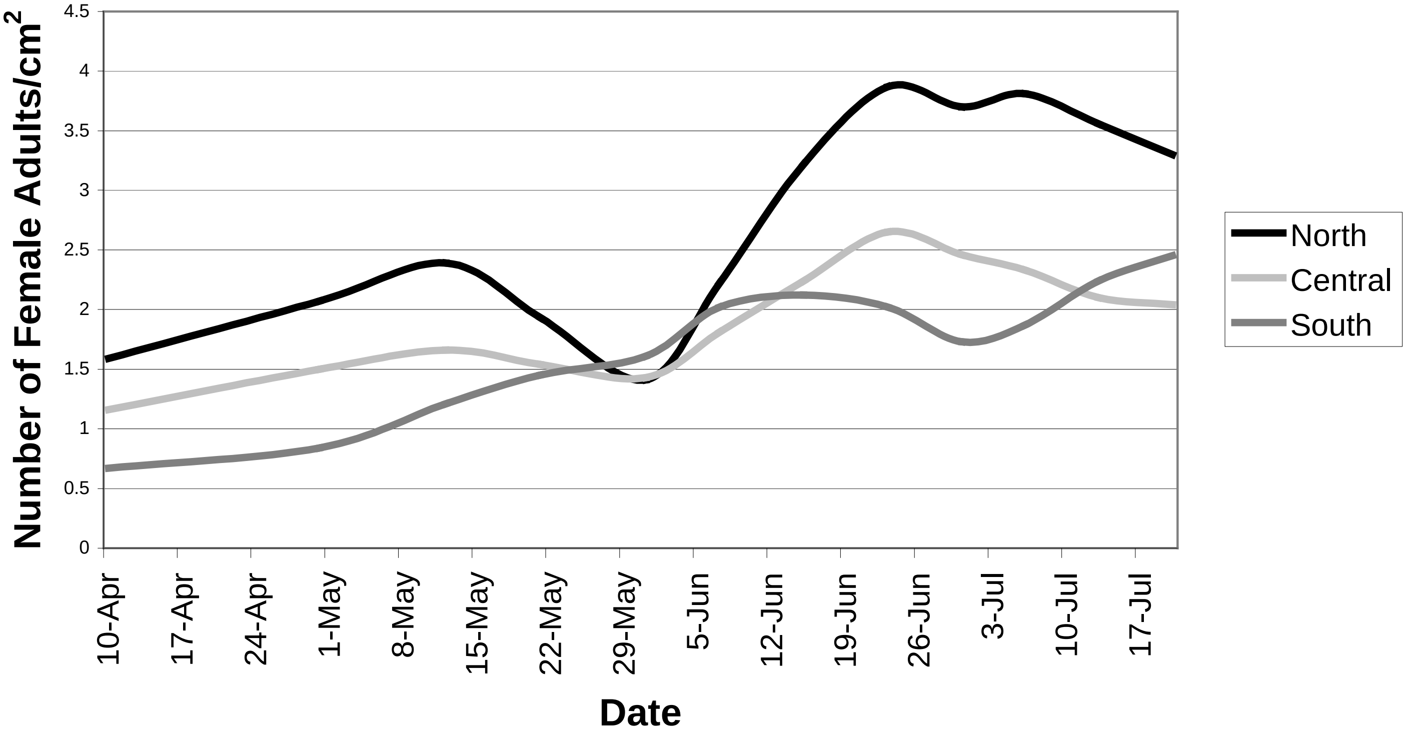

Figure 7. Abundance distributions of adult female *Daphnia pulex* from 1976 at Crawford Lake at three sampling stations. *D.pulex* abundance data taken from Prepas and Rigler, 1978.

Table 4. Two-Way ANOVA for variation of *D.pulex* abundance regarding sampling dates and stations sampled using Excel (2000). The p-value for both factors (sampling date and station sampled) is significant and the null hypothesis can be rejected.

Source of Variation	SS	DF	MS	F	P-value
Sampled Date	11.73	11	1.07	7.45	<0.00*
Station Sampled	7.64	2	3.82	26.71	<0.00*
Error	3.15	22	0.14		
Total	22.52	35			

*Significant difference

Table 5. Pair wise comparison of p-values obtained from One-Way ANOVA (in Excel 2000) for the significance between *Daphnia* abundance and stations sampled. Top: *D.rosea*. Bottom: *D.pulex*.

	North Station	**Central Station**	**South Station**
North Station	-	<0.00*	0.68
Central Station	0.009*	-	0.00*
South Station	0.002*	0.29	-

* Significant difference

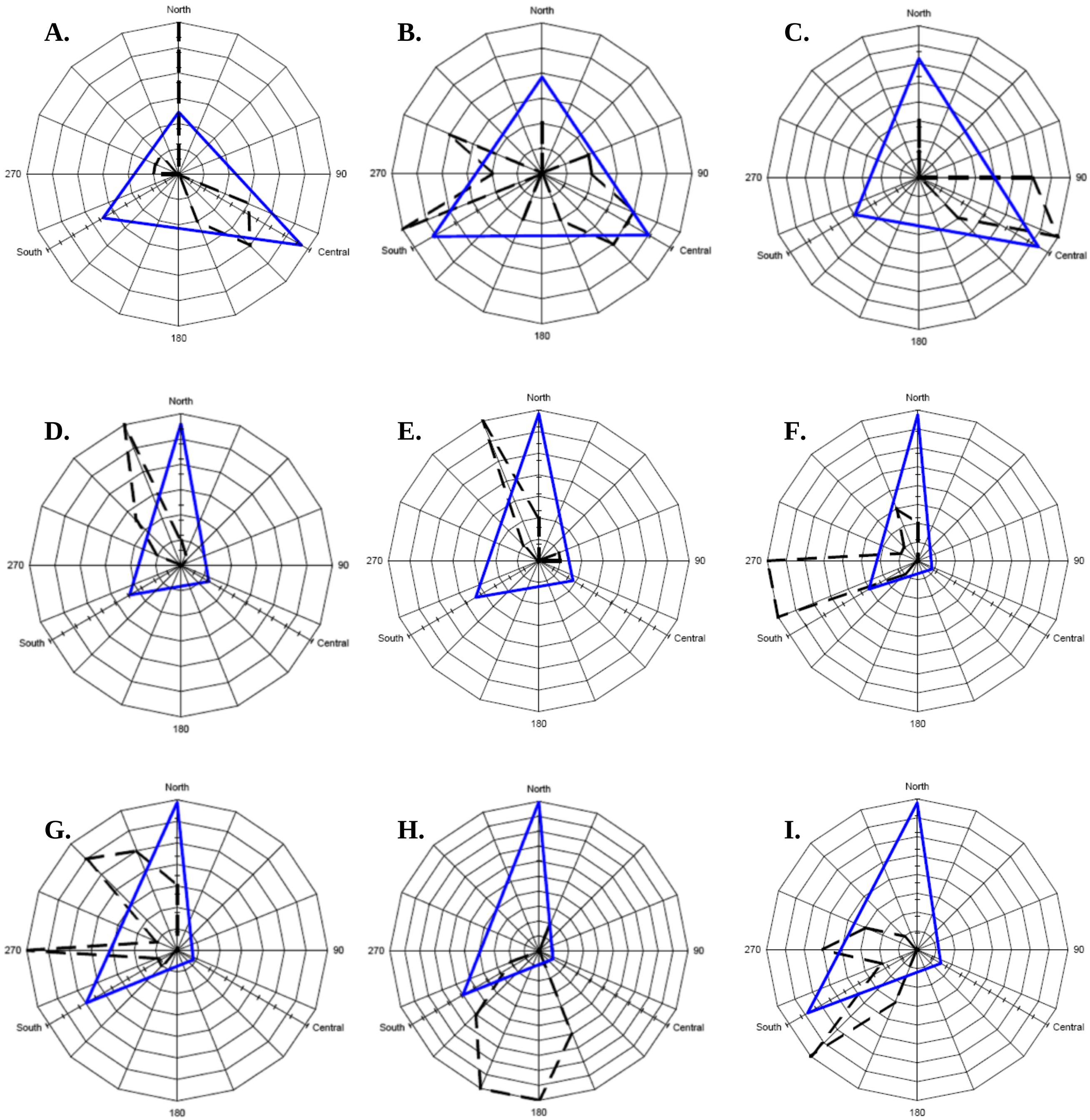

Figure 8a. Total wind directions 24 hours prior to each sampling event and the abundance of *D.rosea* at three sampling stations on Crawford Lake from 1975. A-I represents sampling events on 29-May, 04-Jun, 11-Jun, 20-Jun, 25-Jun, 03-Jul, 09-Jul, 16-Jul and 23-Jul respectively. Dashed black lines represent total tally of wind directions. Blue solid lines represent the orientarion of each sampling station, North, Central and South and the abundance of *D.rosea* (scale in relative number of individuals along the notched line) at each station from the epicentre of the graph and outward. Wind direction scale is in standard compass rose directions (degrees). Wind directions taken from Toronto Lester B. Pearson International Airport from 1975 (43°40'N, 79°38'W) (NCDIA 2008). *D.rosea* abundance data taken from Prepas and Rigler, 1978.

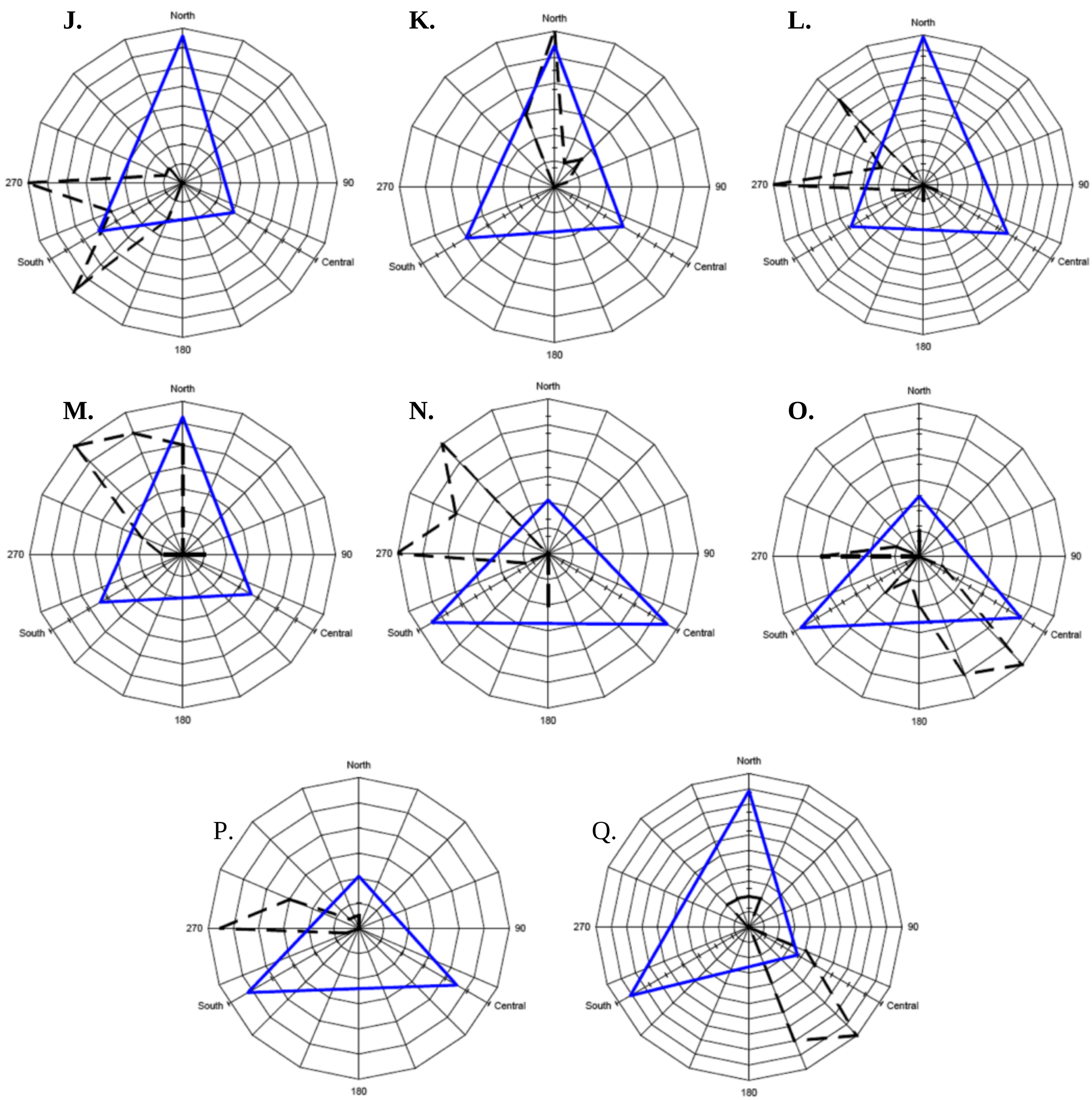

Figure 8b. Total wind directions 24 hours prior to each sampling event and the abundance of *D.rosea* at three sampling stations on Crawford Lake from 1975. J-Q represents sampling events on 31-Jul, 06-Aug, 14-Aug, 20-Aug, 10-Sept, 20-Sept, 28-Sept and 05-Oct respectively. Dashed black lines represent total tally of wind directions. Blue solid lines represent the orientation of each sampling station, North, Central and South and the abundance of *D.rosea* (scale in relative number of individuals along the notched line) at each station from the epicentre of the graph and outward. Wind direction scale is in standard compass rose directions (degrees). Wind directions taken from Toronto Lester B. Pearson International Airport from 1975 (43°40'N, 79°38'W) (NCDIA 2008). *D.rosea* abundance data taken from Prepas and Rigler, 1978.

Table 6. Summary of wind characteristics during the 1975 study period at Crawford Lake, the highest and lowest abundance of *D.rosea* observed at a particular sampled station and the hypothesis outcome. Alphabetical letter (left of date) represents the Radar-type graph from Figure 8. *Italics* indicates a rejection of the hypothesis. Wind characteristics taken from Toronto Lester B. Pearson International Airport (43°40'N, 79°38'W) (NCDIA 2008).

	Date	**Wind Speed at Sample Event (km/h)**	**Daily Wind Speed* (km/h)**	**Major Daily Prevailing Wind Direction****	**Highest Abundance of *D.rosea* species (station)**	**Lowest Abundance of *D.rosea* species (station)**	**Hypothesis Acceptance? (Yes/No)**
A	29-May	21	37	North	Central	North	Yes
B	*04-Jun*	*21*	*37*	*Southwest*	*Central, South*	*North*	*No*
C	11-Jun	10	40	East	North, Central	South	Yes
D	*20-Jun*	*14*	*9*	*North*	*North*	*Central*	*No*
E	*25-Jun*	*19*	*39*	*North*	*North*	*Central*	*No*
F	03-Jul	24	34	West	North	Central	Yes
G	*09-Jul*	*3*	*45*	*Northwest*	*North, South*	*Central*	*No*
H	16-Jul	23	9	South	North	Central	Yes
I	23-Jul	13	34	Southwest	North, South	Central	Yes
J	31-Jul	23	13	West	North	Central	Yes
K	*06-Aug*	*16*	*45*	*North*	*North*	*Central, South*	*No*
L	*14-Aug*	*3*	*37*	*West*	*North*	*Central, South*	*No*
M	*20-Aug*	*16*	*47*	*Northwest*	*North*	*Central, South*	*No*
N	10-Sept	3	8	West	Central, South	North	Yes
O	*20-Sept*	*16*	*34*	*South*	*Central, South*	*North*	*No*
P	28-Sept	11	8	West	Central, South	North	Yes
Q	*05-Oct*	*3*	*5*	*South*	*North, South*	*Central*	*No*

* For the combined 24 hours up to the sampling event.
** Refer to Figure 8 for the illustration of the main daily prevailing wind direction (denoted by the longest dashed black line beginning from the epicentre of the graph and moving outward).

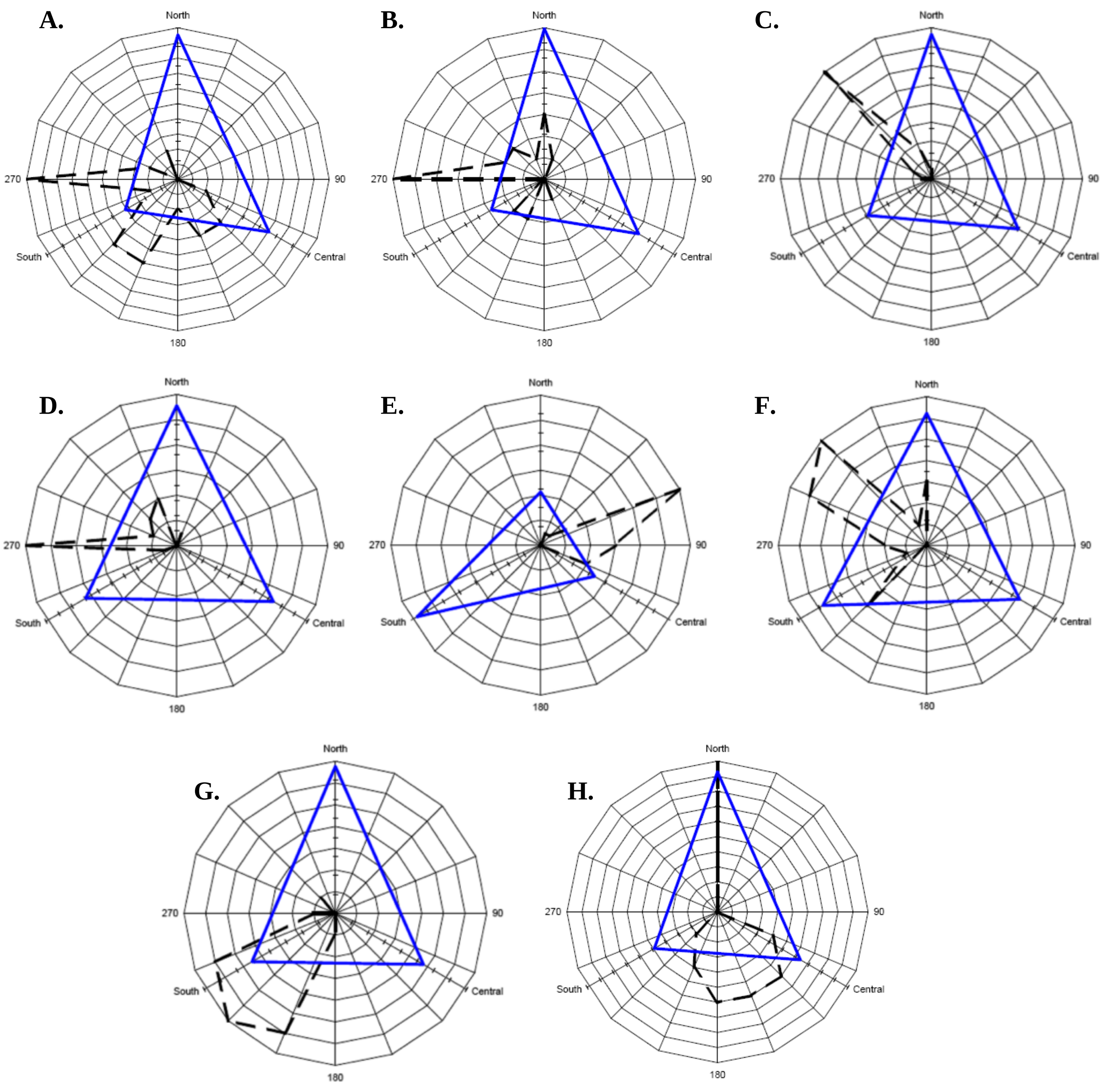

Figure 9a. Total wind directions 24 hours prior to each sampling event and the abundance of *D.pulex* at three sampling stations on Crawford Lake from 1976. A-H represents sampling events on 10-Apr, 30-Apr, 12-May, 21-May, 31-May, 07-Jun, 15-Jun and 23-Jun respectively. Dashed black lines represent total tally of wind directions. Blue solid lines represent the orientation of each sampling station, North, Central and South and the abundance of *D.pulex* (scale in relative number of individuals along the notched line) at each station from the epicentre of the graph and outward. Wind direction scale is in standard compass rose directions (degrees). Wind directions taken from Toronto Lester B. Pearson International Airport from 1975 (43°40'N, 79°38'W) (NCDIA 2008). *D.pulex* abundance data taken from Prepas and Rigler, 1978.

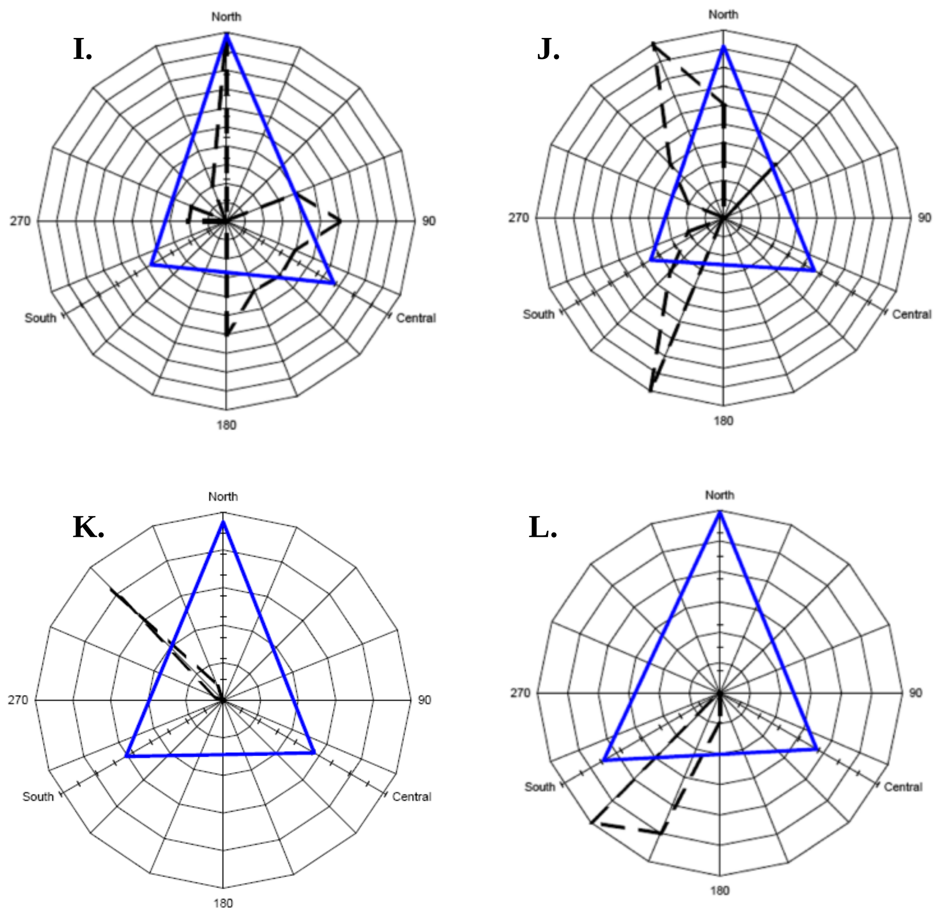

Figure 9b. Total wind directions 24 hours prior to each sampling event and the abundance of *D.pulex* at three sampling stations on Crawford Lake from 1976. I-L represents sampling events on 30-Jun, 06-Jul, 13-Jul and 20-Jul respectively. Dashed black lines represent total tally of wind directions. Blue solid lines represent the orientation of each sampling station, North, Central and South and the abundance of *D.pulex* (scale in relative number of individuals along the notched line) at each station from the epicentre of the graph and outward. Wind direction scale is in standard compass rose directions (degrees). Wind directions taken from Toronto Lester B. Pearson International Airport from 1975 (43°40'N, 79°38'W) (NCDIA 2008). *D.pulex* abundance data taken from Prepas and Rigler, 1978.

Table 7. Summary of wind characteristics during the 1976 study period at Crawford Lake, the highest and lowest abundance of *D.pulex* observed at a particular sampled station and the hypothesis outcome. Alphabetical letter (left of date) represents the Radar-type graph from Figure 9. Wind characteristics taken from Toronto Lester B. Pearson International Airport (43°40'N, 79°38'W) (NCDIA 2008).

	Date	**Wind Speed at Sample Event (km/h)**	**Daily Wind Speed* (km/h)**	**Max Daily Prevailing Wind Direction****	**Greatest Abundance of *D.pulex* species (station)**	**Lowest Abundance of *D.pulex* species (station)**	**Hypothesis Acceptance? (Yes/No)**
A	10-Apr	26	63	West	North	South	Yes
B	30-Apr	19	39	West	North	South	Yes
C	12-May	27	50	Northwest	North	South	Yes
D	21-May	29	53	West	North, Central, South	-	Yes
E	31-May	14	10	East	South	North, Central	Yes
F	07-Jun	23	45	Northwest	North, Central, South	-	Yes
G	15-Jun	23	51	Southwest	North	South	Yes
H	23-Jun	16	7	North	North	South	Yes
I	30-Jun	26	42	North	North	South	Yes
J	06-Jul	10	7	North & South	North	South	Yes
K	13-Jul	29	56	Northwest	North	Central, South	Yes
L	20-Jul	26	34	Southwest	North	Central	Yes

* For the combined 24 hours up to the sampling event.

** Refer to Figure 9 for the illustration of the main daily prevailing wind direction (denoted by the longest dashed black line beginning from the epicentre of the graph and moving outward).

\- No lowest abundance found.

Appendix A

Table A1. Standard compass rose wind direction categories.

Wind Direction Category	Range (in degrees)
N	360, 0-22.4
N-NE	22.5-44.9
NE	45-67.4
E-NE	67.5-89.9
E	90-112.4
E-SE	112.5-134.9
SE	135-157.4
S-SE	157.5-179.9
S	180-202.4
S-SW	202.5-224.9
SW	225-247.4
W-SW	247.5-269.9
W	270-292.4
W-NW	292.5-314.9
NW	315-337.4
N-NW	337.5-359.9

Appendix B

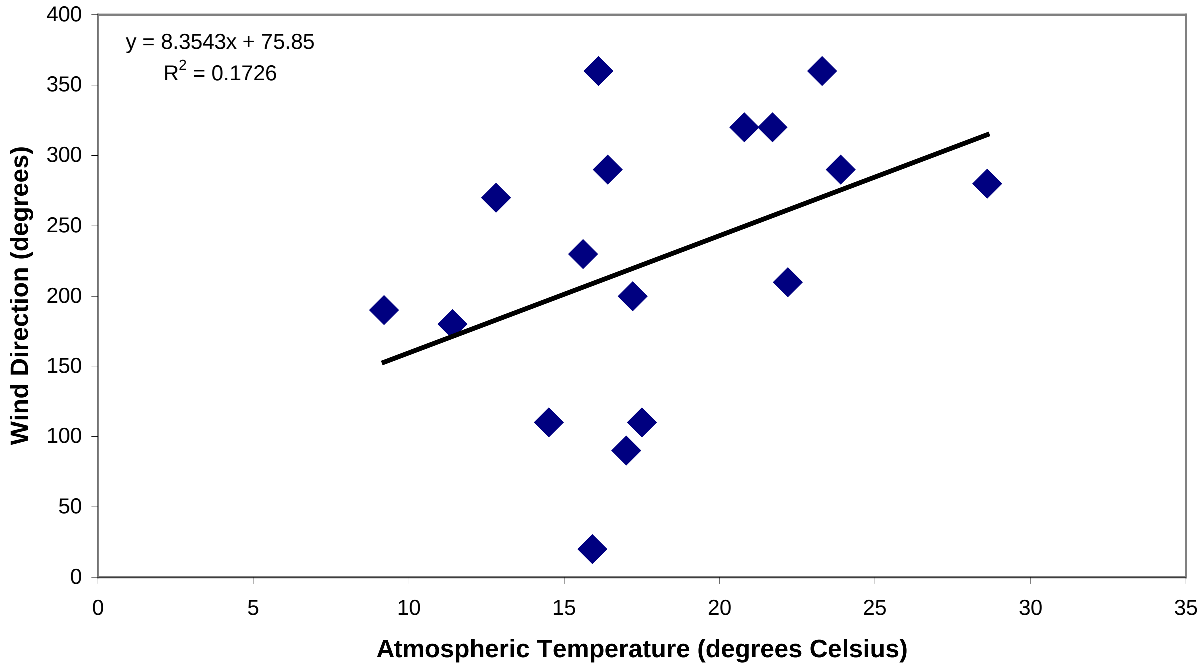

Figure B1. Relationship between atmospheric temperature and wind direction for the study period in 1975 at Crawford Lake. Data taken from Toronto Lester B. Pearson International Airport (43°40'N, 79°38'W) (NCDIA 2008).

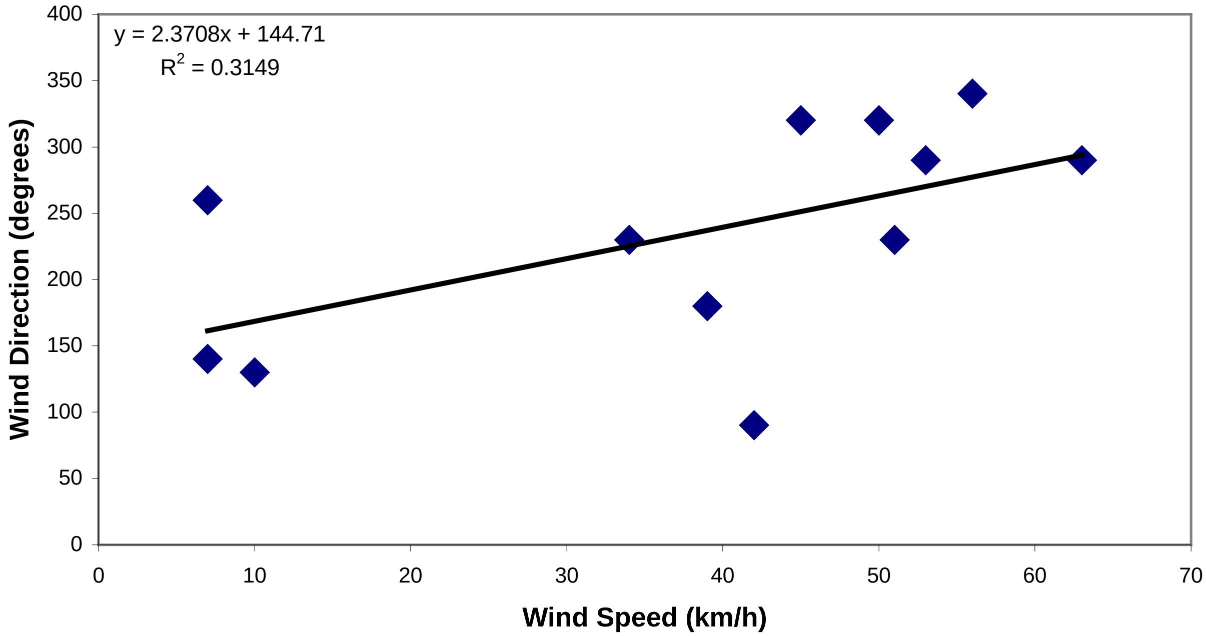

Figure B2. Relationship between wind direction and wind speed for the study period in 1976 at Crawford Lake. Data taken from Toronto Lester B. Pearson International Airport (43°40'N, 79°38'W) (NCDIA 2008).