Chapter 2:
Can the prediction of seasonal and long-term zooplankton abundance in Harp Lake be improved using the wind field at daily steps?

Abstract

The predictability of zooplankton abundance under wind-driven currents has been explored, but what has not been explored is how the distributions change over the long-term in response to changes in wind fields. In this study, I sought relationships between the wind field and fortnightly abundances of 8 zooplankton species at a mid-lake station in Harp Lake, Ontario from 1980 to 2004. Over this time period, average wind speed has declined by 25%, which is consistent with the long-term trends over the Northern Hemisphere (Vautard et al. 2010), while direction has shifted 21 degrees towards the north. Multiple linear regressions were generated to predict seasonal and interannual changes in daily zooplankton abundance combining year, Julian day, chemistry and, finally, wind speed and direction. Wind field metrics were included in the models for 6 of the 8 species, although improvements in predictive power were modest. We suspect that the decrease in wind speed has contributed to a change in zooplankton heterogeneity in the lake, and thus a change in lake-wide abundance estimates derived from a single station. Zooplankton are patchily distributed, but most long-term monitoring programs sample only at one station. My work suggests that we may well be able to correct for some of the bias due to a changing wind field, and make small but significant improvements in the predictability of abundance of zooplankton species if we consider wind as a driver.

Introduction

Zooplankton are rarely included among the list of target study organisms in large-scale environmental assessment programs (e.g., Jeppesen et al. 2011). Major bioassessment programs in Europe (Jeppesen et al. 2011), Canada and the United States have been designed to monitor effects of environmental stressors at large scales (Allen et al. 1999; Hughes et al. 2000; EC 2010). For example, the Canadian Aquatic Biomonitoring Network (CABIN) maintained by Environment Canada is a national program designed to assess the condition and biodiversity of Canadian aquatic biota using nationally standardized protocols for data collection (EC 2010). CABIN recognizes many types of biological indicators as suitable for bioassessment, including invertebrates, macrophytes, algae, zooplankton and fish (EC 2010). However, benthic invertebrates, not zooplankton, are recommended by CABIN as the most useful indicators to assess the health of aquatic ecosystems, mainly because benthic invertebrates are easily collected, are found in streams and lakes, reflect site-specific impacts and respond to a wide range of stressors (EC 2010). Similarly, the Environmental Monitoring and Assessment Program (EMAP-surface waters) supported by the United States Environmental Protection Agency (USEPA) has also recommended approaches for monitoring and assessing the nation's lakes and rivers (Hughes et al. 2000). Unlike CABIN, EMAP does not have a standardized protocol for assessment and monitoring of ecological integrity of waters (Hughes et al. 2000; McDonald 2000). Instead, EMAP develops survey approaches that change dependent on the multiple stressors present in the lake/river in question (Hughes et al. 2000; McDonald 2000).

EMAP methodology and survey protocols are based on various ecological indicators, including water chemistry, physical habitat, periphyton assemblages, sediment community metabolism, benthic macroinvertebrate assemblage, aquatic vertebrate assemblages and fish tissue contaminants (Lazorchak et al. 2000). Despite the vast array of ecological indicators used by EMAP, zooplankton is not found on the list of beneficial indicators that can be used to assess water integrity. In fact, the newly implemented European Water Framework Directive (EU WFD) has also entirely disregarded zooplankton as a biological quality element (BQE) for the assessment of water quality (Jeppesen et al. 2011).

The main reason cited for the exclusion of zooplankton from these national bioassessment programs is their lack of production of useful information (Allen et al. 1999). But in their review, Jeppensen et al (2011) and O'Connor et al. (2000) clearly demonstrate the falsity of this conclusion. Zooplankton respond in predictable ways to many anthropogenic drivers. Still, zooplankton have not appeared to be as useful as other indicators in large scale synoptic surveys designed to choose indicators for biomonitoring (Hughes et al. 2000). I believe this may not be due to the inherent lack of usefulness of zooplankton as biomonitors. Rather I hypothesize it is due to problems with sampling procedures that have been employed in these assessments, and in particular their inadequate reflection of zooplankton distributions in time and space. As reviewed in Chapter 1, a single sampling visit to a single station (Allen et al. 1999), cannot fully capture zooplankton distribution nor dynamics. Therefore, I believe that zooplankton communities have yet to be given a fair chance to be recognized as providing beneficial

biological indictors in national and international biomonitoring programs. Research

projects involving zooplankton distributions and dynamics need to embrace the 'multiple

driving forces' hypothesis of zooplankton distributions in order to reflect ecosystem

dynamics (Pinel-Alloul and Ghadouani 2007). This particular hypothesis states that

plankton distribution patterns are driven by many processes that include biotic and abiotic

elements, including both anthropogenic and meteorological factors (Pinel-Alloul and

Ghadouani 2007).   Many aquatic ecologists acknowledge that there are many chemical

and physical processes that influence plankton distributions, and suggest caution be

exercised in the absence of any of these elements when interpreting or exploiting their

results (Frank and Leggett 1982; Cloern et al. 1992; Romare et al. 2005; Pinel-Alloul and

Ghadouani 2007; Gulati et al. 2008). For example, Allen et al. (1999) found that

zooplankton abundance did not significantly correlate with broader-scale factors, e.g.,

climate change. Not surprising, Allen et al. (1999) collected zooplankton samples from a

single vertical net tow. As they sampled at only 1 station, I suggest that inadequate

sampling may explain why Allen et al. (1999) failed to detect a climate signal in their

zooplankton data. In addition to sampling issues, changes in water mass movements

linked to the large local reduction in wind speed, may also have influenced their detection

and therefore their possible response.

    It is well known that wind influences zooplankton distributions, but it has rarely

been evaluated as a predictor of zooplankton abundance in long-term data sets

(Sollberger and Paulson 1991; MacKenzie and Leggett 1991; Pinel-Alloul and

Ghadouani 2007). Winds move surface waters and thereby affect the distribution of

seston, including zooplankton. If zooplankton are sampled at 1 station, the method used

in many bioassessment programs, there is no chance of capturing the spatial dynamics of

zooplankton populations. If the wind field changes over year, single-station programs

may produce not only inaccurate but also biased results, which may be a consequence of

sampling error and inaccurate portrayals of zooplankton dynamics.

In Chapter 1, I showed that changes in the wind field over Harp Lake between

1980 and 2003 did not improve the prediction of the abundance of zooplankton

populations at annual steps. However, it remains quite possible that the wind may

influence zooplankton abundance at shorter yearly scales (Yan 1986), a possibility best

tested by examining correlations between daily abundance and the wind field on actual

sampling day or the preceding few days. Here I explore this possibility, again using Harp

Lake. Knowing that the Harp Lake community has changed annually in response to the

Bythotrephes invasion (Yan et al 2001), I model the daily abundance of zooplankton

species using first year (that also accounts for the *Bythotrephes* effect in addition to long-

term wind effects), and day of year (to account for the known seasonal dynamics of

zooplankton in north temperate lakes). Starting by modelling these long- and shorter

term known temporal effects, I can then determine if any residual variance may be linked

to the wind. I hypothesize that animals found deeper in the water column should be

affected less by the wind than epilimnetic taxa, since the wind-induced currents and

turbulence decline with depth (Rothschild and Osborn 1988). Thus *D. mendotae* and *L.

sicilis* that are deeper in the water column during the day (Young and Yan 2008) should

have residual abundance that is negatively correlated with wind because under less water

mixing or lower wind speeds, animals should be able to hold their position or that

heterogeneity increased and as a result of sampling at one station, animals may have been

missed.

Wind affects currents that are already in motion. Fast and slow wind speeds can

move animals or allow animals to move themselves. A negative relationship between

abundance and the predictor wind speed result in more animals at low wind speeds and

vice versa (Figure 2.1). When there is a positive relationship between abundance and the

predictor wind speed, animals are less abundant at low wind speeds (appear patchy,

Figure 2.2 – low wind speeds), while at high wind speeds, animals are more abundant

(homogeneously distributed Figure 2.2 – high wind speeds). Without the influence of

wind on the motion of already moving currents, animals may still be heterogeneously or

homogeneously distributed in the water. In the first case, we have fast animals that can

appear patchy or heterogeneously distributed since they are able to withstand the strength

of the current (Figure 2.3, case 1). In the second case, slow animals are homogeneously

distributed in the water because they are not able to withstand the current (Figure 2.3,

case 2).

To detect any effect of wind, we must first consider both the long-term and

seasonal correlations with zooplankton abundance, but it is also possible that zooplankton

are responding to changes in chemistry. As mentioned in Chapter 1, Ca, TP, and SO_4 are

decreasing and pH and NaCl are increasing in Harp Lake (Yan and Pawson 1997). To

correct for any effect of changes in water quality on zooplankton abundance, I examined

17 water chemistry variables that were assessed in Harp Lake from 1980 to 2004 on the

dates and at the same station that zooplankton were also collected by the DESC crew. Most of these variables have changed over the last few decades with over 50% of the variables increasing while 35% have decreased and the remaining 15% are relatively stable (Palmer et al. 2011). Despite all the published work showing long-term changes in zooplankton in Harp Lake (Yan et al. 2001, Yan et al. 2008), there is still unexplained variance, which may be attributable to the wind. My purpose was to discern if seasonal and annual changes in abundance of zooplankton populations determined at the one mid-lake station in Harp Lake could be better predicted when considering the effect of wind in addition to year, day of year, and water chemistry. I approached this objective by: (1) identifying the variation in the long-term data that could be attributable to year and day of year, i.e. long-term changes presumably attributable to the *Bythotrephes* invasion and to normal phenological patterns (Yan and Pawson 1997), (2) correlating the remaining variation in daily abundance with the wind field on the day of sampling and up to two days before sampling, and (3) determining if short-term wind effects contributed significantly to multiple linear regression models predicting daily zooplankton abundance after variance attributable to year, day of year and water chemistry were considered. Harp Lake served as an optimal site for this work given its many years of fortnightly zooplankton data, with modest changes in water chemistry (Yan et al. 2008), and a well understood change in zooplanktivory from the invading *Bythotrephes* (Yan et al. 2001).

Methods

Harp Lake is a small dimictic lake (71.4 ha) that is located at 45°23'N and 79°07'W. It has a mean depth of 13.3 m and a maximum depth of 37.5 m (Yan and Pawson 1997). This Canadian Shield lake is monitored by the Ontario Ministry of Environment's Dorset Environmental Science Centre (MOE's DESC). The lake has 6 inflows and 1 outflow to the Northeast.

The chemistry of Harp Lake has changed between 1980 and 2004 (Arnott et al. 1999; Molot and Dillon 2008; Paterson 2008; Yan et al. 2008). Ca has slightly decreased from 3.02 to 2.87 mg/L (Molot and Dillon 2008; Yan et al. 2008), while total phosphorus (TP) and dissolved organic carbon (DOC) have declined from 9.02 to 6.35 µg/L and 4.02 to 3.47 mg/L, respectively (Yan et al. 2008). Conductivity, Fe, K, Mg and SO_4 have also decreased modestly (Molot and Dillon 2008). Other parameters have increased, for example Na (0.84 to 1.37 mg/L) and Cl (0.79 to 2.7 mg/L) from the de-icing of nearby roads (Molot and Dillon 2008). There have been both increases and decreases in the abundances of zooplankton species at annual steps (Yan and Pawson 1997; Yan et al. 2002; Yan et al. 2008; Young and Yan 2008), attributed mainly to the 1993 invasion by the non-indigenous zooplanktivore *Bythotrephes* (Yan et al. 2001). The abundances of smaller, less efficient grazers declined, while larger zooplankton (e.g., *D. mendotae*) increased.

Zooplankton were collected biweekly in a series of vertical net tows (from 6m, 6m, 13m, 21m and 30m) that are subsequently combined to produce a bathymetrically-weighted composite at a single station at the deepest portion of the lake during the ice-

free season. The net is138.43 cm long, and 12.4 cm in diameter and is constructed of 76

um mesh (Girard et al. 2007). Sample volumes were calculated from the measured net

filtration efficiency (Girard et al. 2007). A minimum of 250 animals were counted and

identified in each sample, with subsample volumes adjusted so that no one species or

copepodid life stage represented more than 20% of the total count (Girard et al. 2007).

All raw data for zooplankton abundance and chemistry can be found in Appendix 5.

As explained in Chapter 1, Harp Lake has experienced changes in the wind field

over the study period assuming that data taken from Muskoka Airport can be applied to

the lake. At the Muskoka Airport, wind speed has decreased by 25% (4.0 to 3.0 m/s)

while the wind direction has shifted more to the North from the Northeast (33 degrees to

12 degrees). The decrease in wind speed is consistent with the Northern Hemisphere

atmospheric declines observed from an analysis of 822 surface weather stations between

1979-2008 (Vautard et al 2010). Vautard et al. (2010) suggests that the reason for the

changes in the wind field is partially due to a change in surface roughness due to changes

in land use.

Zooplankton And Wind Data

I used 1980-2004 zooplankton data from Harp Lake (Yan and Strus 1980; Yan

and Pawson 1997; Yan et al. 2008). I used the same zooplankton species as in Chapter 1,

selecting common species that differed in physical and behavioural characteristics. All

ages of cladocerans were used in this study; however, only adult copepods were used

because the immatures were not identified to species. I expected within-year model fits to

reflect the omission of the immature copepods for some species, a trend I hoped to

capture with polynomial regression since this method omits predictors that do not significantly contribute to the model.

Wind data were taken from the National Climate Data and Information Archives. George and Edwards (1976) suggested that the distribution of plankton in a shallow reservoir, Eglwys Nynydd, could be influenced by wind data from the previous day, and Petruniak (2009) indicated that the distribution of *Bythotrephes* in Harp Lake was best explained by considering the previous two days of wind data. Therefore, hourly data from the sampling day, and for 1 and 2 days prior to the sampling day were tabulated, and daily means were calculated as simple averages of all hourly data for the respective day. As in chapter 1, I used the wind data from the Muskoka Airport, since the Harp Lake anemometer was affected by forest growth around the MET station (refer to Chapter 1, page 25).

Statistical Analyses

Objective 1: Can the variation in daily zooplankton abundance be explained by year and day of year from 1980 to 2004?

Abundance of the 8 chosen species was available from 1980 to 2004 in Harp Lake over the 291 sampling dates (sample size), where each data series had occasional blanks (Table 2.1). These blanks or "missing data" were replaced with the detection limit for the count on the sample date, e.g., the abundance that would have been reported if 1 animal had been identified in the largest sub-sample counted. An explanation of how the blanks were treated can be found in Appendix 1. Refer to Table 2.2 for a summary of the annual averaged abundance trends in Harp Lake after the missing data were replaced with the

lowest detection limits. There were significant changes in 6 of the 8 species over year.

H. glacialis and *D. thomasi* did not show any significant trends in abundance over year

using linear regression.

In order to determine annual and seasonal contributions to abundance, multiple

linear regression models were used. Based on the works of Kleinbaum et al. (1988) and

Birkes and Dodge (1993), I generated the best statistical model that helped explain the

most variation in abundance with respect to the year and day of year. As the dependent

variable I used log-transformed abundances, including detection limit values replacing

missing values, of each of the species. Independent variables were: year (nominal scale:

1-25)(Yr), day of year (Julian day)(DOY), Yr^2 to Yr^5, DOY^2 to DOY^5, YrxDOY, and

$(YrxDOY)^2$. Polynomial orders up to 5 were used because the model that was best fit

was based on the AIC values, which indicated that some models were best at an order of

5. The Analyse-it add-on for Excel (AI) (Analyse-it Software, Ltd. 2011) and

Palaeontological Statistics (PAST) (Hammer et al. 2010) were utilized for the model

generation. Two programs were used because each provided its own unique contribution

to the computation of the models: AI (Analyse-it Software, Ltd. 2011) gave a graphical

output of the model and the generated residuals, while PAST (Hammer et al. 2010) gave

a value for the AIC. The r^2, F-stat, t-stat and residual assumptions (normal distribution,

independence (sum=0)) were the criteria used to assess the fitness of the models. AIC

was used to corroborate the fitness of the models and to finalize the choice of the model.

VIF values were not used in these computations because a majority of the models derived

had polynomial terms and would therefore score very high for multi-collinearity.

Objective 2: Can the remaining variation in abundance be correlated/associated with the wind field?

The residual abundances from the regression models (or from the long-term mean abundance if no regression models were produced) were correlated with the wind speed using Spearman correlations (r_s), and with the wind direction using Pearson correlations (r). All correlations were evaluated at p = 0.05. The wind data that were correlated with the residual abundance were the daily average of hourly readings on the sampling date, and one and 2 days prior to the sampling date. I analysed the daily averages on the three days as opposed to taking the 1,2 and 3 day averages in order to better isolate the change in abundance with respect to a particular wind day. AI (Analyse-it Software, Ltd. 2011) was used for the correlations with wind speed, while Oriana 4.0 (Kovach Computing Services 2010) was used for wind direction. The correlations between the residual abundance and wind direction were generated using bivariate linear-circular associations that output a Pearson r-value with an associated p-value. (See equation 1.3 for these calculations and Appendix 2 for how to identify an association between the residuals and the wind direction). A separate Appendix was included in order to interpret the associations because more data (daily data) were used rather than just annual averaged values between 1980-2004. Refer to Appendix 3 for these associations.

Objective 3: Can zooplankton abundance be predicted by year, day of year, chemistry and wind, in Harp Lake?

I began by ranking the 17 chemistry variables to eliminate the influence of scale and to standarize them. I used the principal component analysis routine in PAST (Hammer et al. 2010) to summarize the co-variance of the 17 variables into a smaller

number of orthogonal components. I used the scree plot in PAST (Hammer et al. 2010) to determine how many principal components to include. The first 2 principal components had the greatest variation explained among the chemistry variables according to the scree plot; however, I used 5 principal components in the regression to predict daily zooplankton abundance because the explained variation stabilized after 5 principal components in the scree plot, which may indicate that 5 components are potentially important.

I constructed various multiple linear regression models to determine if the abundance of each species could be predicted by: seasonality and long-term change (year/day of year) alone; water chemistry (chemistry) alone; the wind field alone; year/day of year and chemistry combined; year/day of year and wind combined; chemistry and wind combined; and year/day of year, chemistry and wind combined. I used stepwise regression for the more complex models because I wanted to estimate the contribution of each predictor to the r^2 value for the model. All other models in this study were constructed by fitting the best model using the t-stat and F-stat for the entire model. I did this because the purpose of these models was to analyze the masking effect between predictors.

I used the residual abundance generated from the year/day of year and chemistry models in order to determine if the remaining variation in abundance for all chosen species correlated with the wind field. I did this to evaluate the additional explanatory power of wind on abundance based on models that corrected for year/day of year alone

(Objective 1 and 2) and those that corrected for year/day of year and chemistry (Objective 3).

In the year/day of year, chemistry and wind MLR models, I forced a wind parameter to help predict abundance over year/day of year and water chemistry (ranked PCs). The goal was to obtain a model that had the greatest number of significant predictors that also included the wind field. Those models that did not add a wind parameter were rejected.

To examine the adequacy of the stepwise multiple linear regression (MLR) model, I generated a criterion flow chart that would assist me in choosing the best model (Figure 2.4). To choose the best regression models in AI, I first eliminated predictor terms that were not significant (defined by the t-stat and p-value). Adequate models adhered to the following criteria: they had the lowest AIC values, their Variance Inflation Factor (VIF) suggested little multi-collinearity, the residuals were normally distributed, the F-stat for the whole model was significant, the t-stat for each predictor was significant, the r^2 value was as high as it could be given satisfaction of the previous criteria. In each case where a draft model was rejected, the regression was re-fit and re-tested with the new terms. It is important to note that any models generated without a wind factor were omitted, and the regression was re-run. For instance, if DOY, PC1 and PC2 were included in the model, but no wind factor was included, I continued the search for models that might include the wind. I admit this decision is unusual; however, the rationale of this study was to determine if zooplankton ecologists were in error by never considering the wind in models designed to predict long-term changes in zooplankton

abundance. I chose to give wind every chance to enter the models, as long as it did

explain a significant component of the variance, and of course, I could compare these

models with the earlier models I generated which included only year/day of year and

chemistry. In other words, I wanted to test wind effects.

A problem with stepwise regression is that the larger, more complex model that I

started with included terms that may not necessarily have added a significant contribution

to the model but still increased the r^2. I dealt with this issue by monitoring the

significance of the t-stat for each predictor included in each draft model. To begin the

model choice process, predictors with a t-stat with $p<0.20$ were sequentially included to

avoid missing terms that might become significant in the final model. I used a p-value of

0.20 after numerous trials because this was the highest p-to-include that resulted in

eventual inclusion of predictors in the final model.

When multi-collinearity was an issue, indicated by a high VIF, a compromise was

sought between the predictor's unique contribution to the model and the magnitude of

multi-collinearity. The VIF values were generated in SYSTAT SigmaStat because AI or

PAST did not provide them. The model itself was not disregarded if the VIF values were

high because even though the r^2 value may be inflated, there is still a possible chance that

the inflated r^2 may still result in a significant model.

Those species that had residual abundance that correlated with a particular wind

parameter (speed and/or direction) were considered as potential species that may have

wind as a predictor within the MLR models. It was anticipated that any

correlations/associations between the residual abundance and the wind speed and direction would lead to the inclusion of wind variables in the MLR models.

Results

Objective 1: Can the variation in long-term abundance be explained by year and day of year?

The long-term abundances of all 8 species varied between 1980-2004 in Harp Lake (Table 2.2, Figure 2.5-2.7). The abundances of *B. tubicen* and *D. birgei* decreased with year/day of year by 2 orders of magnitude, while *D. mendotae* and *L. sicilis* abundance increased over the study period. The remaining species stayed relatively stable over the entire study period (with temporary oscillations due to seasonality) (Figure 2.5). The most dramatic changes in abundance occurred around 1993, when *Bythotrephes* was found in Harp Lake. The long-term abundances of the individual species were relatively similar during the pre-*Bythotrephes* period of time (1980-1992) (Figure 2.6). However, in 1993, the zooplankton community exhibited drastic changes to the composition and abundance of species. Both *B. tubicen* and *D. birgei* decreased greatly with the presence of *Bythotrephes*, whereas, larger species such as *D. mendotae* and *L. sicilis* populations increased (Figure 2.7).

Zooplankton abundance for all 8 species varied seasonally (DOY) (Figure 2.8). Of the 8 species, 5 major trends were observed over the seasonal data. The abundance had either: a dome shaped trend with high abundance in the middle of the seasonal period (*D. mendotae* and *D. birgei*), high abundance at the start of the ice-free season and a progressive decrease later on (*L. minutus* and *D. thomasi*), low abundance at the start of

the ice-free season and a progressive increase later in the season (*T. extensus* and *B. tubicen*), low abundance at the start of the ice-free season and continuous decrease later in the season (*H. glacialis*) or abundance that was stable throughout the ice-free season (*L. sicilis*).   Considering that there were long-term trends and seasonal differences, which varied with species, it was logical to discern how much of the variance in daily zooplankton abundance could be explained by a combination of these two steps, i.e. year and day of year (DOY).

All species abundance could be explained by a combination of DOY and/or Yr in regression models (Figure 2.9abc, Table 2.3). For Figure 2.9ab, abundance was predicted by a single variable (either DOY or Yr), whereas, Figure 2.9c involved a combination of both DOY and Yr variables. For the species, *B. tubicen* and *D. birgei* abundances were best explained by Yr (Figure 2.9a). These species were the most affected by *Bythotrephes*. Approximately 50% of the species abundance required a polynomial fit or multiple predictive terms to best explain abundance. Two of the 8 species had abundance that could be predicted by a combination of independent terms of Yr and DOY (*D. mendotae* and *T. extensus*) (Figure 2.9c). *H. glacialis* and *L. minutus* are best predicted by DOY (Figure 2.9a). These species were most affected by seasonality with increases and decreases in abundances throughout the seasonal period.

Objective 2: Can the remaining variation in abundance be associated with the wind field?

In 21% of cases, the residual abundance generated from the year/day of year models was significantly correlated with wind speed or direction (Table 2.4). Residual

abundances of *B. tubicen* and *T. extensus* were not correlated with the wind field. In contrast, the residuals of *L. minutus* abundance were correlated with both wind speed and direction (Table 2.4). *L. minutus* residual abundance was correlated with wind speed on the sampling day and on the two previous days. Two of the three metalimnetic species (*L. minutus* and *D. birgei*) had residual abundances that were correlated with wind speed and direction. Refer to Appendix 4 (Figure 4.3 and 4.4) for the plots between residual abundance and wind speed and wind direction, respectively.

Objective 3: Can zooplankton abundance be predicted by year/day of year, chemistry and wind in Harp Lake?

Based on the scree plot generated in PAST, 2 principal components explained the variation among the 17 chemistry variables from Harp Lake (Table 2.5). Principal component 1 (PC 1) explained 39% of the variance in ranked water quality data, and captured to rising Cl and Na and falling SO_4. PC 2 accounted for 21% of the variance and reflected changes in Gran Alkalinity and Mg.

Of the 56 possible models produced (including year/day of year and/or chemistry and/or wind) to explain variation in abundance, 46 models were generated (Table 2.6). As the models became more complex (e.g., year/day of year and chemistry and wind combined), fewer models were possible. All models combined explained 1-60% of the variation in abundance. *D. mendotae*, *H. glacialis* and *L. minutus* abundances were explained by each of the model types (all 7 types), while *T. extensus* had abundance that was least explained (only 3 of the 7 types).

The abundance of each species could be explained by chemistry (PC 1-5) (Table 2.7) with 7-39% of the variation explained. The small cladocerans (*B. tubicen* and *D. birgei*) had the greatest variation in abundance explained by water chemistry (37 and 39%, respectively). Cladoceran abundance was better explained by water chemistry relative to copepod abundance (23.75:6.25%, on average per species). *L. sicilis* was the only species that had abundance explained by PC5.

Significant models were produced using wind alone for 6 species. On average, 8% of the variance was explained. No significant models were found for *D. birgei* and *T. extensus*, (Table 2.8). The variation in abundance that could be explained ranged from 1-8%. The greatest variation in abundance that could be attributable to wind was for *L. minutus* (8%), whereas the least variation explained was for *D. thomasi* (1%). The majority (4 of 6) of models included an interaction term between wind speed and direction (e.g., Spd24*Dir24).

All species had abundance that could be predicted by a combination of year/day of year and chemistry in MLR models, which included, either Yr, DOY, YrxDOY (an interaction term), and/or PC 1-5 (Table 2.9). *D. mendotae* abundance was predicted by year and PC 3 (DIC and TKN) (r^2=0.14, p<0.0001). *H. glacialis* abundance was predicted by day of year and PCs 1 (NaCl, SO_4) and 3 (DIC and TKN) (r^2=0.12, p<0.0001). *B. tubicen* abundance was predicted by day of year, year, day of year and year interaction term, and PCs 1 (NaCl and SO_4), 2 (Gran_Alk and Mg), and 3 (DIC and TKN) (r^2=0.39, p<0.0001). *D. birgei* abundance was predicted by day of year, year, day of year and year interaction term, and PCs 1 (NaCl and SO_4), 2 (Gran_Alk and Mg), and

4 (DOC and TKN) (r^2=0.60, p<0.0001). *L. sicilis* abundance was predicted by day of

year and PCs 1 (NaCl and SO$_4$), 2 (Gran_Alk and Mg), 4 (DOC and TKN) and 5 (DOC

and TKN) (r^2=0.11, p<0.0001). *L. minutus* abundance was predicted by day of year,

year, day of year and year interaction term, and PC 3 (DIC and TKN) (r^2=0.31,

p<0.0001). *D. thomasi* abundance was predicted by day of year, year and PC 3 (DIC and

TKN) (r^2=0.15, p<0.0001). And finally, *T. extensus* abundance was predicted by day of

year and PC 3 squared (PC 3^2) (DIC and TKN) (r^2=0.19, p<0.0001).

Seven of the 8 species had abundance that could be predicted by seasonality

(excluding, *D. mendotae*) in the year/day of year and chemistry MLR models (Table 2.9).

The majority of the cladoceran species (3/4) had a positive relationship between

abundance and day of year, while the copepods had no particular pattern (slope being 0).

Year was included with day of year in 4 species models (*B. tubicen, D. birgei, L. minutus*

and *D. thomasi*). In all these cases, there was a negative relationship between abundance

and year.

Six of the 8 species had abundance that could be predicted by PC 3 (DIC and

TKN) (excluding, *D. birgei* and *L. sicilis*) in the year/day of year and chemistry MLR

models (Table 2.9). In all instances, the relationship between abundance and PC 3 were

negative. This indicates that lower abundances were found at high concentrations of DIC

and TKN.

The residual abundance generated from the year/day of year and chemistry

models had 11 of the 48 (23%) possible cases correlate with the wind field (speed and

direction) (Table 2.10). *D. mendotae* and *T. extensus* had the largest correlation between

the wind fields (50% of all possible cases or 3 of the 6). For *B. tubicen* and *L. sicilis*,

residual abundance was not explained by the wind field. *T. extensus* had residual

abundance that could be significantly explained by all wind speed days (sample day, 24-

hours prior to- and 48-hours prior to the sample day). In comparison between the

correlations using residual abundance from year/day of year alone and year/day of year

and chemistry combined, there were more significant cases found for the latter (2%

difference or 10 vs. 11 possible cases). Therefore, after considering the variation in

abundance attributable to year/day of year and chemistry, the wind field could still

improve the prediction of abundance.

Five of the 8 species had abundance that could be explained by a combination of

year and day of year and wind (speed and direction) (excluding *L. sicilis*, *D. thomasi* and

T. extensus) (Table 2.11). Among those species, the variation in abundance explained

ranged between 7-54%. All species with a significant model had abundance explained by

DOY. Two of the 3 metalimnetic species had abundance explained by speed on the

sample day (SpdS) (*D. birgei* and *L. minutus*). The year/day of year predictor may be

masking the variation attributable to the wind field because 3 species abundances could

not be explained by both year/day of year and wind combined.

The abundance of 6 of the 8 species was explained by a combination of chemistry

and wind field, ranging from 6-40%. All cladocerans had abundances that could be

explained by PC3. *D. thomasi* and *T. extensus* abundance could not be explained by a

combination of chemistry and wind. In contrast with the chemistry models alone, these

species could be explained by chemistry; therefore it is possible that chemistry is masking the variation attributable to wind.

After acknowledging that wind did explain some of the variation in residual abundance, nine MLR models were generated by forcing a wind variable to predict the abundance. Models were generated for 6 of the 8 species (Table 2.13). *D. mendotae* abundance was predicted using Yr, wind speed 48-hours prior to the sample and wind direction on the sample day (r^2=0.14, p<0.0001). *H. glacialis* abundance was predicted using DOY, PC 3 (DIC and TKN), wind speed and direction 24 hours prior to the sample date and an interaction term for speed and direction 24 hours prior to the sample (Spd24xDir24) (r^2=0.19, p<0.0001). There was multi-collinearity among variables within the *H. glacialis* regression models but these models were not disregarded because the models still had an r^2 value that is significant (VIF values of 7.169, 7.169, and 18.38 for Spd24, Dir24 and Spd24xDir24, respectively). The *D. birgei* model included year, PCs 1 (NaCl and SO_4), 3 (DIC and TKN), and 4 (DOC and TKN), and the wind speed 48 hours prior to the sample (r^2=0.44, p<0.0001). *L. minutus* abundance was predicted using several models: (1) using DOY, PC 2 (Gran_Alk and Mg) and the wind speed on the sample date (r^2=0.09, p<0.0001), (2) using DOY, PC 2 (Gran_Alk, Mg) and the wind speed 48 hours prior to the sample date (r^2=0.11, p<0.0001), (3) using PC 2 (Gran_Alk and Mg) and wind speed 24 hours prior to the sample date (r^2=0.04, p<0.0001), and (4) using PC 2 (Gran_Alk and Mg) and wind direction on the sample date (r^2=0.05, p<0.0001). *L. sicilis* abundance was predicted using wind speed on the sample date with PC 4 (DOC and TKN) (r^2=0.04, p<0.0001). Finally, *D. thomasi* abundance was predicted

using PCs 3 and 4 (DIC, DOC, and TKN) and wind speed 24 hours prior to the sample date (r^2=0.06, p<0.0001). Both *B. tubicen* and *T. extensus* abundance could not be predicted using a model that incorporated a combination of year/day of year, chemistry and wind. These species are the smallest of the 8 species used in this study.

A comparison of the MLR models using year/day of year and chemistry alone and those that included wind, it is apparent that the inclusion of wind did mask some of the predictors that caused patterns in the abundance of the chosen species. Here by masked, I mean the exclusion of a potential predictor that overshadowed the contribution of the wind parameter and is then ignored.   Masking is a common problem in linear regression because after the deletion of a term, other terms may become visible and appear modestly influential, as with wind in this case (Lawrence 1995, Nurunnabi et al. 2011). In the MLR models for year/day of year and chemistry, 6 of the 8 species (excluding *B. tubicen* and *T. extensus*) had a year/day of year and/or chemistry predictor masked by the inclusion of the wind parameters. For instance, *D. thomasi* abundance in the MLR models for year/day of year and chemistry was predicted by –DOY, -Yr, and – PC 3, while the model that included wind had abundance predicted by PC 3 in addition to a wind field parameter (Table 2.8). As a result, by including the wind variable, the variation in abundance that was explained by year/day of year was masked by the inclusion of wind, however PC 3 remained and was not hindered by the wind parameter. Another example would be the species *L. sicilis.*   I predicted *L. sicilis* abundance using year/day of year and chemistry by multiple predictors: +DOY, +PC 1, -PC 2, -PC 4 and +PC 5 (Table 2.6). However, when a wind field parameter was included to explain *L.*

sicilis abundance, all predictors except –PC 4 were dropped (Table 2.8). Again, the inclusion of wind masked year/day of year and/or chemistry that would usually be included in the models to explain abundance.

When the 9 MLR models were evaluated using individual predictors, the majority of the wind variables explained a significant portion of total variance in the data (Table 2.14a,b). In the case of model 1, *D. mendotae* abundance was predicted by Yr, Spd48 and DirS. Both Spd48 and DirS significantly explained, 1.4 and 1.2% of the variation, respectively (Table 2.14a). In the case of model 4, *L. minutus* abundance was predicted by DOY, PC 2 and SpdS. Actually, SpdS contributed more (3%) to the model than the chemistry variable (PC 2, 2%) (Table 2.14a). However modest the contribution, these MLR models demonstrate that wind does contribute to the prediction of abundance.

Discussion

Wind metrics could be used to improve the prediction of daily zooplankton abundance in Harp Lake in addition to year, day of year and chemistry. Year and/or day of year alone, explained 9-54% of the variance in zooplankton abundance. Chemistry alone, explained 4-39% of the variance on abundance. Using all wind days combined (sample day, and 1 and 2 days before the sample day), both wind speed and direction uniquely explained only 0-2% of the variation in the residual abundance. The combination of year/day of year and chemistry explained 11-60% of the variance in zooplankton abundance. While the combination of year/day of year and wind models explained 7-54% of the variance in abundance. After correcting or modeling abundance

against year/day of year and chemistry, the residual abundance correlated with the wind field in 23% of the total possible cases. Knowing that wind may influence residual abundance, 9 MLR models were generated to explain zooplankton abundance using year/day of year, and/or water chemistry and wind for 6 of the 8 species. Frank and Leggett (1982) used degree-day with wind (wind speed on sample day) to explain zooplankton abundance off the Newfoundland coast. However, the usage of long-term data in order to link the relationship between abundance, year/day of year, water chemistry and wind has never been pursued. The present study suggests that it is worth examining the effects of the wind on zooplankton abundance, but it suggests that the understanding gained will be modest.

As previously mentioned, year/day of year alone explained quite a bit of variation in the abundance of the chosen zooplankton species. *B. tubicen*, *D. birgei* and *L. sicilis* had abundance that was explained only by year (Yr) (49, 37 and 9%, respectively). Both small cladocerans (*B. tubicen* and *D. birgei*), had the greatest percentage explained by year, among these three species. This result is consistent with the presence of *Bythotrephes* in Harp Lake and the decline of both these species after 1993 (Yan and Pawson 1997). Therefore, it was expected that the abundance of these species would reflect a stronger change with year than displaying a trend with seasonality or day of year. Yan and Pawson (1997) also found that *L. sicilis* abundance has increased since the invasion of *Bythotrephes* and this is consistent with the results of this study. *D. mendotae* and *T. extensus* abundance was explained by year (*Bythotrephes* presence) and day of year (seasonality) (54 and 20%, for the species respectively). This result suggests that the

abundance of these species is better explained by a yearly change (such as the presence of *Bythotrephes*) and by seasonal events. For example, *D. mendotae* abundance was predicted by a combination of year and Julian day with low abundance early in the season/year and high abundance later on. However, it is surprising that *T. extensus* showed a significant positive relationship explained by year. According to Yan and Pawson (1997), *T. extensus* was among the species that decreased with the presence of *Bythotrephes* in 1993 hence, I expected abundance would continue to fall over time. However, my study extends beyond 1997 (Yan et al. 2001), and *T. extensus* abundance began to increase after 1999.   Why *T. extensus* has recovered from the initial negative impacts of *Bythotrephes* warrants study. This recovery may be due to the largely algal dietary resources of *T. extensus,* particularly the rotifer, *Polyarthra remata* (Dieguez and Gilbert 2002).

Residual abundance generated from the year/day of year models significantly correlated with the wind field (speed and direction) over the region during 1980-2004 for 21% of all possible cases (out of 48: 8 species x 3 wind days x 2 wind field parameters) and explained 0-2% of the variance in the residual abundance. The only species that did not have residual abundance that could be explained to some extent by the wind field were *B. tubicen* and *T. extensus*. This is not surprising because these are the smallest zooplankton species of the 8 (0.038, 0.050 cm, respectively). The small size would allow the animals to be moved around the water column more easily and thereby maintain their homogeneous distribution regardless of their preferred strata (Moreno-Ostos et al. 2009). *B. tubicen* did not significantly correlate with the wind speed. This was unexpected since

this species is capable of quick bursts of 0.408 cm/s (Lagergren et al. 1997). A capacity

for such quick bursts may not be enough for the changes in wind speed to lead to changes

in their distribution. In addition, *B. tubicen* is the only species chosen that is found in the

surface waters during the daytime and would therefore be the most susceptible to the

effects of wind as well as predation (Yan et al. 1997). The lowest wind speed (0.47 m/s

or 47 cm/s) and thereby, the wind force (~1.5% of the wind speed = 0.705 cm/s) over the

surface waters would have been too strong even for maximal bursts performed by this

species (0.408 cm/s).

     L. minutus had residual abundance that was correlated with wind speed and

direction in 4 of the 6 possible cases, including wind speed on the day of sampling and

the previous 2 days. These results are not surprising since *L. minutus* is a medium-sized

(0.089 cm), fast swimming (0.340 cm/s) metalimnetic species (Dieguez and Gilbert 2002,

Muirhead and Sprules 2003). Its location in the water column and size/speed allows this

species to resist the current, which is induced by the wind and in most cases (4 of 6) *L.

minutus* can maintain its position in the water and withstand turbulence and flow.

Imberger and Hamblin (1982) and Gorham and Boyce (1989) have documented that the

turbulence, internal waves (baroclinic waves) and heat transfer are dampened at the base

of the mixed layer (surface waters) that marks the top of the metalimnion. Since the wind

has a dampened effect in the metalimnion, it is reasonable to find the majority of the

metalimnetic species to be able to withstand (or have abundance correlated with) the

wind field (*L. minutus* and *D. birgei*). *H. glacialis* is the only species in the metalimnion

that did not have residual abundance that was significantly correlated with the wind speed

(although 1/3 possible cases for wind direction was significant). This makes sense because *H. glacilais* is known to be very slow, given its gelatinous capsule (Link 1996), and would therefore not be able to resist the wind-induced currents within the metalimnion, even though they are relatively slow.

What does this all say about the importance of the wind on zooplankton abundance? After correcting for year/day of year, residual abundance can be used to explain an additional portion of the variation in zooplankton abundance. Knowing that the wind may explain some variation in zooplankton abundance, it is possible that it is not just a mere coincidence as suggested in Chapter 1 discussion. Therefore, the addition of wind into models, along with year/day of year and other predictors (e.g., anthropogenic factors), may help further illuminate our understanding of zooplankton in their aquatic ecosystems.

Residual abundance remaining from the year/day of year and chemistry models was significantly correlated with the wind field (speed and direction) for 23% of all possible cases (11 of 48 cases) and explained 0-2% of the variance in the residual abundance. The wind field better predicted the residual abundance from the year/day of year and chemistry models compared to the year/day of year models alone (23% vs. 21%; 11 vs. 10 cases). Surprisingly, *T. extensus* had residual abundance that significantly correlated with all wind speed days. This is unexpected because *T. extensus* residual abundance did not correlate with any aspect of the wind field for the year/day of year models alone. This may be a result of the masking of the wind field by chemistry, when explaining the variation in abundance. For instance, the year/day of year models alone

did not incorporate any variation in abundance due to chemistry, however when chemistry was considered a predictor, the variation in abundance due to the wind field became evident. After correcting for year/day of year and chemistry, *T. extensus* abundance could be explained by the wind field.

The majority of the species (5 of the 7) that had residual abundance that could be explained by wind direction on a particular wind day were the same for the year/day of year alone and year/day of year and chemistry models (*D. mendotae*-DirS, *H. glacialis*-Dir24, *D. birgei*-Dir24, *L. minutus*-DirS and *D. thomasi*-DirS). That variation associated water chemistry did not mask the variation in residual abundance explained by wind direction. For instance, *H. glacialis*, *D. birgei* and *D. thomasi* had residual abundance that was explained by wind direction on the same wind days (e.g., Sample day) when corrected for the year/day of year alone models as well as the year/day of year and chemistry models. If water chemistry were masking the variation in abundance attributable to the wind field, the residual abundance of these species would not be correlated with the wind field.

By forcing wind into MLR models in addition to year/day of year and chemistry it appears that some predictors can be masked by the wind (e.g., year or day of year). However, when wind was given a chance (or termed as "forcible inclusion"), nine models were successfully generated to include either year/day of year and/or water chemistry and wind. Each of these models will be discussed below. To simplify the understanding behind the predictor and its relationship with abundance, an overall discussion of the predictors will be organized by: year/day of year, water chemistry with principal

components and finally wind as opposed to discussing each model. However, it is important to note that each model was derived individually. When discussing the models and the relationship between abundance and a predictor, the annual averaged Harp Lake water chemistry or abundance information can be found in Tables 2.2 and 2.15.

Wind did not load into any MLR models to predict the abundance of *B. tubicen* or *T. extensus*. This is not surprising considering that their residual abundance after correcting for year/day of year did not correlate with the wind field (note: only models that contained a wind field predictor were chosen). Both these species are very small. *B. tubicen* is capable of fast bursts but resides in the epilimnion, which is more exposed to the wind (George and Edwards 1976). However, it is surprising that *T. extensus* did not show a predictive relationship between abundance and the wind field because it resides in the hypolimnion (Barbiero et al. 2005). Those species lower in the water column are less susceptible to wind-induced currents and could therefore potentially withstand any effect of changes in the wind. This difference in current versus swim speed may be the reasoning behind the inability of *T. extensus* to withstand any currents and therefore be homogeneously distributed over spatial and temporal scales. Small zooplankton species that are either too slow to overcome the current or too close to the surface waters (mixing layer) are potentially important species that may be used in bioassessment programs with confidence that any changes in wind will not confound interpretation of their abundance data.

Year and day of year were important variables that were included in the models of 4 of the 6 remaining species. To start, the presence of *Bythotrephes* in 1993 in Harp Lake

caused zooplankton to either out swim this invader or that the animal was large enough to compete for resources amongst other conspecifics. Yan and Pawson (1997) found that larger cladocerans increased in number after the appearance of *Bythotrephes* and that smaller species declined. Therefore, it is expected that the large cladoceran *D. mendotae* would prevail in the presence of *Bythotrephes* and smaller species such as *D. birgei* would decline. However, Schulz and Yurista (1995) found that *Bythotrephes* actually preferred larger daphniids, such as *D. mendotae*, therefore *D. mendotae* body size would not be a likely reason for its success over time. Also, *D. mendotae* is known to avoid *Bythotrephes* (Pichlova-Ptacnikova and Vanderploeg 2011) and is most likely the reason why *D. mendotae* increased with year in Harp Lake. Therefore using year in order to better explain species that have increased or decreased would be important when predicting their future abundance in Harp Lake.

H. glacialis and *L. minutus* both were negatively associated with day of year. *H. glacialis* abundance rose for the first 50 days and then fell gradually thereafter. In particular, cladocerans are known to have thermal limits and they are unable to live at temperatures as high as 30 degrees (Throp and Covich 2010). These animals are more adapted to cooler temperatures, therefore as the summer progresses (or day of year), the temperature increases and the animals begin to decline or the spring food production is over and the resources are limited (Throp and Covich 2010). These increases in temperature are especially important since the climate is continuously warming, which is also observed in Harp Lake surface waters. At 1 m depth, the average surface temperature is increasing with year (refer to Chapter 1, page 67). This may explain why

there is a negative relationship between *H. glacialis* abundance and day of year. It is also

possible that the gradual decline in abundance over the summer may be food related.

They have a burst of production in the spring associated with the spring algal bloom and

then limp along the rest of the year (Throp and Covich 2010). In the case of *L. minutus*,

the negative association between abundance and day of year is an artefact of the MOE's

sample counting and the life history of this species. Calanoids have 6 naupliar and 6

copepodid life stages (Throp and Covich 2010). Adults only were identified to species in

this study while immatures were counted but not identified to species. Therefore I could

not include immature life stages in the models. The addition of these life stages may

have increased the abundance estimate of *L. minutus* during the ice-free season and

changed its relationship with DOY. In summary, both year and DOY can be useful

predictors of daily abundance of zooplankton.

Excluding *D. mendotae*, all species with successful MLR models included

chemistry, i.e. PC1, 2, 3 and/or 4. PC1 mainly summarized changes in NaCl and SO_4,

and loaded into the model for *D. birgei* abundance. High salinities (e.g., 30 psu), do

impact the reproductive life stages of *Diaphanosoma*. For example, the life span of *D.*

birgei decreased from 24 days to 5 days at higher salinities (5, 17, 25 and 30 psu,

Achuthankutty et al. 2000). Ca is known to influence the sensitivity of zooplankton to

salt (Rahaman 2006); however Achuthankutty et al. (2000) did not evaluate salinity with

respect to Ca levels. At the present time, the salinity in Harp Lake is increasing due to

the de-icing of winter roads that surround the lake (Yan et al 2008). However, the

salinity in Harp Lake is still far from the extreme levels of the salinity tested in

Achuthankutty et al. (2000) (Harp Lake average salinity ~0.00356 psu, 1000 times lower than damaging thresholds). Therefore, based on the low levels of NaCl in Harp Lake, I propose that salinity is not directly affecting *Diaphanosoma* abundance. Nevertheless, after correcting for the *Bythotrephes* effect using year, the negative relationship between *D. birgei* abundance and PC1 is still present and therefore even a small amount of NaCl may be affecting *D. birgei* abundance.

As the next constituent of PC1, SO_4 levels in Harp Lake are decreasing as SO_2 emissions in eastern North America fall, yet sulphate is not toxic. Therefore the link between SO_4 and abundance is not causal. *D. birgei* has been found in waters with SO_4 levels much higher than those in Harp Lake (up to 24.5 mg/L in Northern lakes) (Keller and Pitblado 1989). Pinel-Alloul et al. (1990) also observed a positive correlation (r=0.40) of *Diaphanosoma* with SO_4 in Quebec lakes. Since SO_4 is decreasing in Harp Lake, there is a positive relationship for *D. birgei*. Therefore, the link between SO_4 and *D. birgei* abundance is not apparent.

L. minutus was the only species that had PC2 (explained by Gran_Alk and Mg) included in the MLR models. This is not surprising since *L. minutus* dominates in waters that have high alkalinity (e.g., 191 mg/L as $CaCO_3$, Shaw and Kelso 1992). In fact the levels of alkalinity are increasing in Harp Lake, i.e. with higher alkalinity, more *L. minutus*. PC2 is also correlated with Mg, which is decreasing in Harp Lake from 1.02 mg/L to levels as low as 0.80 mg/L, however modest. According to Keller and Pitblado (1989), *L. minutus* can dominate waters that have Mg levels as high as 15 mg/L.

Therefore it is unlikely that the link between *L. minutus* and Mg is a cause/effect relationship.

PCs 3 and 4, associated with inorganic and organic carbon and TKN were included in models for *D. birgei*, *H. glacialis, L. sicilis* and *D. thomasi*. All these species had abundance that increased with TKN and DOC, and decreased with DIC (PC3). In Harp Lake, DOC and TKN are positively correlated ($rs=0.19$, $p<0.0001$), therefore I must discuss them jointly. Both *D. birgei* and *H. glacialis* were more abundant when TKN levels were low to moderate (110-1120 µg/L vs. >2300 µg/L) (Keller and Pitblado 1989). Keller and Pitblado (1989) reported that in northern Ontario lakes, 82-84% of *Diaphanosoma* were found in lakes where TKN levels were between 110-1120 µg/L and only 48% of the lakes contained this species when TKN peaked at 2300 µg/L. Likewise, 71-90% of the *H. glacialis* were also found at low TKN levels, with only 42% of higher-TKN lakes containing this species (Keller and Pitblado 1989). In the study by Keller and Pitblado (1989), *D. thomasi* abundance was present in almost all the lakes (86-94%) at all ranges of TKN. In Harp Lake, the highest level of TKN was 261 µg/L and higher abundances were found at lower TKN levels.

Four of the 8 zooplankton species had a negative correlation between abundance and DIC/DOC in the MLR models (*H. glacialis, D. birgei, L. sicilis* and *D. thomasi*). A possible reason for this negative relationship could be related to strata location. All these species are found lower in the water column, below the epilimnion where DIC/DOC levels are higher (Kamjunke et al. 2004). *H. glacialis* and *D. birgei* are found in the metalimnion during the day (Tessier 1983, Doulka and Kebayias 2008), while *L. sicilis*

and *D. thomasi* are found in the hypolimnion (Barbiero et al. 2005, Young and Yan 2008). Those species that inhabit the metalimnion are subjected to dampened turbulence from wind-induced currents and thereby less turbidity, which leads to increased levels of particulate matter (and higher DIC/DOC levels). Unlike the metalimnetic species, *D. thomasi* particularly thrives in deep, clear waters where turbidity is at its lowest (Balcer et al. 1984, Lytle and Snoeyink 2003). In fact, *D. thomasi* has been found to negatively correlate with the turbidity of water (r=-0.30) (Pinel-Alloul et al 1990). It is understandable that metalimnetic and hypolimnetic species that reside below the epilmnion would be negatively associated with DIC/DOC, since levels are found to be higher below the surface waters (Kamjunke et al. 2004). Therefore, when studying zooplankton, using DIC/DOC and TKN as predictors to estimate abundance would be worthy of study since zooplankton respond to levels dependent upon their location in the water.

Both wind speed and direction were forcibly included as predictors that explained zooplankton abundance. The prediction of abundance of 6 of the 8 species could be improved by the inclusion of a wind parameter within a MLR model in addition to year/day of year and/or water chemistry. Wind speed was a better predictor than wind direction. Wind direction on the sample day was included as a predictor for 2 of the species (*D. mendotae* and *L. minutus*), whereas wind speed was included in the models of all the species. The abundances of *D. mendotae*, *D. birgei* and *L. sicilis* were negatively correlated with wind speed on the sample date or 48 hours prior to sampling. The wind effect (which was significant) for each of these species was 2, 2 and 1%, respectively.

This negative relationship indicates that animals are more abundant at lower wind speeds and fewer animals are present at higher wind speeds (Figure 2.1). This may indicate that animals can hold their position in the water under low wind-induced mixing. Under high wind mixing, animals may become transported elsewhere in the water column (upwelled or downwelled, depending on their original strata location). For instance, *D. mendotae* abundance was negatively associated with wind speed 48 hours prior to the sample taken. Since this species is found in the hypolimnion (Young and Yan 2008), low wind speeds would cause slower currents in the surface waters that cannot penetrate through the metalimnion (Heaps and Ramsbottom 1966) and therefore, the internal wave movements of the hypolimnion cease or weaken. At higher wind speeds or more turbulent waters, there is a better chance that the hypolimnion is oscillated back and forth with a frequency of the internal wave period (Antenucci and Imberger 2003). The internal wave period in Harp Lake was 160 minutes in the summer of 2007 (Petruniak 2009). This means the thermocline tilts back and forth from one end of the lake to the other approximately every 3 hours. In a 48-hour period, the internal wave at the metalimnion would have oscillated 16 times. This oscillation causes animals in the water to become transported upwind or downwind depending on their location in the water. For *D. mendotae*, the high wind speeds cause the movement of the internal wave at the metalimnion and animals are transported downwind and upwelled, unless they are able to resist being pushed upward (Waife and Frid 1996) (Figure 2.1). This is the same case with *L. sicilis* (except this species is always hypolimnetic), however abundance was negatively associated with the wind speed on the sample day. *D. birgei* is found in the metalimnion (Doulka and

Kebayias 2008), where the water movement is dampened due to the temperature gradient and therefore results in decreased turbulence (Elci 2008). Therefore, both the metalimnion and hypolimnion experience a similar amount of wind-induced turbulence and animals found within those strata would react similarly to the wind speeds.

H. glacialis, *L. minutus* and *D. thomasi* had abundance that positively correlated with the wind speed on either the sample date, 24-hours prior to- and/or 48-hours prior to the sample being taken (variance explained for the wind variable: 2, 4 and 1 %, respectively). This positive relationship indicates that animals were less abundant at lower wind speeds and more abundant, earlier in the records, when wind speeds were higher (Figure 2.2). This may indicate that animals cannot hold their position in the water under high wind speeds because the wind is too strong and is penetrating through to the metalimnion (Colebrook 1960). Under lower wind speeds, animals are able to hold their position in the water and become patchy (heterogeneously distributed) (Rinke et al. 2007). Both *H. glacialis* and *L. minutus* are found within the metalimnion and therefore follow the dynamics portrayed in Figure 2.8, where animals are patchy at low wind speeds and homogeneous at high winds speeds. Even though *D. thomasi* is found in the hypolimnion, this species demonstrates the same pattern as mentioned above with the metalimnetic species. A possible reason why *D. thomasi* does not share the same negative relationship with its fellow hypolimnetic species could be that this particular copepod is able to swim faster than the other species (Visser et al. 2009). According to Link (1996), even the largest cladoceran, *D. mendotae* was captured 80% of the time in a study of fish-zooplankton contact rates. The smallest cyclopoid was only captured 65%

of the time (Link 1996). Therefore, it is reasonable to suggest that the cyclopoid *D. thomasi* is capable of holding its position in the hypolimnion during low wind speeds compared to its hypolimnetic conspecifics.

Wind direction on the sample day was the only parameter that improved predictions of abundance of *D. mendotae* and *L. minutus*. The explanation for this result is unclear. Why were these the only 2 species that had abundance significantly predicted by wind direction? Why only on the sample day? Further sampling with the consideration of the wind effect on depth would help address these questions.

The inclusion of wind in MLR models helps predict zooplankton abundance beyond year/day of year and chemistry. On average, the inclusion of wind in the 9 MLR models significantly adds 2.4% to the prediction of abundance beyond year/day of year and chemistry, with a total of 22% for all 9 models combined. On larger lakes, the wind effect may be even bigger or smaller. When wind is a considerable factor in a study that may bias results, such as for large lakes, e.g. Lake Ontario, the effect of the wind on species distributions may well be predictable. . If wind can have a predictable effect on zooplankton abundance, we can correct for its influence.

Given the comparisons between year/day of year and chemistry and wind, the order of importance of factors that are needed to predict daily abundance can be hypothesized using the 9 MLR models. Year and day of year have the greatest effect on the change in abundance (of the 9 MLR models, average contribution = 6.6%), while chemistry appears to be less important than year/day of year (4.3%). Wind may matter less when predicting abundance compared to year/day of year and chemistry, but its level

of importance still remains (2.4%). The use of Harp Lake as a study site for documenting the distribution of zooplankton is beneficial because the chemistry has not changed largely over the last 25 years. However, the invasion of *Bythotrephes* may have inflated the effect of year on the abundance of zooplankton species within Harp Lake. Without the *Bythotrephes* invasion, wind might have been more important in the MLR models as year/day of year masked wind as a predictor of abundance.

Sampling zooplankton once at a single station is adequate for capturing a yearly effect because the regression models in this study document a great deal of variation in abundance attributable to year. However day of year and wind may suffer from infrequent samples because seasonality and the wind field change throughout the calendar year. Examining patterns using few sampling days at a single station may not capture the fluctuations in the life history of animals (seasonal) or as the climate warms (decadal). On the other hand, wind can fluctuate daily, even hourly and with few sampling dates, the wind can have a varying effect on zooplankton depending on the strata in which, they are located and the strength of the wind itself. Water chemistry is less of a concern regarding the sampling efficiency in Harp Lake, since the changes observed are more similar over time and less drastic compared to lakes with major water chemistry issues (drastically changing chemistry concentrations). Zooplankton are not used in large bioassessment projects, therefore this study has provided insight to further explore wind as a contributor within aquatic ecosystems as well as demonstrating that zooplankton do in fact react to many predictors.

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Table 2.1: The number of sampling dates available for the chosen species between 1980 and 2004 in Harp Lake, Ontario out of a total of 291 sampling dates.

Species	Total Number of Sample Dates With Abundance Recorded	Percentage of Data Available
D. mendotae	247	85
H. glacialis	200	69
B. tubicen	138	47
D. birgei	132	45
L. sicilis	171	59
L. minutus	268	92
D. thomasi	278	96
T. extensus	263	90

Table 2.2: Summary table of the zooplankton species chosen in Harp Lake between 1980-2004 using the data after substituting the blank values with the lowest detection limit (LDL), N=25 years.

Species	Average Abundance for all years (#/m^3)	Abundance Range between 1980-2004 (lowest to highest)	Spearman Correlation between Abundance and Year (r, p-value)	TREND
D. mendotae	579.17	11.44 – 3194.00	0.35, p<0.0001	Increasing
H. glacialis	326.81	5.12 – 3736.40	0.01, p=0.8268	Slightly Increasing
B. tubicen	282.13	3.37 – 9116.47	-0.53, p<0.0001	Decreasing
D. birgei	383.88	4.88 – 1145.87	-0.56, p<0.0001	Decreasing
L. sicilis	121.95	21.81 – 617.20	0.19, p=0.0010	Increasing
L. minutus	690.26	21.71 – 6623.63	-0.19, p=0.0014	Decreasing
D. thomasi	220.97	82.61 – 623.67	-0.09, p=0.1297	Slightly Decreasing
T. extensus	430.84	69.00 – 1520.92	-0.16, p=0.0069	Decreasing

Table 2.3: Regression models predicting abundance of zooplankton species between 1980-2004 using multiple steps: year (Yr) and day of year (DOY).

Species	Model	r^2	Fstat/p-value
D. mendotae	LogAbundance = -4.911+0.06748*DOY-0.0001566*DOY^2+0.03223*Yr	0.54	111.15/<0.0001
H. glacialis	LogAbundance = -30.77+0.5781*DOY-0.003663*DOY^2+1.0046x10^{-5}*DOY^3-1.0215x10^{-8}*DOY^4	0.38	43.62/<0.0001
B. tubicen	LogAbundance = 2.647-0.7458*Yr+0.2187*Yr^2-0.02312*Yr^3+0.0009979*Yr^4-1.5169x10^{-5}*Yr^5	0.37	33.67/<0.0001
D. birgei	LogAbundance = 3.033-0.8475*Yr+0.2391*Yr^2-0.02513*Yr^3+0.001081*Yr^4-1.6389x10^{-5}*Yr^5	0.41	39.83/<0.0001
L. sicilis	LogAbundance = 1.57+0.004171*Yr^2-0.0001594*Yr^3	0.09	14.87/<0.0001
L. minutus	LogAbundance = 55.3-1.389*DOY+0.01421*DOY^2-6.9942x10^{-5}*DOY^3+1.6453x10^7*DOY^4-1.4772x10^{-10}*DOY^5	0.37	32.80/<0.0001
D. thomasi	LogAbundance = 2.67-0.002261*DOY	0.09	28.25/<0.0001
T. extensus	LogAbundance = 1.534+0.004308*DOY-0.011*Yr	0.20	36.48/<0.0001

Table 2.4: Spearman correlation coefficients between the residual abundance of zooplankton and the wind field using the residual abundance generated from the year/day of year models*. Significance denoted by a p-value<0.05 with 95% confidence.

Species	Day	Wind Speed[a] (rs)	Wind Speed (p-value)	Day	Wind Direction[b] (r)	Wind Direction (p-value)
D.mendotae	Sample	0.02	0.7856	Sample	0.117	**0.0190***
	24 Hrs	0.02	0.7770	24 Hrs	0.055	0.4220
	48 Hrs	0.03	0.6265	48 Hrs	0.058	0.3810
H.glacialis	Sample	0.03	0.5831	Sample	0.052	0.4590
	24 Hrs	0.06	0.3070	24 Hrs	0.108	**0.0340***
	48 Hrs	0.06	0.3090	48 Hrs	0.094	0.0770
B.tubicen	Sample	-0.02	0.7958	Sample	0.070	0.2390
	24 Hrs	0.08	0.1992	24 Hrs	0.077	0.1840
	48 Hrs	-0.07	0.2065	48 Hrs	0.072	0.2200
D.birgei	Sample	-0.04	0.5365	Sample	0.042	0.6080
	24 Hrs	-0.02	0.7352	24 Hrs	0.148	**0.0020***
	48 Hrs	-0.14	**0.0184***	48 Hrs	0.038	0.6560
L.sicilis	Sample	-0.02	0.6778	Sample	0.074	0.2060
	24 Hrs	0.02	0.7852	24 Hrs	0.106	**0.0380***
	48 Hrs	-0.06	0.3092	48 Hrs	0.082	0.1410
L.minutus	Sample	0.13	**0.0246***	Sample	0.119	**0.0170***
	24 Hrs	0.14	**0.0141***	24 Hrs	0.09	0.0990
	48 Hrs	0.15	**0.0127***	48 Hrs	0.038	0.6550
D.thomasi	Sample	0.01	0.8078	Sample	0.111	**0.0290***
	24 Hrs	0.06	0.3297	24 Hrs	0.027	0.8070
	48 Hrs	0.01	0.8845	48 Hrs	0.049	0.4950
T.extensus	Sample	0.07	0.2090	Sample	0.040	0.6370
	24 Hrs	0.09	0.1322	24 Hrs	0.054	0.4340
	48 Hrs	0.08	0.1498	48 Hrs	0.074	0.2060

[a]Pearson correlation coefficients using Analyse-it add-on for Excel
[b]Bivariate linear-circular association coefficients using Oriana 4.0

Table 2.5: PCA summary from the 17 chemistry variables from Harp Lake, Ontario and the summary proportions of the greatest variance.

Principal Components	Eigenvalues	% variance explained by the component	Chemistry Variable	Value
PC1	6.65	39.17	Cl	0.3281
			Na	0.3589
			SO_4	-0.3502
PC2	3.59	21.16	Gran_Alk	0.3869
			Mg	0.4263
PC3	1.46	8.59	DIC	-0.6733
			TKN	0.4210
PC4	1.03	6.07	DOC	0.6350
			TKN	0.4230
PC5	0.70	4.14	DOC	-0.4847
			TKN	-0.5371
SUM		**79.14**		

Table 2.6: Summary of all possible regression models between zooplankton abundance and predictor(s) in Harp Lake during 1980-2004. Bolded values are the highest r^2 value between the models for each species. The detailed model compositions are found in Tables 2.3, 2.7-2.9, 2.11-2.12, respectively.

Species	Year/Day of Year		Chemistry		Wind Field		Year/Day of Year & Chemistry*		Year/Day of Year & Wind Field*		Chemistry & Wind Field*		Year/Day of Year & Chemistry & Wind Field*	
	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value	r^2	p-value
D. mendotae	**0.54**	**<0.0001**	0.12	<0.0001	0.04	0.0035	0.14	<0.0001	**0.54**	**<0.0001**	0.14	<0.0001	0.17	<0.0001
H. glacialis	**0.38**	**<0.0001**	0.07	<0.0001	0.05	0.0079	0.12	<0.0001	0.07	0.0002	0.10	<0.0001	0.19	<0.0001
B. tubicen	0.37	<0.0001	0.37	<0.0001	0.05	0.0008	**0.39**	**<0.0001**	0.09	<0.0001	0.17	<0.0001	---	---
D. birgei	0.49	<0.0001	0.39	<0.0001	---	----	**0.60**	**<0.0001**	0.27	<0.0001	0.40	<0.0001	0.44	<0.0001
L. sicilis	0.09	<0.0001	0.09	<0.0001	0.02	0.0458	**0.11**	**<0.0001**	---	---	0.06	0.0007	---	---
L. minutus	**0.37**	**<0.0001**	0.04	0.0014	0.08	<0.0001	0.31	<0.0001	0.10	<0.0001	0.09	<0.0001	0.11	<0.0001
D. thomasi	0.09	<0.0001	0.05	0.0013	0.01	0.0469	**0.15**	**<0.0001**	---	---	0.06	0.0004	---	---
T. extensus	**0.20**	**<0.0001**	0.07	0.0002	---	---	0.19	<0.0001	---	---	---	---	---	---

*Must include each of the variables in order to be considered.

Table 2.7: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using chemistry. Computations were done in AI and the r^2 is based on the entire model. PC-principal component.

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 2.311 - 0.1873*PC2 - 0.1563*PC3	0.12	19.45/p<0.0001
2	*H. glacialis*	LOGAbund= 1.984 - 0.1424*PC3 - 0.1026*PC4	0.07	10.42/p<0.0001
3	*B. tubicen*	LOGAbund= 1.801 - 0.1727*PC1 + 0.3382*PC2 - 0.1734*PC3	0.37	55.11/p<0.0001
4	*D. birgei*	LOGAbund= 1.864 - 0.2281*PC1 + 0.3893*PC2 - 0.179*PC3 - 0.1103*PC4	0.39	45.59/p<0.0001
5	*L. sicilis*	LOGAbund= 1.822 + 0.05134*PC1 - 0.07999*PC2 - 0.06627*PC4 + 0.06866*PC5	0.09	7.05/p<0.0001
6	*L. minutus*	LOGAbund= 2.419 + 0.1113*PC2 - 0.08596*PC4	0.04	6.75/p=0.0014
7	*D. thomasi*	LOGAbund= 2.187 - 0.06788*PC3 - 0.05696*PC4	0.05	6.83/p=0.0013
8	*T. extensus*	LOGAbund= 2.31 - 0.09239*PC1 + 0.09292*PC2 + 0.06623*PC4	0.07	6.96/p=0.0002

Table 2.8: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using wind. Computations were done in AI and the r^2 is based on the entire model. Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 2.06 + 0.003223*Dir24 - 0.0005582*Spd24xDir24	0.04	5.77/p=0.0035
2	*H. glacialis*	LOGAbund= 1.011 + 0.1758*Spd24 + 0.004333*Dir24 + 0.002011*Dir48 - 0.0009114*Spd24xDir24 - 0.0003226*Spd48xDir48	0.05	3.20/p=0.0079
3	*B. tubicen*	LOGAbund= 1.435 + 0.1816*Spd24 - 0.0003309*Spd24xDir24	0.05	7.31/p=0.0008
4	*D. birgei*	No model could be produced	---	---
5	*L. sicilis*	LOGAbund= 1.697 + 0.00156*DirS - 0.0002718*SpdSxDirS	0.02	3.12/p=0.0458
6	*L. minutus*	LOGAbund= 1.86 + 0.07736*SpdS + 0.09806*Spd48	0.08	12.06/p<0.0001
7	*D. thomasi*	LOGAbund= 2.072 + 0.03548*Spd24	0.01	3.98/p=0.0469
8	*T. extensus*	No model could be produced	---	---

Table 2.9: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using year/day of year and chemistry. Computations were done in AI and the r^2 is based on the entire model. Yr-year, DOY-day of year, PC-principal component, DOYxYr-an interaction term between the 2 predictors.

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 1.906+0.03092*Yr-0.1232*PC3	0.14	24.12/p<0.0001
2	*H. glacialis*	LOGAbund= 2.666-0.003192*DOY-0.09933*PC1-0.1654*PC3	0.12	12.81/p<0.0001
3	*B. tubicen*	LOGAbund= 0.9111+0.008117*DOY-0.01972*Yr-5.0148x10^{-8}*DOYxYr-0.1275*PC1+ 0.2149*PC2-0.1733*PC3	0.39	30.86/p<0.0001
4	*D. birgei*	LOGAbund= -1.769+0.03066*DOY-0.0377*Yr-2.0749x10^{-7}*DOYxYr-0.1399*PC1+ 0.1657*PC2-0.1292*PC4	0.60	70.82/p<0.0001
5	*L. sicilis*	LOGAbund= 1.57+0.001178*DOY+0.0634*PC1-0.08953*PC2-0.09121*PC4+ 0.06728*PC5	0.11	6.78/p<0.0001
6	*L. minutus*	LOGAbund= 6.419-0.02635*DOY-0.02216*Yr+1.6422x10^{-7}*DOYxYr-0.09522*PC3	0.31	31.85/p<0.0001
7	*D. thomasi*	LOGAbund= 2.837-0.002546*DOY-0.008081*Yr-0.09486*PC3	0.15	16.77/p<0.0001
8	*T. extensus*	LOGAbund= 1.416+0.004375*DOY-0.04074*PC3^2	0.19	34.62/p<0.0001

Table 2.10: Spearman correlation coefficients between the residual abundance of zooplankton and the wind field using the residual abundance generated from the year/day of year and chemistry models. *Significance denoted by a bolded p-value<0.05 with 95% confidence.

Species	Day	Wind Speed[a] (rs)	Wind Speed (p-value)	Day	Wind Direction[b] (r)	Wind Direction (p-value)
D.mendotae	Sample	-0.05	0.3766	Sample	0.11	**0.030***
	24 Hrs	-0.02	0.7542	24 Hrs	0.113	**0.025***
	48 Hrs	-0.12	**0.0338***	48 Hrs	0.1	0.056
H.glacialis	Sample	0.02	0.7658	Sample	0.064	0.310
	24 Hrs	0.04	0.5010	24 Hrs	0.13	**0.007***
	48 Hrs	-0.03	0.5561	48 Hrs	0.038	0.666
B.tubicen	Sample	0.07	0.2555	Sample	0.043	0.589
	24 Hrs	0.11	0.0685	24 Hrs	0.06	0.358
	48 Hrs	0.04	0.4621	48 Hrs	0.081	0.149
D.birgei	Sample	0.06	0.3463	Sample	0.063	0.319
	24 Hrs	-0.03	0.6544	24 Hrs	0.116	**0.021***
	48 Hrs	0.07	0.2241	48 Hrs	0.102	0.051
L.sicilis	Sample	-0.02	0.6909	Sample	0.062	0.326
	24 Hrs	0.03	0.6352	24 Hrs	0.08	0.159
	48 Hrs	-0.05	0.4423	48 Hrs	0.089	0.100
L.minutus	Sample	0.06	0.3216	Sample	0.103	**0.047***
	24 Hrs	0.06	0.2775	24 Hrs	0.117	**0.019***
	48 Hrs	0.08	0.1519	48 Hrs	0.029	0.783
D.thomasi	Sample	0	0.9440	Sample	0.102	**0.049***
	24 Hrs	0.04	0.5306	24 Hrs	0.029	0.785
	48 Hrs	-0.03	0.6340	48 Hrs	0.064	0.303
T.extensus	Sample	0.12	**0.0370***	Sample	0.056	0.410
	24 Hrs	0.13	**0.0245***	24 Hrs	0.069	0.253
	48 Hrs	0.14	**0.0212***	48 Hrs	0.098	0.064

[a]Pearson correlation cefficients using Analyse-it add-on for Excel
[b]Bivariate linear-circular association coefficients using Oriana 4.0

Table 2.11: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using year/day of year and wind. Computations were done in AI and the r^2 is based on the entire model. Yr-year, DOY-day of year, DOYxYr-an interaction term between the 2 predictors. Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= -3.237 + 0.03546*DOY + 0.03486*Yr - 2.4122E-007*DOYxYr + 0.08675*Spd48 + 0.001246*DirS - 0.0002767*Spd48xDir48	0.54	56.24/p<0.0001
2	*H. glacialis*	LOGAbund= 1.753 - 0.002374*DOY + 0.1611*Spd24 + 0.004597*Dir24 - 0.001007*Spd24xDir24	0.07	5.75/p=0.0002
3	*B. tubicen*	LOGAbund= 0.7884 + 0.002977*DOY + 0.1155*Spd24	0.09	14.11/p<0.0001
4	*D. birgei*	LOGAbund= -2.859 + 0.03215*DOY - 2.1328x10^{-7}*DOYxYr + 0.1108*SpdS	0.27	36.20/p<0.0001
5	*L. sicilis*	No model could be produced	---	---
6	*L. minutus*	LOGAbund= 2.311 - 0.001887*DOY + 0.06754*SpdS + 0.09267*Spd48	0.10	10.76/p<0.0001
7	*D. thomasi*	No model could be produced	---	---
8	*T. extensus*	No model could be produced	---	---

Table 2.12: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using chemistry and wind. Computations were done in AI and the r^2 is based on the entire model. PC-principal component, Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 2.556 - 0.1648*PC2 - 0.1528*PC3 - 0.07561*Spd48	0.14	15.56/p<0.0001
2	*H. glacialis*	LOGAbund= 1.223 - 0.1388*PC3 - 0.09718*PC4 + 0.1697*Spd24 + 0.004238*Dir24 - 0.000912*Spd24xDir24	0.10	6.39/p<0.0001
3	*B. tubicen*	LOGAbund= 1.459 - 0.1696*PC1 - 0.187*PC3 + 0.1046*Spd24	0.17	19.34/p<0.0001
4	*D. birgei*	LOGAbund= 1.645 - 0.2366*PC1 + 0.4097*PC2 - 0.1718*PC3 - 0.106*PC4 + 0.002421*Dir48 - 0.0003716*Spd48xDir48	0.40	32.12/p<0.0001
5	*L. sicilis*	LOGAbund= 1.711 - 0.06733*PC4 + 0.0656*PC5 + 0.001468*DirS - 0.0002666*SpdSxDirS	0.06	4.95/p=0.0007
6	*L. minutus*	LOGAbund= 1.868 - 0.08215*PC4 + 0.07219*SpdS + 0.1004*Spd48	0.09	9.75/p<0.0001
7	*D. thomasi*	LOGAbund= 2.058 - 0.07305*PC3 + 0.0397*Spd24	0.06	6.35/p<0.0001
8	*T. extensus*	No model could be produced	---	---

Table 2.13: Stepwise multiple linear regression models to better predict zooplankton abundance in Harp Lake using year/day of year, chemistry and/or wind. Computations were done in AI and the r^2 is based on the entire model. Yr-year, DOY-day of year, PC-principal component, Spd-wind speed, Dir-wind direction, S-sample day, 24-24 hours prior to the sample day, 48-48 hours prior to the sample day, and Spd24xDir24-an interaction term between the 2 predictors. *These models are not included in Table 2.6 because they do not include all predictors (year/day of year, chemistry and wind).

Model #	Species	Model	r^2	Fstat/p-value
1	*D. mendotae*	LOGAbund= 1.905 + 0.02893*Yr-0.1261*PC3-0.06867*Spd48+0.001295*DirS	0.17	15.03/p<0.0001
2	*H. glacialis*	LOGAbund= $1.604-8.6698 \times 10^{-11}$*DOY^4+0.153*Spd24+0.003793*Dir24-0.0008904* Spd24*Dir24-0.1537*PC3	0.19	13.01/p<0.0001
3	*D.birgei*	LOGAbund= 2.842-0.06529*Yr-0.1292*PC1-0.246*PC3-0.1066*PC4-0.009998*Spd48^2	0.44	45.64/p<0.0001
4	*L.minutus*	LOGAbund= 2.723-0.002419*DOY+0.1141*PC2+0.06788*SpdS	0.09	9.82/p<0.0001
5	*L.minutus*	LOGAbund= 2.65-0.002402*DOY+0.01047*PC2+0.08737*Spd48	0.11	11.52/p<0.0001
6	*L.minutus**	LOGAbund= 2.218+0.09001*PC2+0.0617*Spd24	0.04	6.49/p<0.0001
7	*L.minutus**	LOGAbund= 2.148+0.1056*PC2+0.00141*DirS	0.05	7.49/p<0.0001
8	*L.sicilis**	LOGAbund= 1.886-0.0693*PC4-0.005608*SpdS^2	0.04	5.28/p<0.0001
9	*D.thomasi**	LOGAbund= 2.058-0.07305*PC3+0.0397*Spd24	0.06	6.35/p<0.0001

Table 2.14a: A summary of the MLR model breakdown for each predictor based on each of the 9 models in Table 2.13. Blank values indicate that SigmaStat did not compute.

Model	Species	Predictors	VIF	Individual r^2	Individual Tstat/p-value*	Model Fstat/p-value	Model r^2
1	*D. mendotae*	Yr	1.113	0.11	5.57/<0.0001	15.03/<0.0001	0.18
		PC 3	1.024	0.03	-3.159/0.0020		
		Spd48	**1.083**	**0.02**	**-2.23/0.0270**		
		DirS	**1.023**	**0.02**	**2.33/0.0210**		
2	*H. glacialis*	DOY[4]	---	0.11	-5.90/<0.0001	13.01/<0.0001	0.19
		PC 3	1.029	0.06	-4.22/<0.0001		
		Spd24	**7.169**	**0.00**	**-0.06/0.9542**		
		Dir24	**7.168**	**0.00**	**1.48/0.1387**		
		Spd24xDir24	**18.38**	**0.02**	**-2.61/0.0096**		
3	*D. birgei*	Yr	1.158	0.29	-10.67/<0.0001	45.64/<0.0001	0.44
		PC 1	1.053	0.02	-3.50/0.0005		
		PC 3	1.025	0.10	-6.81/<0.0001		
		PC 4	1.001	0.01	-3.02/0.0027		
		Spd48^2	**1.079**	**0.02**	**-2.51/0.0127**		
4	*L. minutus*	DOY	1.053	0.04	-3.34/0.0009	9.82/<0.0001	0.09
		PC 2	1.072	0.02	2.95/0.0035		
		SpdS	**1.069**	**0.03**	**2.95/0.0034**		

*These values were generated as the variable was included in the model.

Table 2.14b: A summary of the MLR model breakdown for each predictor based on each of the 9 models in Table 2.13.

Model	Species	Predictors	VIF	Individual r^2	Individual Tstat/p-value*	Model Fstat/p-value	Model r^2
5	*L. minutus*	PC 2	1.068	0.01	2.27/0.0237	6.49/0.0017	0.04
		Spd24	**1.068**	**0.03**	**2.78/0.0058**		
6	*L. minutus*	DOY	1.041	0.04	-3.34/0.0009	11.52/<0.0001	0.11
		PC 2	1.081	0.03	2.72/0.0070		
		Spd48	**1.068**	**0.04**	**3.86/0.0001**		
7	*L. minutus*	PC 2	1.003	0.03	2.76/0.0061	7.49/0.0007	0.05
		DirS	**1.003**	**0.02**	**2.68/0.0077**		
8	*L. sicilis*	PC 4	1.003	0.03	-2.66/0.0083	5.28/0.0056	0.04
		SpdS^2	**1.003**	**0.01**	**-1.85/0.0653**		
9	*D. thomasi*	PC 3	1.009	0.03	-3.04/0.0026	6.35/0.0004	0.06
		PC 4	1.000	0.02	-2.35/0.0195		
		Spd24	**1.009**	**0.01**	**2.00/0.0469**		

*These values were generated as the variable was included in the model.

Table 2.15: Summary table of the chemistry variables in Harp Lake, Ontario from 1980 – 2004. N=25 years.

Chemistry Variables	Annual Average	Data Range from 1980-2004 (lowest to highest)	Spearman Correlation between Data values and Year (rs, p-value)	TREND
Gran_Alk (mg/L)	3.48	2.84 – 3.98	0.44, p<0.0001	Increasing
Ca (mg/L)	2.85	2.65 – 3.06	-0.55, p<0.0001	Decreasing
Cl (mg/L)	1.94	0.79 – 3.14	0.87, p<0.0001	Increasing
Cond (µS/cm)	35.86	32.76 – 38.72	0.51, p<0.0001	Decreasing
DIC (mg/L)	1.51	1.20 – 1.98	0.08, p=0.2382	Slightly Increasing
DOC (mg/L)	3.80	3.47 – 4.10	0.23, p=0.0006	Increasing
Fe (µg/L)	63.57	35.91 – 124.70	-0.74, p<0.0001	Decreasing
K (mg/L)	0.52	0.46 – 0.57	-0.49, p<0.0001	Decreasing
Mg (mg/L)	0.88	0.80 – 1.02	-0.37, p<0.0001	Decreasing
Na (mg/L)	1.62	0.84 – 2.25	0.93, p<0.0001	Increasing
NH_4/NH_3 (µg/L)	10.23	0.50 – 25.38	0.61, p<0.0001	Increasing
NO_3/NO_2 (µg/L)	105.61	78.31 – 150.00	0.39, p<0.0001	Increasing
TKN (µg/L)	218.31	166.32 – 260.67	0.15, p=0.0246	Increasing
pH	6.29	6.12 – 6.61	0.65, p<0.0001	Increasing
TP (µg/L)	6.58	4.90 – 9.50	-0.60, p<0.0001	Decreasing
SiO_3 (mg/L)	1.45	0.93 – 1.91	0.65, p<0.0001	Increasing
SO_4 (mg/L)	7.01	5.86 – 8.45	-0.86, p<0.0001	Decreasing

Wind Condition	Wind Behaviour		Wind & Animal Result
Low Wind Speeds	Wind → Epi Meta Hypo	Wind is slow → →	- Animals are more abundant at lower wind speeds. - Animals can hold their position in the water and withstand the currents
High Wind Speeds	Wind → Epi Meta Hypo	Wind is fast → → Animals being upwelled Animals resisting being upwelled and being concentrated at one end of the lake	- Animals are less abundant at higher wind speeds. - Animals are either resisting being upwelled and are being concentrated at one end of the lake OR the animals are being upwelled.

Figure 2.1: Hypothetical wind dynamics in Harp Lake – A negative relationship between abundance and the predictor wind speed.
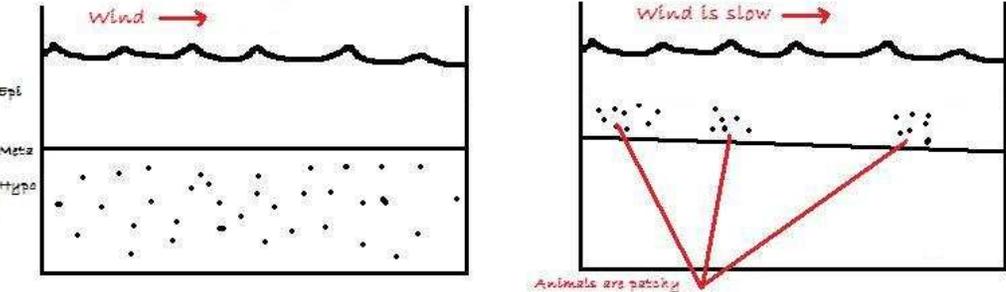
Wind Condition	Wind Behaviour	Wind & Animal Result
Low Wind Speeds		- Animals are less abundant at low wind speeds - Animals are able to withstand the current speeds and become patchy (hold their position in the water)
High Wind Speeds		- Animals are more abundant at high wind speeds - Animals are not able to withstand the current speeds and they are homogeneously distributed in the water column
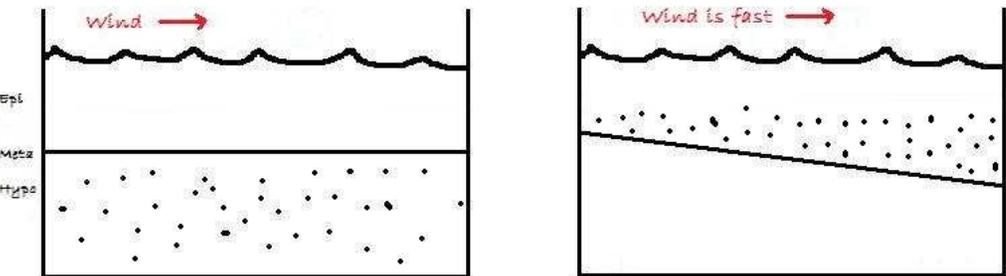
Figure 2.2: Hypothetical wind dynamics in Harp Lake – A positive relationship between abundance and the predictor wind speed.

Possibilities	Abundance Dynamics	Animal Result
Case 1 - Fast Animals		*Animals are moving* *Without wind, the currents are still in motion* *Animals that can swim faster than the current would be able to hold their position in the water and become patchy*
Case 2 - Slow Animals		*Animals are being moved* *Without wind, the currents are still in motion* *Animals that cannot swim faster than the current would not be able to hold their position in the water become homogeneously distributed in the water*
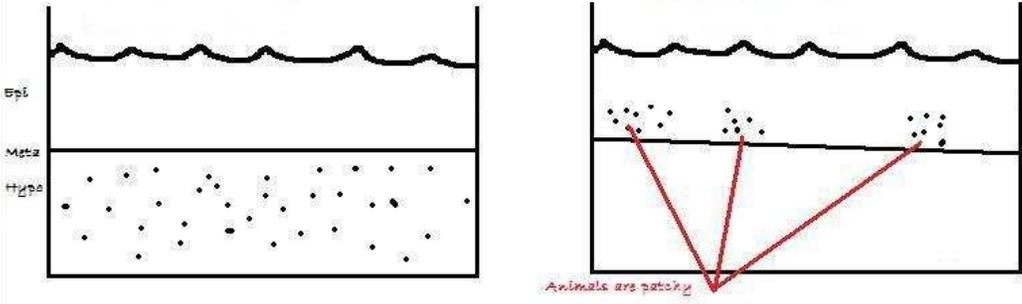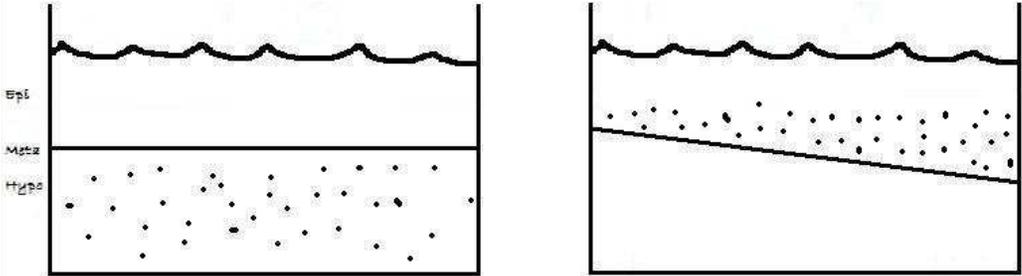
Figure 2.3: Hypothetical abundance dynamics in Harp Lake without wind.
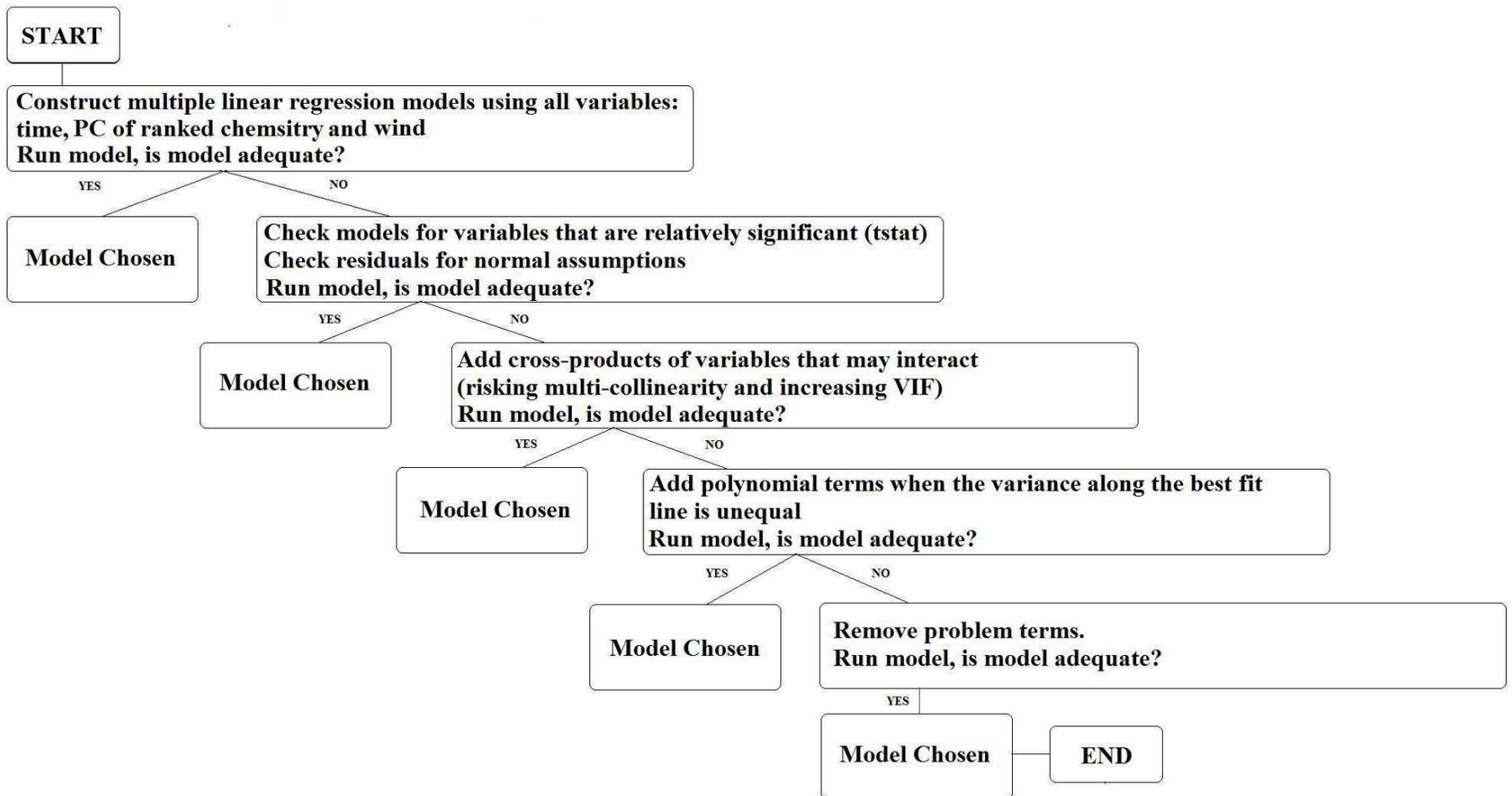
Figure 2.4: Flow chart of the decision making for the multiple regression models in order to better predict zooplankton abundance in Harp Lake, Ontario using year/day of year, chemistry and wind.
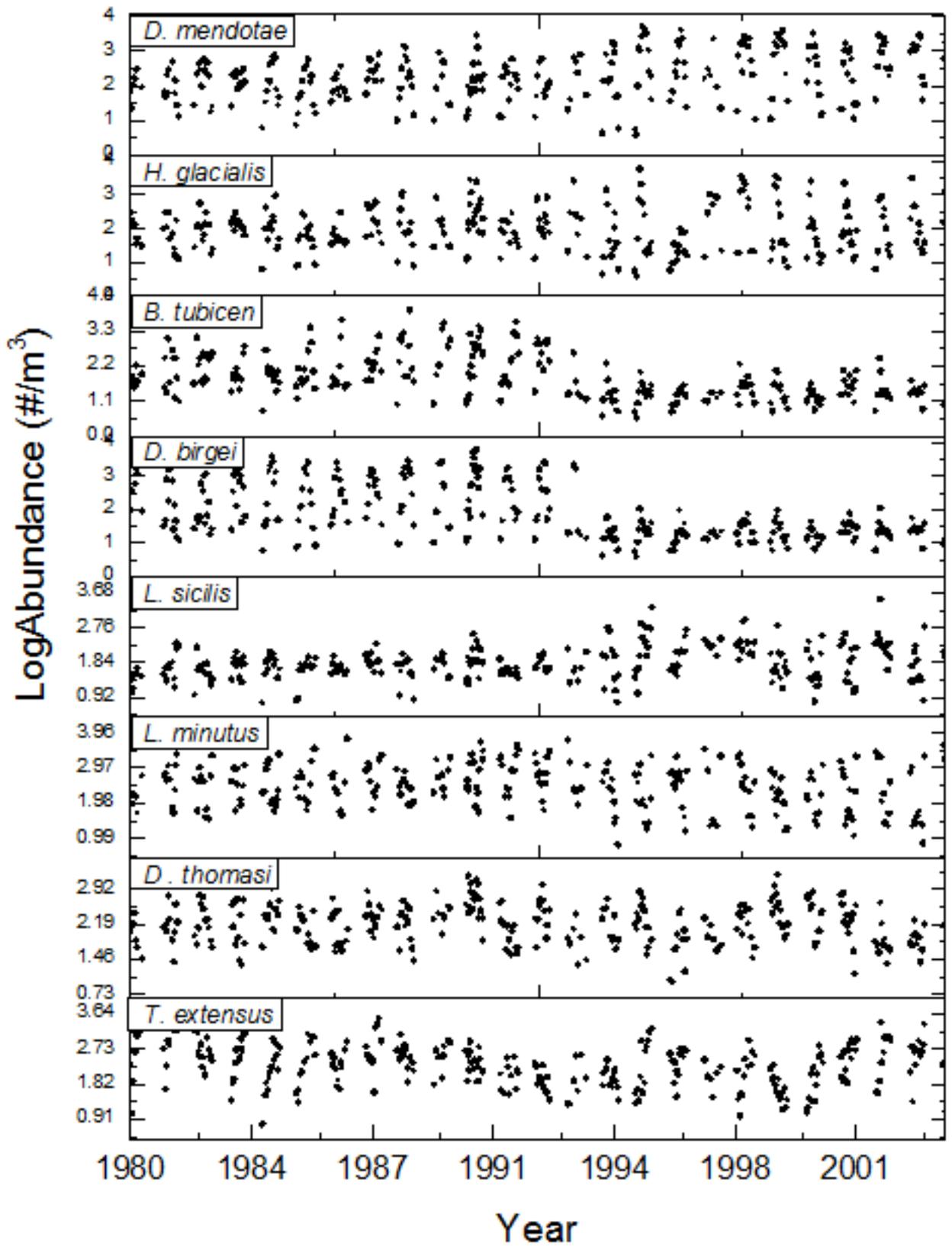
Figure 2.5: Long-term patterns in the chosen zooplankton species in Harp Lake, Ontario between 1980-2004.
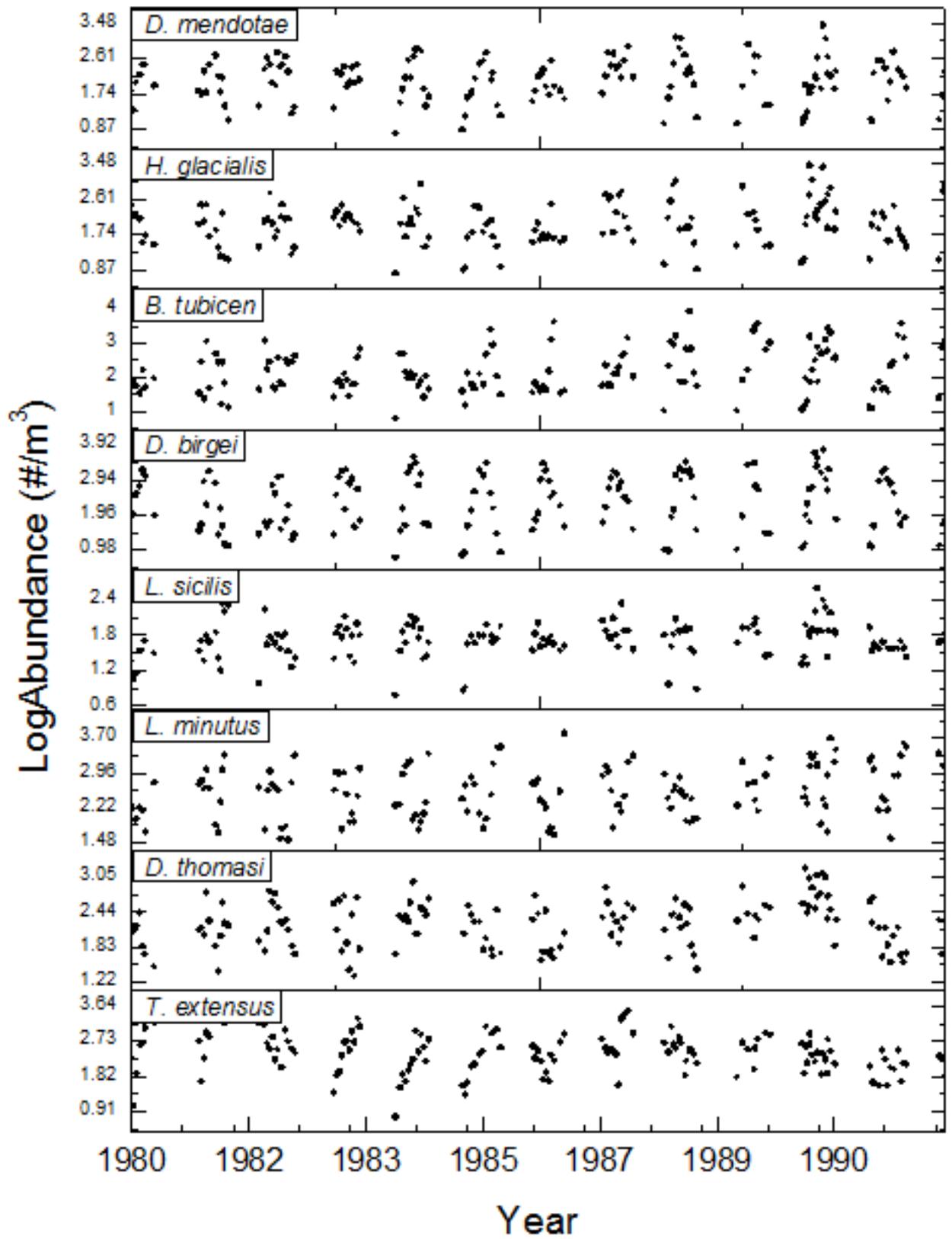
Figure 2.6: Long-term patterns in the chosen zooplankton species in Harp Lake, Ontario between 1980-1992 (pre-*Bythotrephes* presence).
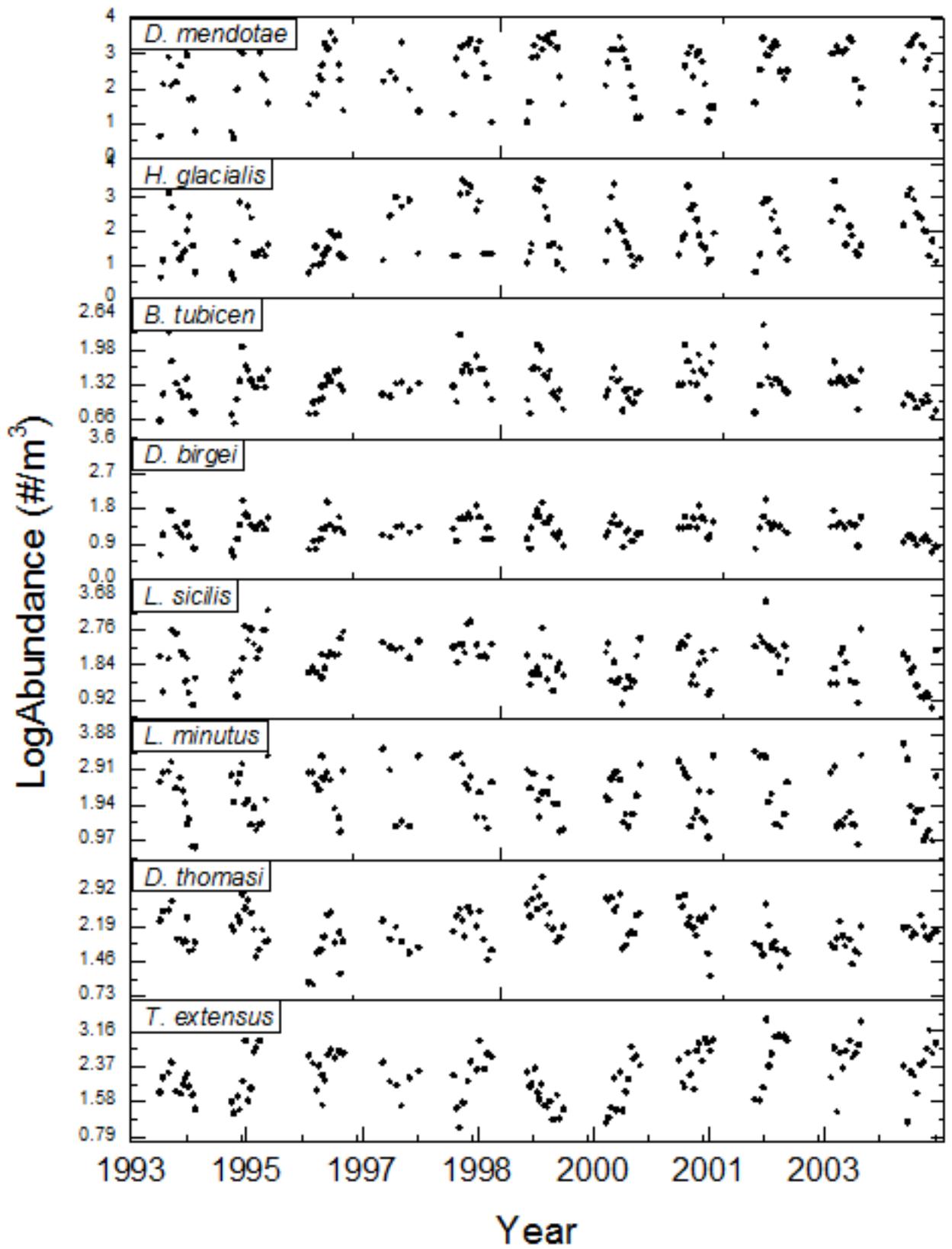
Figure 2.7: Long-term patterns in the chosen zooplankton species in Harp Lake, Ontario between 1993-2004 (post-*Bythotrephes* presence).
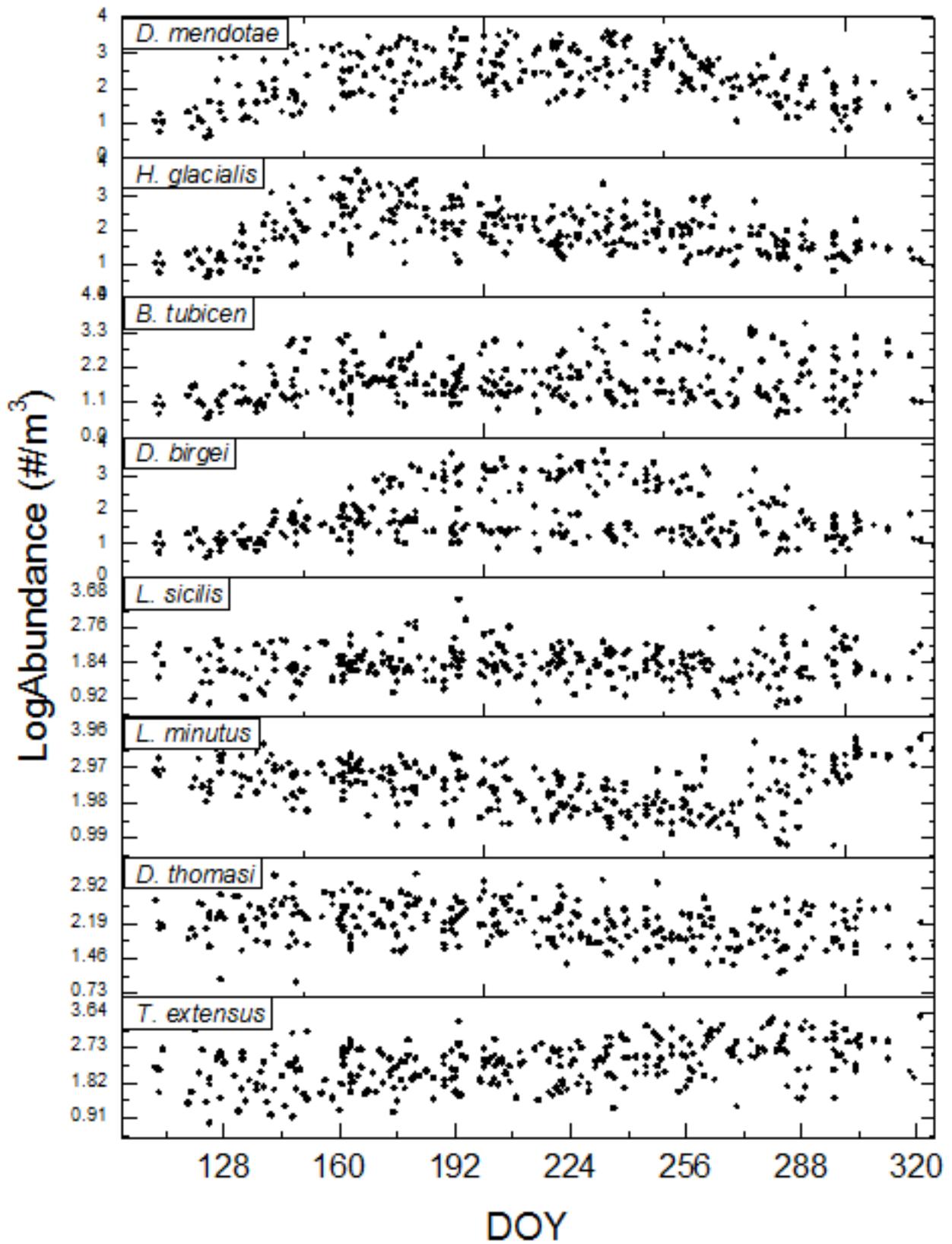
Figure 2.8: Long-term patterns in the chosen zooplankton according to day of year (DOY) in Harp Lake, Ontario between 1980-2004.
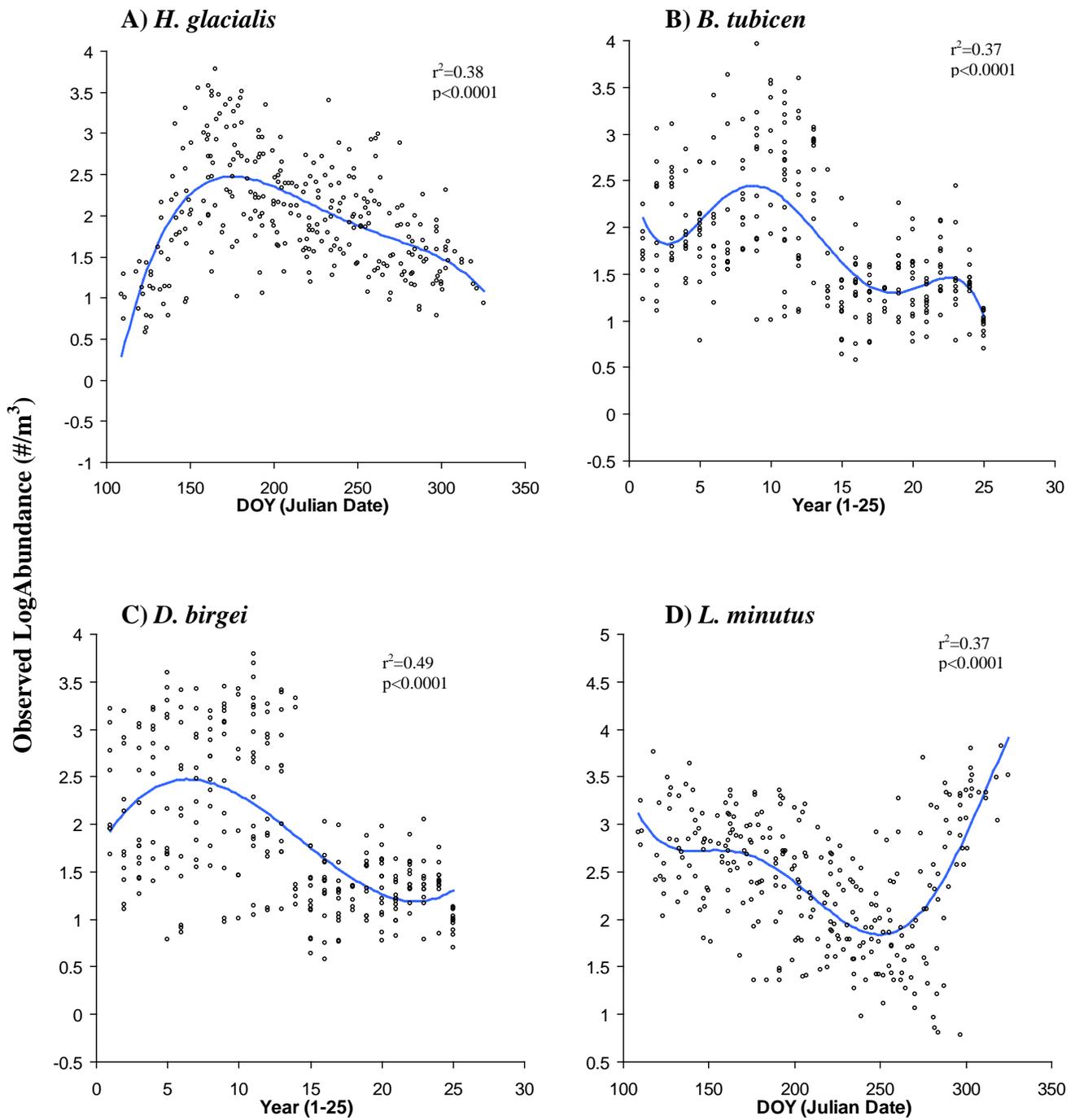
Figure 2.9a: Regression models that best fit the data using the abundance of zooplankton species using multiple steps: year (1-25) and day of year (Julian date).

E) *D. thomasi*
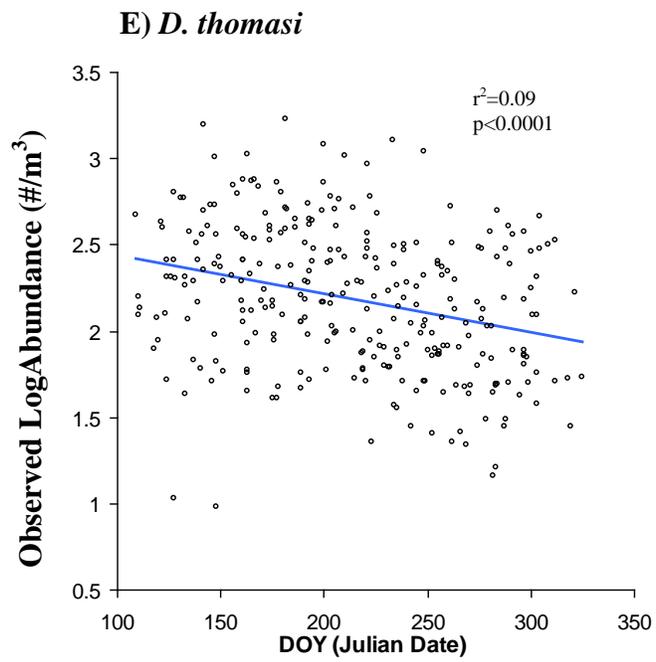
Figure 2.9b: Regression models that best fit the data using the abundance of zooplankton species using multiple steps: year (1-25) and day of year (Julian date).
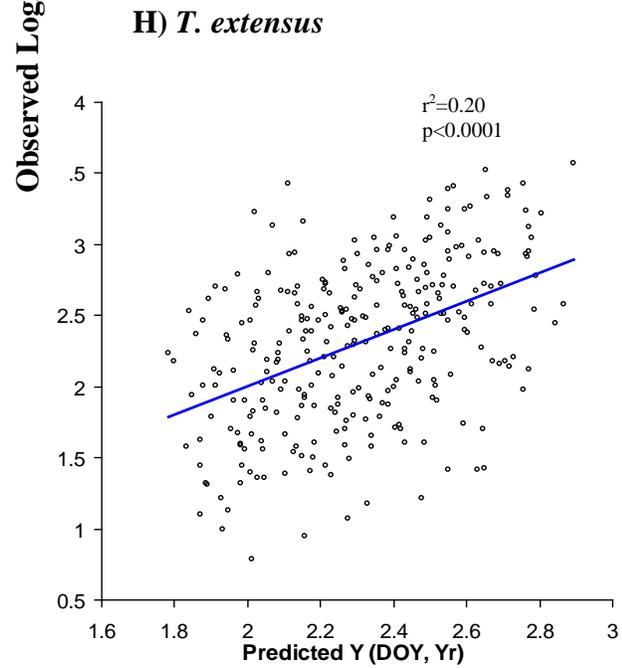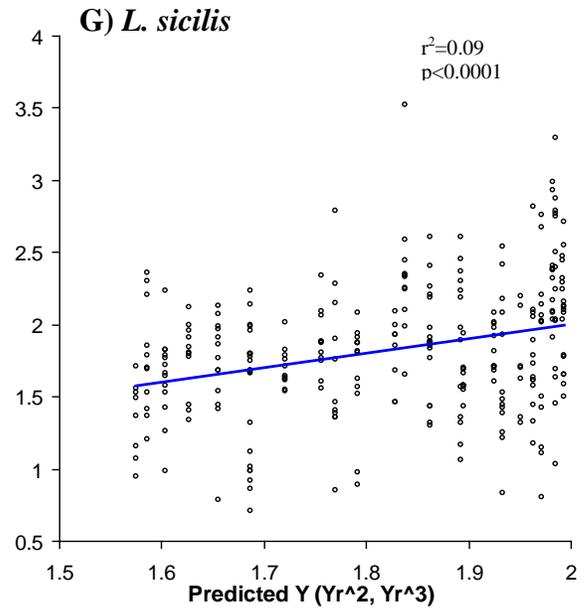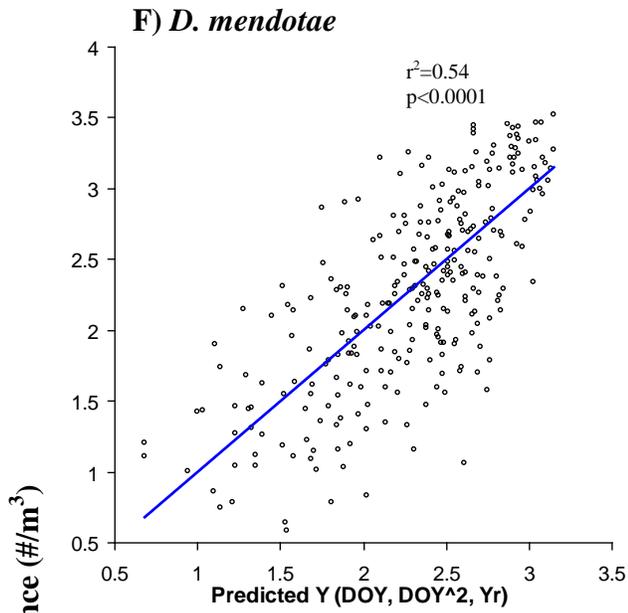
Figure 2.9c: Regression models that best fit the data using the abundance of zooplankton species using multiple steps: year (1-25) and day of year (Julian date).