

# Aerial dispersal of invertebrates on Svalbard and the influence of weather

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Master thesis in ecology

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# Abstract

A total of 20 water traps were set out at four locations around Longyearbyen on the High Arctic island Spitsbergen. The traps sampled aerially dispersed invertebrates during the summer of 2008. These trapping locations were in relatively close proximity to weather stations that recorded the local variations in weather. During the summer, the traps caught 102 Acari, 47 Collembola, 8 Aphidoideae and 5 Araneae as well as 10979 Nematocera, 177 Brachycera and 36 Hymenoptera. The effect of weather on aerial dispersal rates of invertebrates was studied and three general hypotheses were tested, that (1) aerial dispersal rates of wingless invertebrates will increase with wind speed, (2) aerial dispersal rates for all invertebrates will increase with temperature, (3) Collembola aerial dispersal will increase with relative humidity. To study the relationship between invertebrate catches and weather variables, canonical correspondence analysis, multiple regression and linear regression methods were used. Based on our results, we conclude that relative humidity has a positive effect on Collembola dispersal rates and the related hypothesis is accepted. The effect of wind speed on Collembola dispersal is negative and this is thought to be because of a negative relationship between wind speed and relative humidity. The hypothesis that increased wind speed has a positive effect on Collembola aerial dispersal is rejected. Brachycera and Hymenoptera respond positively to temperature and the related hypothesis is accepted. The explanation is thought to be the presence of temperature threshold values under which winged insects are not able to take flight. On average, warmer temperatures mean winged insects are able to spend more time flying. Wind speed has a negative relationship with Brachycera and Hymenoptera dispersal and this is thought to be because of an avoidance strategy where Brachycera and Hymenoptera avoid taking to the air or fly at lower altitude as flying into winds represents a risk of being swept away from a preferred habitat. Analysis did not find any significant relationships between Acari aerial dispersal and weather and due to errors in the study related to site location and hidden variables, no conclusions are drawn regarding Nematocera dispersal and how it is affected by weather. Catch densities of Aphidoideae and Araneae were considered too low for statistical testing.



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# 1 Introduction

Aerial dispersal of invertebrates has tremendous ecological importance in many ecosystems (Vanschoenwinkel et al. 2008) and a range of wingless invertebrates are adapted to and actively facilitate their own dispersal by wind, for example the European red mite *Panonychus ulmi* or the caterpillars of the Gypsy moth *Lymantria dispar* which are both able to drift on winds with the help of silken strands (Jeppson et al. 1975, Elkinton and Liebhold 1990). A review paper from 2002 on spider ballooning (Weyman et al. 2002), a term for the way some species of spiders travel through the air while attached to silk threads, suggests that for species inhabiting arable farmlands, ballooning evolved primarily as a risk spreading strategy to maximise survival in unpredictable habitats. This explanation pertains to one group of organisms (spiders) in one general habitat (arable farmlands), but aerial dispersal could benefit flightless arthropods in High Arctic habitats in much the same way. Svalbard is a High Arctic archipelago north of Norway between 74° and 81°N latitude and 10° and 35°E longitude (Hisdal 1998). On Svalbard, habitats are often fragmented. On a large scale, suitable habitats may be broken up by fjords, mountains or glaciers. On a smaller scale relevant to insects and other terrestrial invertebrates, soil may break up when water in the ground expands as it freezes or a habitat may be rendered unsuitable by a change in the direction of a melt water stream (Leinaas 1999). The latter is a common occurrence during summer on the west coast of the island Spitsbergen as streams of melt water flowing down from the mountains into the valleys may change their paths from year to year and also within seasons. Permafrost prevents drainage of water into the soil and such streams may have great effect on the conditions in the active layer (pers. obs.). On Svalbard and elsewhere, aerial dispersal, both passive and by those capable of controlled flight, is important for a number of potential reasons. For invertebrates inhabiting unstable or fragmented habitats, mobility and the ability to disperse will have an important effect on population dynamics. The ability to passively disperse by air could facilitate gene flow between populations or enable the re-colonization of habitat islands where the species has gone extinct. Also, aerial fallout has been credited for being able to sustain species inhabiting habitats poor in sustenance by transfer of organic detritus and prey species from richer neighbouring habitats (Edwards 1987). Finally, long distance aerial dispersal from mainland Europe to Svalbard by visiting Lepidoptera is known to have occurred (Coulson et al. 2002). Long distance aerial dispersal including passive dispersal of invertebrates like Acari, Collembola, Araneae, Rotifera, Tardigrada or

Nematoda, may have played an important part of the re-colonization of the Svalbard islands since the deglaciation after the last ice age. The majority of the Svalbard invertebrate fauna consist of species with wide, circumpolar distributions while endemics are relatively few and few if any species are thought to have survived the last glaciation peak on Svalbard *in situ* (Coulson 2000). In order to shed light on these mysteries as well as others, aerial dispersal has to be studied.

Acari is one of the numerically dominant groups in the mesofauna on much of the west coast of Spitsbergen (Coulson et al. 1996). Outside Svalbard, several Acari species are known to promote their dispersal by winds, particularly ballooning members of the Tetranychidae family (spider mites) (Brandenburg and Kennedy 1982), some predatory mites of the Phytoseiidae family (Johnson and Croft 1981, Jung and Croft 2001) and some of the plant parasitic members of the Eriophyidae family (gall mites) (Bergh and McCoy 1997). A study recovering aerial fallout from snow in West Virginia found a range of Acari from different taxa. Out of a total of the 163 Acari found in the study, 88 were eriophyoids while the remaining 75 represented 29 different species from more than 11 different families (Zhao and Amrine 1997).

Collembola is also a numerically dominant group from the west coast Spitsbergen mesofauna (Coulson et al. 1996). Although there are fewer studies on aerial dispersal of Collembola than there are on Acari, there are studies reporting catches of aeriually dispersed Collembola. One such study from the late 1960s used large nets to sample invertebrates at Point Barrow and Cape Thompson during the summers of 1966 and 1969. Although Collembola were part of the catch, their abundance in the catches was low (Gressitt and Yoshimoto 1974). As a group, Collembola are generally susceptible to mortality from desiccation because most species have water permeable cuticles which cause them to lose body water to the atmosphere through passive osmosis when conditions become dry (Verhoef and Witteveen 1980). It has been suggested that this vulnerability makes them poor aerial dispersers as an adult Collembola riding the winds would be likely to experience hostile conditions too dry to survive (Leinaas 1999). However, a recent study on Collembola aerial dispersal on the Antarctic Peninsula showed that Collembola are dispersed by air and that they are able to survive it. This study used water traps to sample Collembola falling out of the air and all of the nine individuals caught were alive when collected (Hawes et al. 2007).

Aerial dispersal of both Acari and Collembola has been documented on Svalbard. A study sampling aerial fallout on the Midtre-Lovenbre glacier foreland in Kongsfjorden caught both Acari and Collembola, although catch numbers were low. On the foreland, ten water trays sampled aerial fallout in June and July 2003. These trapped six Acari and two Collembola in total (Hawes 2008). An earlier study which did fieldwork at the same glacier foreland in July and August 2001 sampled the air using sticky traps which were set up at seven sites along a transect, ranging from a distance of nearly 1,5 kilometres away from the glacier for the site furthest away to a mere 15 metres distance from the glacier at the closest site. This study failed to catch any Acari or Collembola, but caught Araneae at every site across the foreland (Coulson et al. 2003). These studies may indicate that aerial dispersal of Acari and Collembola are rare events, but the location for the studies may also have been unsuitable. On the foreland, katabatic winds flowing down from the glacier meant that the prevailing wind direction was away from the foreland towards the fjord (Svendsen et al. 2002, Hawes 2008). Also, compared to tundra habitats, the glacier foreland is a generally barren habitat with sparser vegetation the closer you get to the glacier (pers. obs., Hodkinson et al. 2004). Although a previous study on the invertebrate community assembly of the Midtre-Loven foreland found Collembola and mites at all sites across the foreland (Hodkinson et al. 2004), densities were likely lower than one would expect in richer and more vegetated habitats like moist tundra. Collembola densities can vary drastically with habitat quality and densities approaching as many as 800,000 m<sup>-2</sup> individuals have been observed on Svalbard in wet *Carex* tundra (Coulson 2000). Vegetation cover can act as a thermal insulator, preventing heat conduction into the soil beneath (Coulson et al. 1993). Because higher temperatures cause increased rates of evaporation (Navarra 1979), reduced vegetation cover may be expected to lead to drier soil conditions. Drier conditions would generally decrease quality of the foreland habitat to Collembola (Verhoef and Witteveen 1980). Studies show Acari are generally less vulnerable to changes in moisture conditions than Collembola (Hodkinson et al. 1996a), but the barren glacier foreland may also represent a poor habitat to Acari through other factors like general decreased availability of sustenance and poor soil quality. If long range dispersal is rare event and Acari and Collembola density on the foreland is low, a low rate of aerial dispersal is to be expected. However, long range dispersal by wind may still be possible by repeated short range aerial dispersal. Such dispersal could also be behaviourally promoted, for example by climbing vegetation in order to become more wind exposed or by jumping into the air. Depending on the species, such a mode of dispersal could be difficult or dangerous

across potentially hostile habitats like the glacier foreland, causing them to change their behaviour or die at the fringes of the habitat so that they no longer promote their own dispersal. Although this is speculation, it illustrates how aerial dispersal could facilitate dispersal over long distances even if it is highly influenced by local conditions and average dispersal distance is short. Although previous studies suggest that aerial dispersal of Collembola and Acari are relatively rare occurrences, there is reason to believe that such suggestions may underestimate the overall rates of such dispersal and that it may be a more regular occurrence depending on habitat and weather conditions.

Of insects on Svalbard, Diptera are the most species diverse, particularly the family Chironomidae (Coulson 2000). These have a larval stage in freshwater and utilize melt water rivers as larval habitats (Lods-Crozet et al. 2007). A study from France showed that distance to water bodies is the main factor explaining the spatial distribution of Chironomidae and densities and species compositions changed with distance from the streams from which they emerge from the larval stage (Delettre and Morvan 2000).

The aim of this research was to answer one of the most basic questions about aerial dispersal of invertebrates. How is aerial dispersal of invertebrates on Svalbard affected by changes in weather? We had 3 general hypotheses, (1) aerial dispersal rates of wingless invertebrates will increase with wind speed, (2) aerial dispersal rates for all invertebrates will increase with temperature, (3) Collembola aerial dispersal rates will increase with relative humidity.

## 2 Materials and methods

### 2.1 Sites

Fieldwork took place in the period between 21<sup>st</sup> of June and 9<sup>th</sup> of September in 2008 at five locations around Longyearbyen (table 1, fig. 1). These sites were chosen because they are all in relatively close proximity (hundreds of metres) to weather stations that recorded the local weather conditions at each site throughout the fieldwork season.

Table 1 – Field sites and their GPS coordinates

Site	Description	GPS Location (WGS 84)	
1	Jansonhaugen	N78°10.447	E016°18.817
2	Colesdalen	N78°06.923	E015°01.437
3	Adventdalen	N78°12.181	E015°49.714
4	Hotellneset	N78°14.964	E015°24.016
5	Breirosa	N78°09.734	E016°02.217



Fig. 1 - Map showing locations of Jansonhaugen (site 1), Colesdalen (site 2), Adventdalen (site 3), Hotellneset (site 4) and Breirosa (site 5).

Site 1 was located on Jansonhaugen, a small hill at the end of Adventdalen at about 16 kilometres distance from Longyearbyen. A weather station is located on top of the hill some hundreds of metres from the site location. Elevation at the location of the site is approximately 150 metres above sea level. During the fieldwork season, the site was rocky and windy with little vegetation. The Jansonhaugen weather station recorded climate variables every hour for a total of 24 recordings per day uninterrupted throughout the fieldwork season.

Site 2 was close to the shore in Colesdalen, not far from some abandoned buildings related to the history of Russian coal mining. The area was relatively rich in vegetation compared to the other sites and was dominated by grasses. Boat was used to get to the site, but problems with the boat led to a series of failed attempts before the site was finally established. Two of the traps broke at sea. Further problems with transportation made this site comparatively hard to get to and when catches were finally collected, they were already decomposing in the water. For this reason and because samples were collected rarely, no data from site 2 is included in the results.

Site 3 was close to an old northern lights station in Adventdalen where there is a weather station. The location of the site is in the middle of Adventdalen about four to five kilometres away from Longyearbyen at an estimated elevation between 3 and 10 metres above sea level. The site was set up on the 21<sup>st</sup> of June and taken down on September 1<sup>st</sup>, 2008. The area was relatively dry with vegetation dominated by *Salix polaris*. At the old northern light station, climate data was recorded every ten minutes. However, the weather station stopped recording between august 14<sup>th</sup> at 02:40 in the morning and resumed operation on august 19<sup>th</sup> at 07:18 in the morning.

Site 4 was close to the Isfjorden shoreline at Vestpynten to the west of Longyearbyen Airport. A weather station at the airport recorded weather during the fieldwork season. The site was in a west-facing slope above a rocky beach. At the site, distance from the sea was roughly estimated to be between 30 and 40 meters. Elevation was roughly measured to be about four to six meters above sea level. The site was in a tundra habitat dominated by grass and mosses. The site was set up on the 21<sup>st</sup> of June and taken down on the 2<sup>nd</sup> of September 2008.

Site 5 was located above mine 7 on the mountain Breinosa. The location of the site is at approximately 400 meters elevation. The mountain side where the site was located slopes upwards towards the south-east summit which is covered by the glacier Foxfonna. Melt water

produced by the melting snow further up on the mountain ran through the site. This made site 5 comparatively the wettest. The vegetation was dominated by mosses. Weather data from this area was recorded from a weather station at the nearby EISCAT Svalbard Radar station, also located on Breinosa. This weather station recorded climate variables every five minutes and did so uninterrupted throughout the fieldwork season.

## 2.2 Traps

In order to catch aerial fallout at each site, hard plastic boxes were used as traps. Five such traps were put out at each site. These were 26 cm high with a catch surface of 44 x 31 cm. The edges of the boxes had a curved lid with a smear of Vaseline to stop arthropods from climbing in. To keep the traps from moving during gales, four plastic bags per trap filled with rocks were used. These were located outside the traps and secured to them by strings attached through holes drilled through the lids at each corner (fig. 2). The traps were filled with water and enough detergent to break the water surface tension. For most sites, regular tapwater from UNIS was used. The exception was site 1 where freshwater from a meltwater river at the foot of the Jansonhaugen hill was used instead. To collect water from the stream, plastic bottles were used. Great care was taken to fully submerge the bottles under water to minimize the risk of catching invertebrates on the water surface.

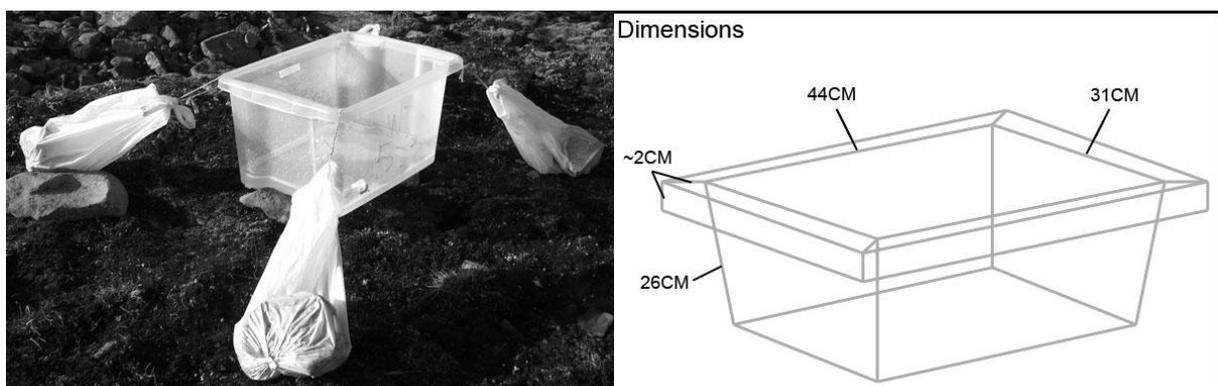


Fig. 2 - Picture and an illustration of a water trap, showing the approximate dimensions in centimetres.

Water traps at each site were sampling for a number of days before the water in them was collected and the traps were refilled. These periods of days differ in timing and duration at each site, but lasted on average between one and two weeks (table 2).

Table 2 - Table shows sampling periods at sites.

	Site 1 - Jansonhaugen	Site 3 – Adventdalen	Site 4 - Vestpynten	Site 5 - Breinosa
Period 1	Jun 25 - Jul 10	Jun 21 - Jun 30	Jun 21 - Jul 2	Jun 24 - Jul 9
Period 2	Jul 11 - Jul 16	Jul 1 - Jul 9	Jul 3 - Jul 9	Jul 10 - Jul 15
Period 3	Jul 17 - Jul 24	Jul 10 - Jul 15	Jul 10 - Jul 17	Jul 16 - Jul 23
Period 4	Jul 25 - Aug 5	Jul 16 - Jul 23	Jul 18 - Jul 23	Jul 24 - Aug 6
Period 5	Aug 6 - Aug 27	Jul 24 - Aug 6	Jul 24 - Aug 7	Aug 7 - Aug 18
Period 6	Aug 28 - Sep 9	Aug 7 - Aug 18	Aug 8 - Aug 19	Aug 19 - Aug 28
Period 7		Aug 19 - Aug 26	Aug 20 - Sep 2	Aug 29 - Sep 2
Period 8		Aug 27 - Sep 1		

## 2.3 Lab work and identification

At the end of each sample period, the content of each trap was poured into a bottle and brought to the lab. In the lab, water from the traps was filtered through a fine 150µm mesh. That which did not pass through the filter was then carefully transferred to glass containers using a squirt bottle with alcohol. These catches were stored on alcohol until they were processed under light microscope. Sites and periods were processed in random order and invertebrate specimens were identified and counted.

## 2.4 Data processing

Weather data from the sites at the old northern lights station, Jansonhaugen and Breinosa was downloaded from the websites of the University Centre in Svalbard ([www.unis.no](http://www.unis.no)) while the weather data from the airport at Vestpynten was downloaded from the web pages of the Norwegian Meteorological Institute (Meteorologisk Institutt). Collected weather data was imported into Microsoft Excel 2007. To describe the different sites and compare the weather at different locations, daily values for a set of climate variables were used. The comparable variables that were recorded at all sites were maximum, average and minimum temperature (°C), average millibars pressure (mbars), average and maximum wind speed (m/s), average relative humidity (%) and wind direction (degrees). For weather comparisons, daily minimum, average and maximum values from all variables except wind direction were compared. Before wind direction was used, the values were sorted to variables describing the general wind directions north, east, south or west. For example, in the wind-direction column, a non-zero value which was either the same as or greater than 315 or lower than 45 would be

registered as a 1 in the column for wind direction north and 0 in the other wind direction columns. Values from 45 and greater, but lower than 135, would be registered as a 1 in the column for wind direction east. Values from 135 and greater, but lower than 225, would be registered as a 1 in the column for wind direction south. Values from 225 and greater, but lower than 315, would be registered as a 1 in the wind direction west column. The proportion of wind coming from the different directions was then calculated by dividing the sum of observations of wind coming from any one direction with the total amount of wind observations across a given time span. These values were then multiplied by 100 to get percentages. When describing or comparing weather at different sites, data from the period 15<sup>th</sup> of June until the 15<sup>th</sup> of September was used.

To explain invertebrate counts with weather data, weather minimum, maximum and average values for periods were used rather than for days (table 2) because the exact date when any one invertebrate fell in the trap was not known, only the time or period the traps had been out when the invertebrate was caught. In addition to the climate variables, the variables period length and number of traps were added to the data set. Number of traps is the amount of traps that were out at any one site during any period. This number was usually five, but there were occasions when samples were lost. A total of 4 traps content was lost due to accidents during collection or processing. One was lost at site 3 in the fourth period from July 16<sup>th</sup> to July 23<sup>rd</sup>. Two were lost in an accident at site 4 during the sixth period from August 8<sup>th</sup> to August 18<sup>th</sup>. One was lost at site 5 in the second period from July 10<sup>th</sup> to July 15<sup>th</sup>. Wind direction data was not used in statistical analysis with invertebrate catches because wind direction at sites was influenced by local conditions and was not considered comparable (fig.7).

## **2.5 Statistical methods**

### **2.5.1 Shapiro-Wilk**

Before being used in multiple regressions, variables were tested for normality. To do this, Shapiro-Wilk tests were carried out in the program Past, version 2.03. Shapiro-Wilk test is a test for normality which tests the null hypothesis that a sample came from a normally distributed population (Shapiro and Wilk 1965). In attempts to achieve normality, some variables were transformed using simple functions in Excel 2007. Of the explanatory

variables, Period length was  $\log(x)$  transformed and average atmospheric pressure was  $\cos(x)$  transformed.

## 2.5.2 Canonical correspondence analysis

Canonical Correspondence Analysis (CCA) was done in R using the Vegan library. CCA is a multivariate descriptive method for data analysis and exploration which is related to PCA (ter Braak 1986). The method requires a data matrix of non-negative elements from which it can calculate an ordination plot with distances between variables from the dataset. In CCA, the whole dataset consists of two datasets, in this case the data set containing the climate variables and the dataset containing the counts for the plant leaves and different taxa. The method calculates the distance between catches and climate variables in a multi-dimensional space. In this multidimensional space, a count variable will have shorter distance to climate variables it responds more to than climate variables it responds less to. It will also be closer to other count variables it is similar to in response and abundance. This multi-dimensional arrangement of count and climate variables is finally represented in a two or three dimensional ordination plot. This reduction of dimensions compromises the accuracy of the spatial arrangement of count and climate variables, but generally it creates a plot where count variables are arranged closer to the climate variables which explain them. In our analysis, the explanatory variables are minimum, average and maximum temperature, average and maximum wind speed, average atmospheric pressure, average relative humidity, period length and the number of traps. The response variables were plant leaves, Acari, Collembola, Brachycera and Hymenoptera. Collembola includes all Collembola species counts and was chosen rather than individual species because separating the species would create several variables with comparatively low abundance. Aphidoideae and Araneae were also excluded because of their low abundance with count numbers generally regarded as too low for statistical analysis. Nematocera were excluded from the analysis because their abundance is many times that of any other taxa. Their inclusion into the plot would push the other taxa away. In addition to the effect variables may have on each other, inclusion of many can make ordination plots seem cluttered.

### **2.5.3 Regression modelling**

To study interactions between climate variables and count variables, different kinds of regression analysis were done in R, version 2.11.1. These are methods for modelling and analysing the relationships between independent (climate) and dependent (count) variables. Such analysis can tell us which climate variables explain the variance in a count variable and how the count variable may be expected to change when a climate variable changes. To create regression models predicting aerial dispersal of different taxa, multiple regression and zero-inflated poisson regression was used. For hypothesis testing of whether the relationship between a climate and a count variable was positive or negative, linear regression was used.

#### **Multiple regression**

Multiple regression assumes normally distributed data. When data was not normally distributed, attempts to achieve normal distributions were done through transformations. To find the best fit models, backwards elimination and forward stepwise regression was performed. This was automated by the StepAIC function in R from the MASS library.

#### **Zero-inflated regression**

Zero-inflated regression is a multiple regression method optimized for data where the dependent variables are poisson distributed and zero-inflated. It creates two models, one that explains and predicts the count data and one which explains and predicts the number of zeros in the dataset. The method may be particularly suitable when there is a source of “certain zeros”, for example if temperatures below a certain threshold value always cause zeros in the count data. Manual backwards elimination and forwards stepwise regression was used to find the best fit models. Also, models with significant predictors in the zero-inflation model were preferred. To do zero-inflated regression in R, the zeroinfl function from the pscl library was used.

## **Vuong test**

To test whether or not the zero-inflated regression models were better than their standard poisson regression model counterparts, Vuong closeness tests were performed using the `lrtest` function in R from the `lmtest` library. A Vuong test compares the predicted probabilities of two models and determines which is the closest or “superior”. It does not tell you which model is truer. After zero-inflated regression models had been made, Vuong tests were made against standard poisson regressions using the exact same variables.

## **Linear regression**

To study single relationships between one count and one climate variable at a time, single linear regressions were used. Linear regression assumes that the response in a count variable to a climate variable is linear, but was also used when visual analysis showed that responses were not. Rather than describe the response of a count variable, linear regression was used for hypothesis testing to check whether a relationship between a climate and count variable was negative or positive. Generally, describing a non-linear response with linear regression leads to underestimation of the significance of the relationship rather than overestimation because the non-linear response will not fit the linear response line as well as linear data might. This is preferable to overestimation errors because it is less likely to find significant positive or negative relationships which are not true. However, using regression to test the relationship between only one independent and one dependent variable at a time may also overestimate the importance of the independent variable in explaining the variance in the dependent variable. However, linear regression was considered reliable enough to tell whether or not a negative or positive relationship between a dependent and an independent variable was significant.

## **2.6 Statistical analysis**

### **2.6.1 Collembola**

The average catch per trap per day for each period was calculated for the two most abundant species, *Agrenia Bidenticulata* and *Sminthurides malmgreni*. This was done by dividing the

total catch of each species from each period with the number of traps and the amount of period days. These numbers were compared (fig. 10).

Collembola count totals were included in CCA analysis (fig. 11).

A model predicting Collembola aerial dispersal was made using zero-inflated poisson regression. The model used the total count of Collembola found in catches and related them to climate variables. To see if the zero-inflation poisson regression model was superior to a standard poisson regression model using the same variables, a Vuong test comparing the two was performed.

Relationships were further analysed and hypotheses were tested by performing linear regressions between catch totals and environmental variables (fig.17).

### **2.6.2 Acari**

The average catch per trap per day for each period was calculated for total Acari (fig. 10).

A model for total Acari aerial dispersal was made using multiple regression. Before regression, the total Acari count variable was transformed with a  $\log(\sqrt{x+1})$  transformation and tested for normality using the Shapiro-Wilk test. The best fit model was found using stepwise regression.

To test hypotheses, linear regressions were made between Acari totals and climate variables. To uncover further significant relationships between, linear regressions were also carried out between Acari totals and climate variables not connected with any of our hypotheses. Of these tests, insignificant results were not documented.

### **2.6.3 Nematocera**

Nematocera were sorted and counted under light microscope. The vast majority (>90%) of Nematocera catches were made up of Chironomid midges (personal observations, not documented).

Nematocera aerial dispersal was modelled using multiple regression. Before regression, the total Nematocera count variable was transformed with a  $\log(x)$  transformation. The count

variable was then tested for normality with a Shapiro-Wilk test. The best fit multiple regression model was found using stepwise regression.

To test the hypothesis that there is a positive relationship between Nematocera dispersal and temperature, linear regressions were done between Nematocera totals and temperature variables. In an attempt to uncover further significant relationships, linear regressions were also carried out between Nematocera totals and climate variables not connected with any of our hypotheses (fig. 13). Of these tests, results that were not significant are not documented.

#### **2.6.4 Brachycera**

Brachycera were sorted and counted under light microscope.

Brachycera aerial dispersal was modelled using multiple regression. Before regression, the total Brachycera count variable was transformed with a  $\log(x+1)$  transformation. The count variable was then tested for normality with a Shapiro-Wilk test. The best fit multiple regression model was found using stepwise regression.

To test the hypotheses that there is a positive relationship between Brachycera dispersal and temperature, linear regressions were done between Brachycera totals and temperature variables (fig. 13). In an attempt to uncover further significant relationships, linear regressions were also carried out between Nematocera totals and climate variables not connected with any of our hypotheses. From these tests, insignificant results are not documented.

#### **2.6.5 Hymenoptera**

Hymenoptera were sorted and counted under light microscope.

A model predicting Hymenoptera aerial dispersal was made using zero-inflated poisson regression. The model used the total count of Hymenoptera found in catches and related them to climate variables. To see if the zero-inflation poisson regression model was superior to a standard poisson regression model using the same variables, a Vuong test comparing the two was performed.

To test the hypotheses that there is a positive relationship between Hymenoptera dispersal and temperature, linear regressions were done between Hymenoptera totals and temperature

variables (fig. 13). In an attempt to uncover further significant relationships, linear regressions were also carried out between Hymenoptera totals and climate variables not connected with any of our hypotheses. From these tests, insignificant results were not documented.

### **2.6.6 Aphidoideae**

Invertebrates identified as Aphidoideae were counted under light microscope and noted. However, catch abundance was considered too low for statistical analysis (table 4).

### **2.6.7 Araneae**

Invertebrates identified as Araneae were counted under light microscope and noted (table 4). However, catch abundance was considered too low for statistical analysis.

# 3 Results

## 3.1 Weather at sites

Climate generally changed in the same way at the different weather stations, but with some variables changing more between sites within the same period of time than other variables.

Table 3 - Climate variable averages and standard deviations from each site.

<b>Climate at sites (15.06.08 - 15.09.08)</b>	<b>Site 1</b>	<b>Site 3</b>	<b>Site 4</b>	<b>Site 5</b>
<b>Atmospheric pressure average (mbars)</b>	<b>981.5</b>	<b>1008.9</b>	<b>1008.8</b>	<b>949.1</b>
Standard deviations	9.5	9.7	9.7	9.3
<b>Average temperature (°C)</b>	<b>3.7</b>	<b>4.9</b>	<b>5.1</b>	<b>1.3</b>
Standard deviations	2.2	1.8	1.7	2.4
<b>Relative humidity average (%)</b>	<b>83.1</b>	<b>75.7</b>	<b>76.5</b>	<b>86.3</b>
Standard deviations	8.7	8.3	10.0	8.6
<b>Wind Speed average (m/s)</b>	<b>4.4</b>	<b>4.3</b>	<b>4.0</b>	<b>3.2</b>
Standard deviations	1.9	1.9	1.9	2.0

### 3.1.1 Atmospheric pressure

For atmospheric pressure, differences between sites stem from differences in elevation rather than differences in distance between sites. Between the 15<sup>th</sup> of June and the 15<sup>th</sup> of September 2008, average pressure at site 3, located at an elevation of less than 10 metres above sea level, was 1008.9 millibars with a standard deviation of 9.7. The average millibars pressure at site 4, also located at less than 10 metres elevation, was 1008.8 with a standard deviation of 9.7. The average millibars pressure at site 1, at approximately 150 metres altitude, was 981.5 with a standard deviation of 9.5. The average millibars pressure at site 5, at approximately 400 metres altitude, was 949.1 with a standard deviation of 9.3. While differences in averages between different altitude sites are higher than the standard deviations within sites, the changes in pressure at the different sites are similar. An approximately 9 millibars increase over the course of a day at site 1 would also occur at site 3, 4 and 5 and changes in average millibars pressure between sites reflect one another.

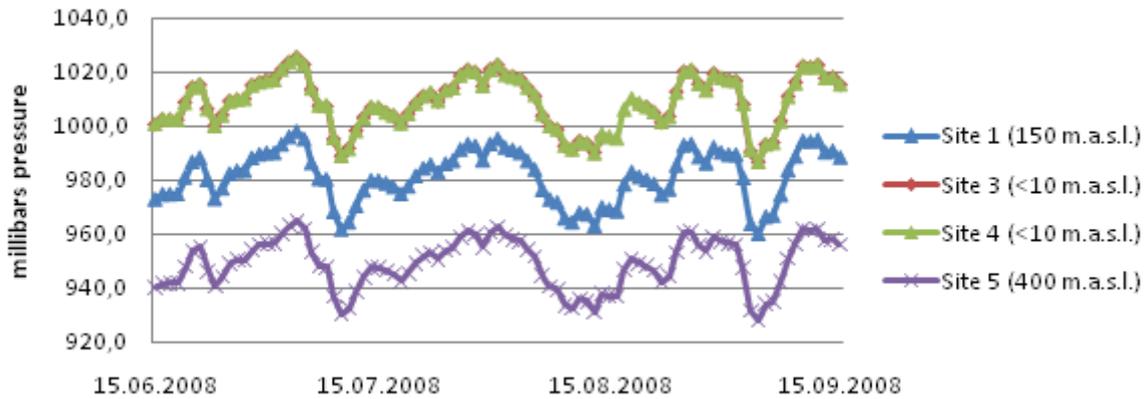


Fig. 3 - Average daily millibars pressure at all sites over time (dd.mm.year). Lines for Site 3 and 4, both located at altitudes below 10 metres above sea level, overlap.

### 3.1.2 Temperature

Temperature generally changed in similar ways across sites. The general trend across all sites was an increase in temperature from early in the season until late July and then a subsequent decrease in temperature into August.

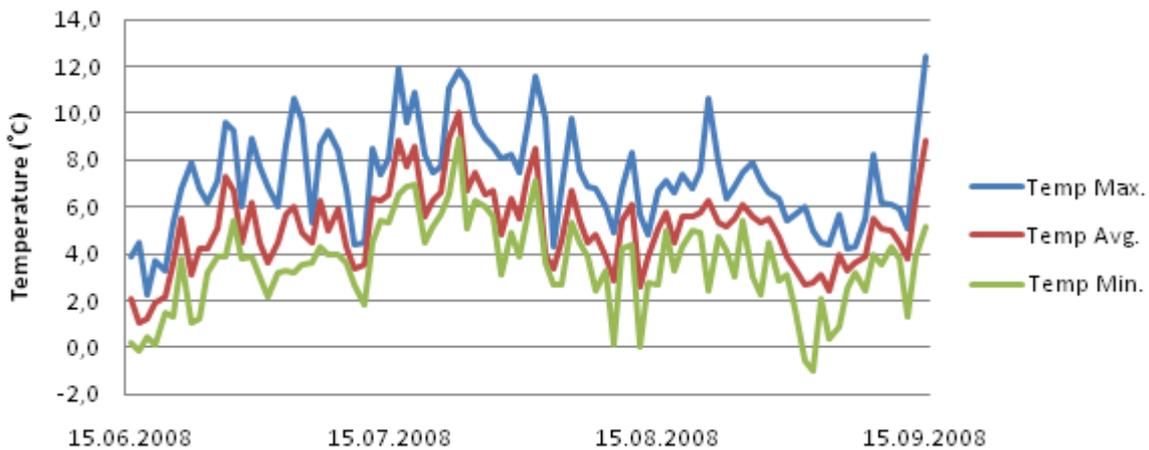


Fig. 4 - Maximum, average and minimum daily temperatures at Vestpynten over time.

Sites 1 and 5 at the highest altitudes had lower average temperatures than sites 3 and 4. From the 15<sup>th</sup> of June until the 15<sup>th</sup> of September, site 3 and 4 had average temperatures of 4.9 and 5.1 respectively. Sites 1 and 3 had average temperatures of 3.7 and 1.3 respectively. While average temperatures most days were lowest at site 5 and highest at site 3 or 4, there were exceptions. On November 3<sup>rd</sup>, site 5 had the highest minimum, average and maximum temperatures. Although site 1 was generally colder than site 3 and 4, there were days when the temperature at the three sites were similar. One such period lasted from the 24<sup>th</sup> until 29<sup>th</sup>

of July. Thus, unlike atmospheric pressure readings, a recorded value at one site could not be assumed to always accurately predict a temperature value at a different site.

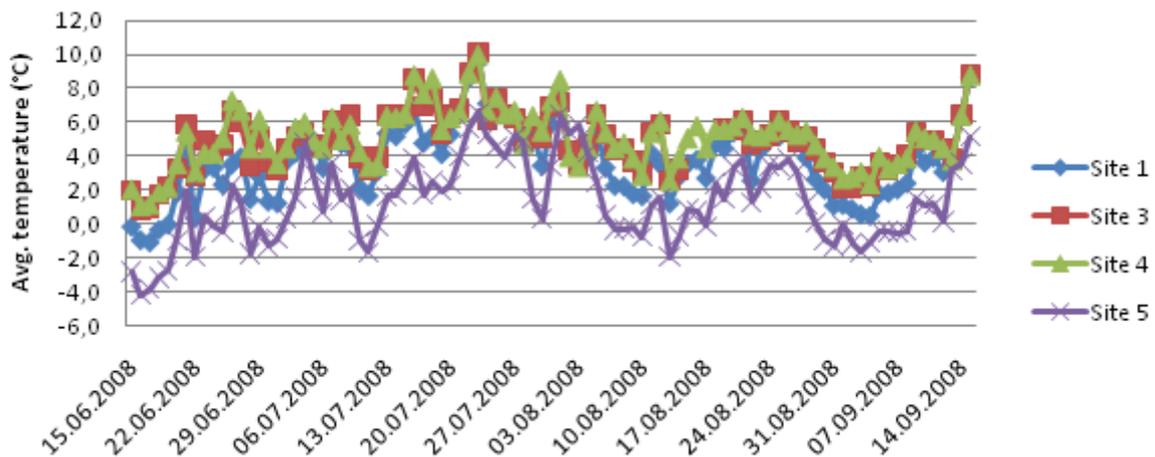


Fig. 5 - Daily average temperature at sites over time.

### 3.1.3 Wind speed

Site 1 was the windiest site with an average wind speed of 4.4 metres per second. Site 3 and 4 had average wind speeds of 4.3 and 4.0 metres per second respectively. Site 5 was the least windy site with an average wind speed of 3.2 metres per second. Generally, sites followed similar patterns in wind intensity and higher wind speed at one site would predict a higher wind speed at a different site.

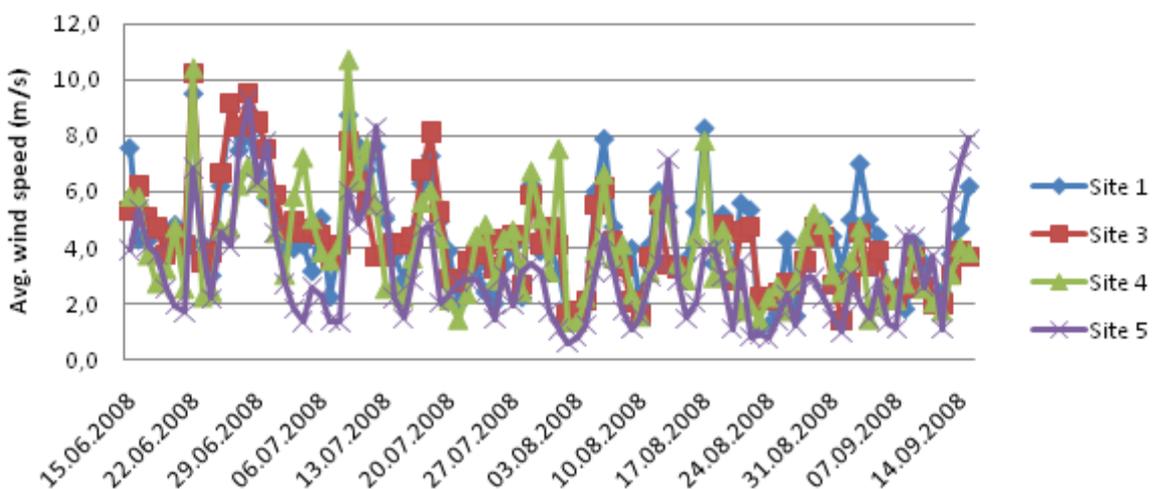


Fig. 6 – Daily average wind speed at sites over time.

There were some exceptions to this general trend. For example on the 2<sup>nd</sup> of July, wind speed at site 4 and 5 were 3.0 and 2.7 respectively. The next two subsequent days, average wind

speed increased at site 4 to 5.8 and 7.2 metres per second. At site 5 however, the wind speed the two subsequent days was reduced to 1.8 and 1.3 metres per second.

### 3.1.4 Wind direction

Over the same period of time, recorded wind direction often differed between sites. When the wind was blowing from the south at one site, for example site 5, it could be registered as blowing from the west at a different site, for example site 4.

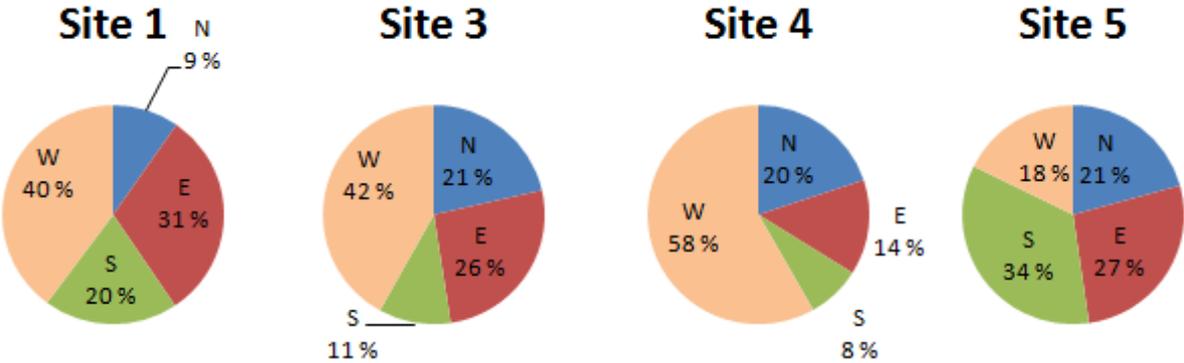


Fig. 7 - Proportion (%) of time the wind blew from any four directions, north (N), east (E), south (S) or west (W), at any site in the period 15<sup>th</sup> of June until 15<sup>th</sup> of September.

The higher altitude sites 1 and 5 have higher relative humidity with an average relative humidity of 83.1 and 86.3 in the period between 15<sup>th</sup> of June until 15<sup>th</sup> of September. By comparison, the average relative humidity during the same period at site 3 and 4 were 75.7 and 76.5.

### 3.1.5 Climate interactions

Some general climate trends are seen at all sites. When atmospheric pressure increases, temperature tends to increase. When temperature increases, relative humidity tends to decrease. There is also a negative trend between relative humidity and average wind speed.

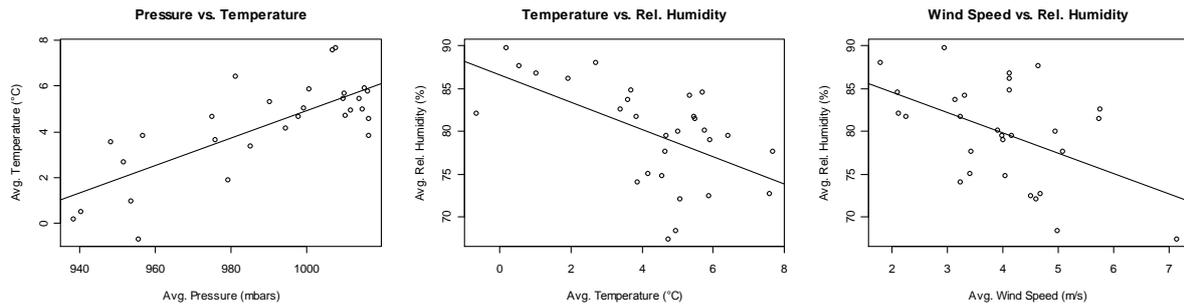


Fig. 8 - Scatterplots with linear trend lines between climate variables, (1) Average millibars pressure vs. Average temperature, (2) Average temperature vs. Average relative humidity, (3) average wind speed vs. Average relative humidity.

## 3.2 Statistical analysis of catches

A number of invertebrates were caught throughout the season with dipterans, specifically Nematocera being the numerically dominant group.

Table 4 - Table showing catch totals from different sites.

Catches	Site 1	Site 2	Site 3	Site 4	Total
Acari	37	40	16	9	102
Large Acari	24	36	2	1	63
Small Acari	13	4	14	8	39
Aphidoidea	1	5	2	0	8
Araneae	1	1	3	0	5
Collembola	1	3	0	43	47
<i>Agrenia bidenticulata</i>	0	1	0	29	30
<i>Folsomia quadrioculata</i>	0	0	0	1	1
<i>Hypogastrura</i> sp.	0	0	0	1	1
<i>Lepidocyrtus lignorum</i>	1	0	0	0	1
<i>Parisotoma notabilis</i>	0	0	0	1	1
<i>Sminthurides malmgreni</i>	0	2	0	11	13
Diptera	579	1900	639	8038	11156
Brachycera	17	28	99	33	177
Nematocera	562	1872	540	8005	10979
Hymenoptera	8	4	21	3	36
Leaves	21	47	19	10	97

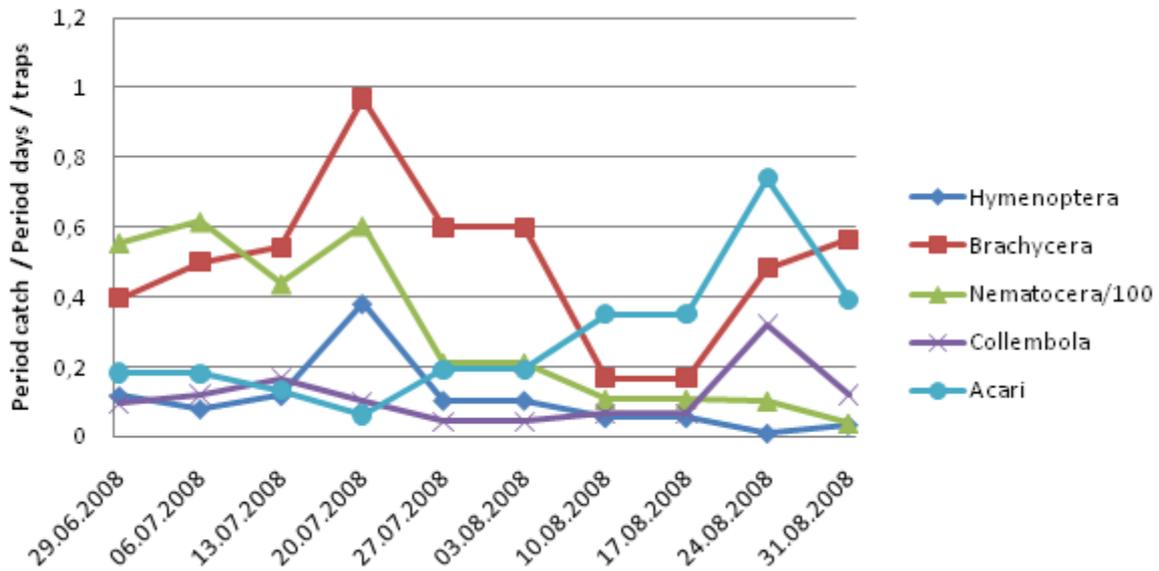


Fig. 9 - Weekly values of average catch per trap per day per period from each site added up. Nematocera have been downscaled by dividing them by 100. When values for catches are the same for two consecutive weeks, the days are from the same sampling period at all sites. Aphidoidea and Araneae whose catch numbers were the lowest are not included. The chart shows a time period when all sites were out.

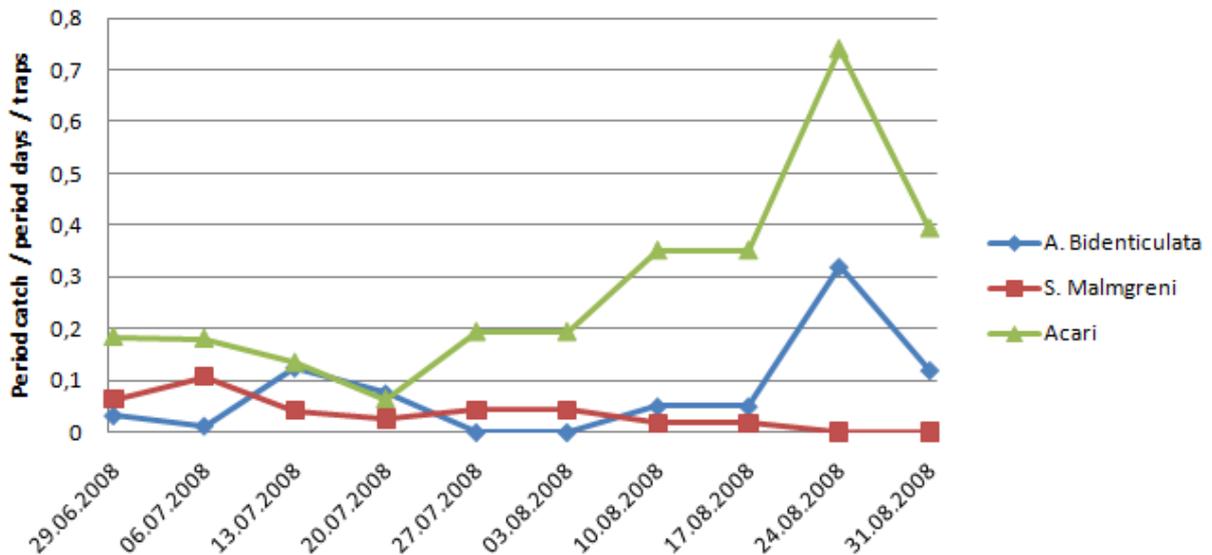


Fig. 10 - Weekly values of average catch per trap per day from all sites added up. When values for catches are the same for two consecutive weeks, the days are from the same sampling period at all sites.

Catches of Nematocerans, Brachycera and Hymenoptera dispersal peaked in July while catches of Acari and Collembola peaked in August. Brachycera also had a secondary August peak. For Collembola, the August peak is solely due to *Agrenia bidenticulata* which is the numerically dominant species in the catches. *Sminthurides malmgreni*, which was the second most caught Collembolan species, had higher catch densities in July.

### 3.2.1 Canonical Correspondence Analysis

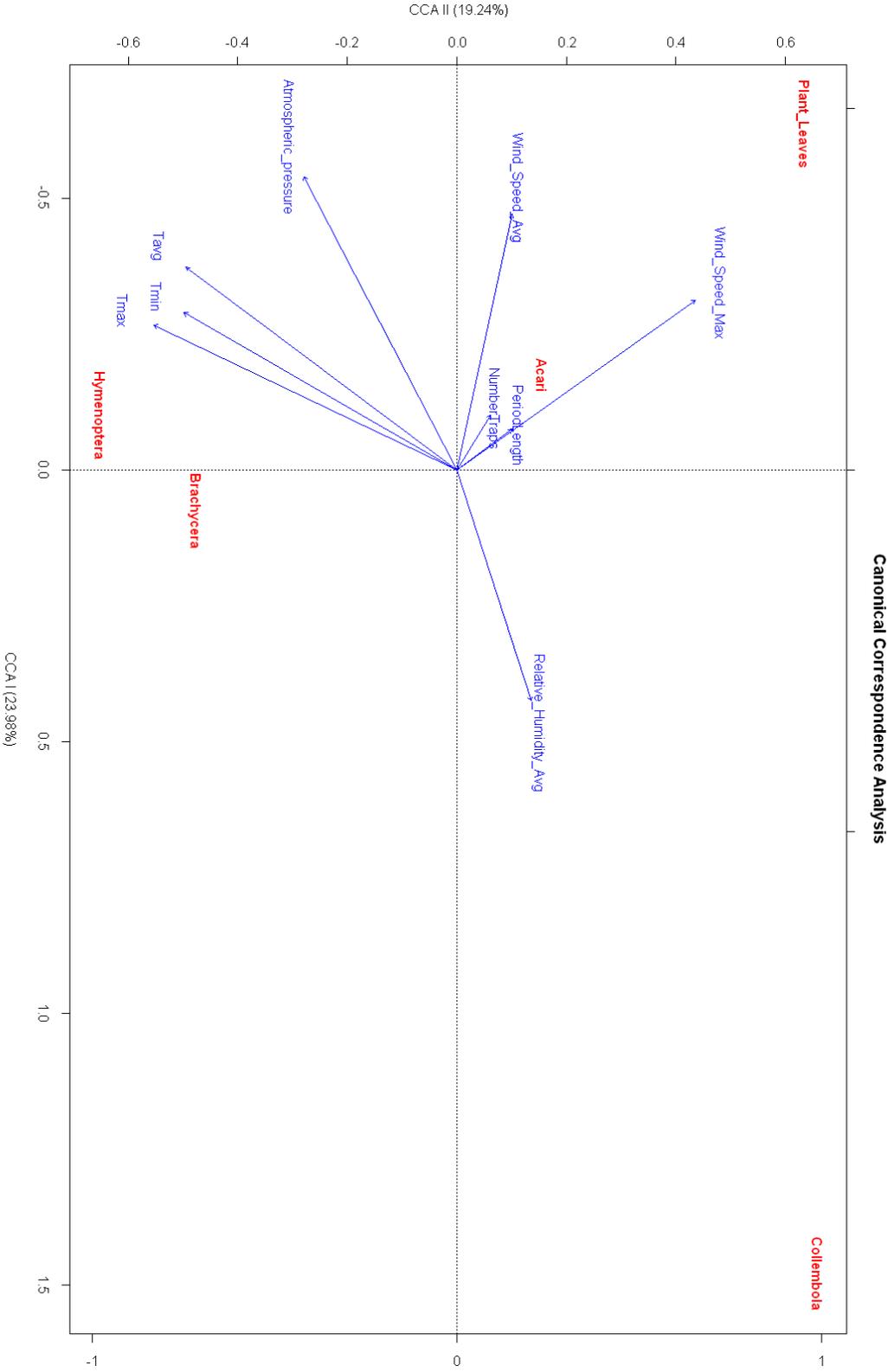


Fig. 11 - Canonical correspondence analysis with climate variables vs. plant leaves, Collembola, Acari, Brachycera and Hymenoptera. Some weather variable names have been shortened to not overlap in the plot. Tavg = Average temperature, Tmin = Minimum temperature, Tmax = Maximum temperature.

### 3.2.2 Collembola

In the CCA ordination plot, Collembola catches are best predicted by average relative humidity (fig. 11).

Zero-inflated regression modelling gave two models, one model explaining catches and one zero-inflation model explaining the presence of zeros in the dataset. The catch data model predicts Collembola by average relative humidity and average wind speed ( $p < 0.05$ ). For average relative humidity, the relationship with catches is positive and the expected change in  $\log(\text{Collembola catch})$  for a one-unit increase in relative humidity average is 0.137. For average wind speed, the relationship with catches is negative and the expected change in  $\log(\text{Collembola catch})$  with a one-unit increase in wind speed is -0.374. In the zero-inflation model, values of zero are significantly predicted by temperature average ( $p < 0.05$ ). The relationship between zeros and average temperature is positive and increased average temperature predicts more zeros in the catch data. Vuong test suggests that the zero-inflated regression model is a significant improvement over a standard poisson regression model ( $p < 0.05$ ).

Table 5 - Linear regression results between Collembola and one climate variable at a time.

Linear reg. : Collembola ~	R <sup>2</sup>	P
Millibars average pressure	0.4	<0.05
Average temperature	0.254	<0.05
Average relative humidity	0.244	<0.05
Average wind speed	0.178	<0.05

For linear regressions, the relationship between Collembola count and average temperature is negative and explains 25.4% of the variation in the catches ( $p < 0.05$ ). The relationship between Collembola catch and wind speed is negative and explains 17.8% of the variation in catches ( $p < 0.05$ ). The relationship between Collembola catch and atmospheric pressure is negative and explains 40% of the variation in catches ( $p < 0.05$ ). The hypothesis that Collembola aerial dispersal increases with temperature is rejected. The hypothesis that Collembola aerial dispersal increases with wind speed is rejected. The relationship between Collembola catches and average relative humidity is positive and explains 24.4% of the variation in catches ( $p < 0.05$ ). The hypothesis that Collembola aerial dispersal increases with

relative humidity is accepted. Only one Collembola, an *Agrenia Bidenticulata*, was caught during a period when average relative humidity was below 80%.

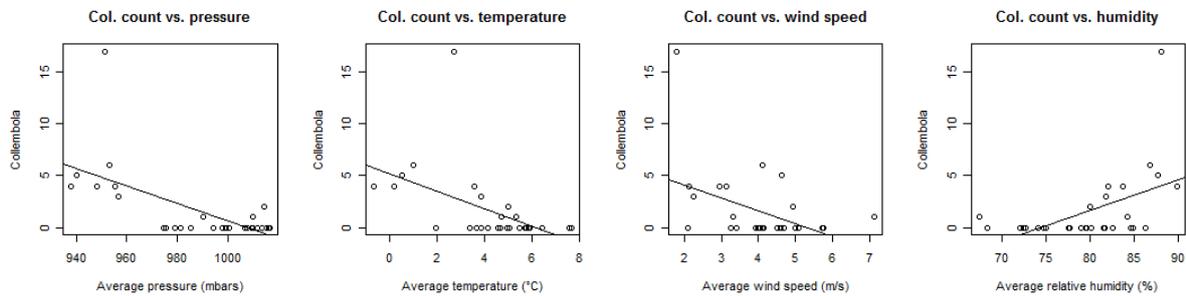


Fig. 12 - Scatterplots with linear regression trendlines between Collembola catch and (1) average pressure (mbars), (2) average temperature (°C), (3) average wind speed (m/s), (4) average relative humidity (%).

### 3.2.3 Acari

According to the CCA plot, Acari aerial dispersal is best explained by either period length or the amount of days the traps were out during any catch period (fig. 11).

Stepwise regression also produced a model with only one predictor variable, period length, which was significant ( $p < 0.05$ ).

Linear regression between Acari count and wind speed variables found no significant relationships. No support was found for the hypothesis that increased wind speed leads to increased Acari aerial dispersal. Linear regression did not find a significant relationship between Acari count and temperature variables. No support was found for the hypothesis that increased temperature leads to increased Acari aerial dispersal. For linear regressions, the only significant relationship found between Acari count and an independent variable was with period length, which explains 17.5% of the variation in Acari catches ( $p < 0.05$ ).

### 3.2.4 Nematocera

Stepwise regression produced a model with only two explanatory variables, average temperature and maximum temperature. A one-unit increase in average temperature predicts a negative -0.278 change in Nematocera catch ( $p < 0.05$ ). However, a one-unit change in maximum temperature predicts a positive change of 0.210 ( $p < 0.05$ ).

Linear regression between Nematocera counts and temperature variables yielded no significant results. No support was found for the hypothesis that Nematocera aerial dispersal increases with temperature. Linear regression shows there is a significant relationship between Nematocera count and atmospheric pressure. This relationship is negative and explains 21% of the variation in Nematocera catches ( $p < 0.05$ ) (fig. 13). For linear regression, no other significant relationships were found between Nematocera count and other climate variables.

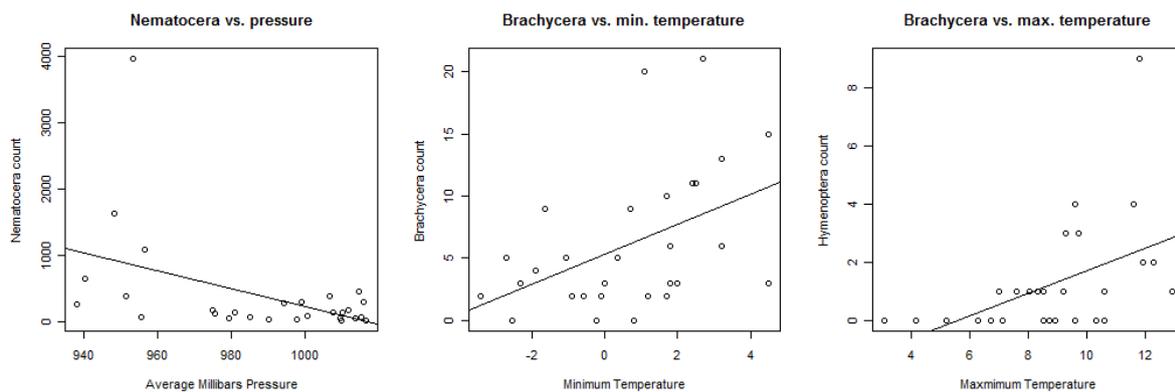


Fig. 13 - scatterplots with linear regression lines showing (1) Nematocera totals vs. Average millibars pressure, (2) Brachycera totals vs. Minimum temperature, (3) Hymenoptera totals vs. Maximum temperature.

### 3.2.5 Brachycera

According to CCA, Brachycera catches are best explained by the minimum, maximum and average temperature (fig. 11).

Stepwise regression produced a model with two explanatory variables, maximum temperature and maximum wind speed. The predicted change in Brachycera catches with a one-unit increase in maximum temperature is a positive 0.212 ( $p < 0.05$ ). The expected change in Brachycera catches with a one-unit increase in maximum wind speed is a negative -0.103 ( $p < 0.05$ ).

Linear regression between Brachycera catches and minimum, maximum and average temperatures were all positive and significant with minimum temperature being the strongest predictor (fig. 13) being able to explain 21.1% of the variation in Brachycera catches ( $p < 0.05$ ). The hypothesis that Brachycera aerial dispersal increases with temperature is

accepted. For linear regressions, no further significant relationships were found with between Brachycera count and non-temperature climate variables.

### **3.2.6 Hymenoptera**

According to CCA results, Hymenoptera catches are best explained by minimum, average and maximum temperature (fig. 11).

Zero-inflated regression produced a model explaining catches with two explanatory variables, maximum temperature and average wind speed. The expected change in Brachycera catches with a one-unit increase in maximum temperature is a positive 0.316 ( $p < 0.05$ ). The expected change in Brachycera catches with a one-unit increase in average wind speed is a negative -0.559 ( $p < 0.05$ ). The best single predictor for the inflation of zeros was average relative humidity with values of zero increasing with increased humidity, but this relationship was not significant ( $p = 0.0574$ ). Vuong test results suggests that the zero-inflated regression model is an improvement over a standard poisson regression model, but this result is not significant ( $p = 0.167$ ).

Hymenoptera catches respond positively with significance to all temperature variables, but are best explained by maximum temperature which explains 22.5% of the variance in catches. The hypothesis that temperature increases dispersal of Hymenoptera is accepted. For linear regressions, no further significant relationships were found with between Hymenoptera count and non-temperature climate variables.

# 4 Discussion

## 4.1 Weather

The weather variables used in this study are not independent of each other, but all interconnected cogs in the great climate machinery where one turning like *this* causes another to turn like *that*. As such, a response in invertebrate dispersal to one climate variable may tie to a response in another. For this reason, an attempt at understanding how weather explains invertebrate dispersal should start with an attempt at understanding how the climate variables act and interact.

### 4.1.1 Atmospheric pressure

Atmospheric pressure is highest closest to the surface of the earth and decreases upwards through the atmosphere (fig. 3). This is because in a still column of air, the weight of the air above will make pressure highest in the bottom of the column (Navarra 1979). Judging from our results, the daily average pressure differences between sites stem almost exclusively from differences in elevation. If all sites had been at the same elevation, it is likely to assume all readings of daily average pressure would have been overlapping like the values from Vestpynten and Adventdalen do (fig. 3), with no significant difference between them.

### 4.1.2 Temperature

Looking at temperature averages, the low elevation sites were warmer and the high elevation sites colder (table 3, fig. 5). This is in part explained by the relationship between the gasses that make up the air and the atmospheric pressure. When atmospheric pressure increases, a parcel of air is compressed tighter by the surrounding air and the energy pushing the molecules together cause them to move faster, making the parcel of air warmer. When pressure is reduced, the opposite happens and the declining pressure causes the parcel of air to expand. The expanding parcel of air uses some of its energy to push at the surrounding air, causing the molecules to slow down and the air parcel to cool (Navarra 1979). This explains in part why temperatures decline with elevation. While this describes the trend over time at the fieldwork sites, there were deviations from this general pattern, as demonstrated by the day August 3<sup>rd</sup> when all temperature readings were highest on Breinosa. During this day, the

lower elevation sites likely experienced cool, foggy conditions during much of the day while the site at Breinosa was sun exposed. Similar weather conditions during other days may also account for other deviations from the general trend and indeed, such conditions were observed in the field, although the specific dates and durations of such occurrences were not noted.

### **4.1.3 Wind speed**

Average wind speed was highest at the lower elevation sites in the Adventdalen valley (Northern Lights station and Jansonhaugen) and lowest at Breinosa (table 3, fig. 6). This may be due to the channeling effect the valley has on winds and wind speed inside valleys may increase significantly if overall wind direction is parallel to the valley (Ruel et al. 1998).

### **4.1.4 Relative humidity**

Relative humidity was highest on Breinosa and lowest at the old northern lights station (table 3). Because relative humidity is intimately interconnected with temperature, explaining why this is so must include an explanation of how these variables relate to each other. Air is able to transport water, but the capacity of a parcel of air to do so decreases with temperature. If a parcel of air with a relative humidity of 50% is cooled while the amount of moisture in the air remains constant, the relative humidity will increase. This is because when the capacity of the air to transport water decreases while the amount of water vapour stays the same, the parcel of air becomes more saturated (Navarra 1979). The fact that Jansonhaugen and Breinosa are the coldest sites due to their higher elevation also helps explain why they have highest relative humidity. Although lower temperatures cause less water evaporation, the addition of a specific amount of water vapour to a parcel of air at the coldest sites would on average cause a higher increase in relative humidity than at our warmest sites. Also, as mentioned in the site description, the relatively cold Breinosa site was relatively wet site with melt water running through it, although this was not the case on Jansonhaugen.

Our results show that relative humidity is also negatively affected by wind speed (fig. 8). The rate of evaporation tends to increase with wind speed as air motions above a water surface carry water vapour away from the interface (Navarra 1979), decreasing the relative humidity above it. This effect in larger scale could explain why relative humidity has a negative relationship with wind speed at our sites. Moisture added to the air by evaporation may be removed from a site and replaced with drier air by wind. The details of such an effect would

depend on the presence of drier air masses around or above the site as well as wind speed and direction, but an overall negative effect on relative humidity may explain the general pattern present in our weather data.

#### **4.1.5 Climate interactions**

Pressure and temperature share a positive relationship (fig. 8). Undoubtedly adding to this is the fact that the lowest pressure sites are also the coldest. However, this relationship may be expected to be true even if all sites had been at the same elevation. As cold air descends in a high pressure zone, it is relatively having previously lost its moisture as it ascended in a low pressure zone and high atmospheric pressure is associated with clear weather (Navarra 1979). During the summer months, clear weather means more sun exposure which commonly leads to warmer days. During winter and polar night, the cold descending air in a high pressure zone may instead be associated with clear conditions and biting cold. However in low pressure zones as relatively warm and moist air ascends, it cools down and the capacity for transporting water is reduced. The relative humidity goes up until the air becomes saturated and clouds condense (Navarra 1979). During summer, such cloudy conditions block sunlight and temperatures may decline as a result. For this reason, a positive relationship between atmospheric pressure and temperature during the summer months may be true.

Our results show that relative humidity and average temperature share a negative relationship (fig. 8). Adding to this is undoubtedly the fact that the coldest site is also the most humid. One might also expect this to be true if there is a positive relationship between pressure and temperature because relative humidity shares a negative relationship with pressure and lower pressure on average leads to more humid conditions. However, the relationship between pressure and temperature may be more complex and warm days can co-occur with low pressure and-or high humidity. The strength of the relationship should not be taken at face value.

## 4.2 Aerial dispersal of invertebrates

### 4.2.1 Collembola

Collembola numbers are largely made up by two species which account for over 90% of the total catch, *Agrenia bidenticulata* and *Sminthurides malmgreni*. Both species are surface active, have strong furculas and are capable of jumping into the air (pers. obs.). No proof of long distance dispersal events was found in our studies, although our results do not exclude the possibility of such events. All species caught were native to Spitsbergen and catch species and densities are likely to in part reflect the local surface active Collembola fauna. A likely explanation why a Collembola such as an *Agrenia bidenticulata* was caught in a trap is that it was present somewhere in the vicinity of the trap and was caught by the wind as it jumped. A gust may have carried it for a short distance through the air before dropping it.

With all statistical results combined, humidity, temperature, pressure and wind speed all seem able to predict Collembola aerial dispersal, but the different statistical methods emphasize different weather variables. Looking at the overall results from all statistical methods combined, Collembola aerial dispersal is positively related with relative humidity and negatively related to temperature, pressure and wind speed. As these different weather variables are dependent on and share trends with each other, it is likely that the way they interact has affected the results. For this reason, interpretation of the results is done with caution.

The strong negative relationship with average millibars pressure is believed to largely come from two reasons. The Breinosa site where Collembola catches largely come from has the lowest average pressure. The highest pressure recordings at this site were comparable to the lowest at Jansonhaugen, the site with the second highest elevation. Comparing the pressure at Breinosa to the lowest elevation sites, we see that they are completely detached and the highest values observed at the Breinosa site are never recorded at the northern lights station or at Vestpynten. This means that even if Collembola were caught during days when pressure was relatively high compared to average Breinosa pressure values, the values would be low compared to those from the other sites. Because Collembola were always caught in a

comparatively low pressure environment, a negative relationship between Collembola aerial dispersal and pressure may be expected, even if the direct effect of pressure on dispersal is negligible. Based on these results, the explanatory power of atmospheric pressure on Collembola aerial dispersal is not interpreted as being a direct effect of pressure on collembolans, but one may still be able to predict dispersal by pressure through interactions with the other weather variables. Average pressure relates to the other climate variables in such a way that a decline in pressure correlates with favourable conditions for Collembola dispersal in temperature, humidity and wind speed. However, in our results, the value of 40% predictory power is likely to be exaggerated.

Temperature is the only significant predictor for values of zeros in the zero-inflation model, meaning that higher temperatures leads to more values of zero when we are trying to catch aerially dispersed Collembola. The reason for this is likely because most Collembola are caught at the site with the lowest average temperature, and anything else in the environment at Breinosa which promotes aerial dispersal of Collembola may be reflected in the seeming importance of temperature as a predictor. A study on the effect of elevated temperatures on soil microarthropods showed that temperatures required for killing the Collembola species in the study was about 35-40 degrees Celcius when relative humidity was high, but that the lethal temperature shifted downwards when conditions were dry. The study concluded soil microarthropods appear able to cope with higher temperatures and that significant changes in the microarthropod communities are more likely to be associated with changes in soil moisture status (Hodkinson et al. 1996a). We believe that the predictory power of temperature on dispersal largely comes from the interaction between temperature and humidity and moisture. When increased temperatures cause drier conditions, it may have an adverse effect on Collembola dispersal if this causes them to retreat from wind exposed surfaces to more humid microhabitats. However, studies outside Svalbard have also shown that catch densities from suction sampling of Collembola has a positive effect with temperature (Frampton et al. 2001). Although our results show with significance that temperature has a negative relationship with Collembola aerial dispersal, the truth may be too complex for such a general statement and may rely on a context involving species and how rising temperatures occur with other weather conditions, particularly relative humidity. Further studies should be conducted before accepting or rejecting the negative effect of temperature on Collembola dispersal as true.

Both the zero-inflated poisson regression model and linear regression showed wind speed to be a significant predictor with a negative relationship with Collembola aerial dispersal. We believe the power of wind speed as a predictor on Collembola aerial dispersal comes from its interaction with moisture and humidity. At our study sites, higher wind speeds tend to cause drier conditions for Collembola (fig. 8) which is likely to have a negative effect on Collembola activity on exposed surfaces where they can be caught by the wind. This supports our rejection of the hypothesis that increased wind speeds lead to increased rates of Collembola aerial dispersal.

We conclude that from our set of weather variables, relative humidity is the most important predictor for Collembola dispersal. It is the only variable whose significance as a predictor is supported by the CCA analysis, the zero-inflated poisson regression model and linear regression. Collembola have water permeable cuticles and are generally susceptible to desiccation if conditions become dry (Verhoef and Witteveen 1980), although the susceptibility to cuticular water loss differs between species (Hertzberg and Leinaas 1998). An earlier study from Svalbard concluded that for the Collembola species *Onychiurus arcticus*, uptake of water from a saturated atmosphere happens faster than uptake of free, liquid water in the environment (Hodkinson et al. 1994). A likely explanation for why relative humidity relates positively to relative humidity is that humid air conditions allow Collembola to be active on surfaces where they can get caught by the wind without drying out, hence high relative humidity is thought to promote Collembola activity. This supports our acceptance of the hypothesis that Collembola dispersal increases with humidity.

#### **4.2.2 Acari**

A total of 102 Acari were caught at sites with the highest catch totals from Jansonhaugen and the old northern light station in Adventdalen and the lowest catches from the site at Breinosa. No significant relationships were found between total Acari dispersal and any weather variable. According to CCA, the multiple regression model and linear regressions, the only variable able to predict Acari aerial dispersal was period length. The relationship was positive, predicting that the longer traps are out, the more Acari they will catch. This is something one should expect if arthropods disperse regardless of what the weather conditions are. If on the other hand arthropods only disperse under certain weather conditions, the amount of days a trap is out should be of less relevance. Rather, having the trap out during a

time period when the right conditions occur would be important. Previous studies on Svalbard microarthropods that include Collembola and mite species have shown that mites are generally more robust than Collembola when it comes to coping with higher temperatures and drought (Hodkinson et al. 1996a). Such robustness is a likely explanation why no significant relationship between Acari dispersal and climate could be found. Compared to collembolans, Acari aerial dispersal responds less to weather and takes place under a wider range of environmental conditions. However, although our results failed to find any significant relationships between Acari aerial dispersal and weather, we do not exclude the possibility that such relationships may exist.

### **4.2.3 Nematocera**

The best fit multiple regression model found for Nematocera identifies both average and maximum temperatures as predictors for Nematocera dispersal. This is partly caused by the nematoceran catch numbers during the first trapping period at Breinosa which caught more nematocerans than any other period at any other site. The total catch for the period was 3964 nematocerans. By contrast, the period with the second highest catch, also at Breinosa, caught 1624. Breinosa is the coldest site and so the average temperature compared to all sites during this period is low. However, the maximum temperature registered at that site during the same period is relatively high. Thus, the highest registered catch number of Nematocerans happened at the site which was coldest, but during a period which recorded a relatively high maximum temperature during that period. A likely explanation for the pronounced abundance of Nematocera in the traps at this site during this period is that emergence from the larval stage took place within this period. Nematocera like mosquitoes and the chironomid midges have a freshwater larval stage. A study on chironomid midge dispersal in agricultural landscapes in France showed that densities of chironomids were higher closer to the water source from which they emerge (Delettre and Morvan 2000). The Breinosa site was the wettest site with a meltwater stream running through it and was likely a suitable habitat for freshwater larvae. This indicates that proximity to water is an important hidden variable in our study and may be more important than any of our weather variables. Although linear regression showed pressure to be a significant predictor with a negative relationship to Nematocera dispersal, the response to pressure is likely affected and exaggerated by the hidden variable. Most nematocerans were caught at Breinosa, likely because nematoceran adults emerge from the freshwater streams and pools at the site. Because the site also distinctly has the lowest

average pressure, part of the positive effect on Nematocera catches from traps being close to water is interpreted as stemming from the pressure difference between Breinosa and other sites. Thus, our own results remain inconclusive in regards to how weather affects Nematocera dispersal. However, previous studies from Svalbard identified temperature as the major predatory climate variable on Nematocera biomass (Hodkinson et al. 1996b).

#### **4.2.4 Brachycera**

Brachycera were caught at all sites, but were most abundant in the traps at Vestpynten which caught more than half the total catch. According to CCA analysis, Brachycera count responds to temperature. This is confirmed by linear regressions which show that there is a positive relationship between Brachycera count and all temperature variables with minimum temperature being the strongest predictor. The warmer it was during a trapping period, the more brachyceran flies the traps caught. Temperature is likely to have a positive relationship with dispersal because the thoracic flight muscles of insects generally need to reach a threshold temperature before the insects are capable of flight (Pedgley 1982). During a warmer period, temperatures are likely to stay above this threshold for longer than during colder periods, allowing the brachycerans to fly around more. This supports our acceptance of the hypothesis that Brachycera dispersal is positively affected by temperature.

The best fit multiple regression model for Brachycera aerial dispersal also identifies average wind speed as a significant predictor in addition to average temperature. The relationship is negative and so an increase in wind speed is predicted to reduce Brachycera aerial dispersal rates. As temperature and wind speed share a slightly positive trend, this is not due to the effect wind speed has on temperature. Instead, the likely explanation is that when it is windy, Brachycera spend less time in the air or fly at lower altitudes. Flying into faster winds increases the risk of an insect getting transported away from its favoured habitat by wind. An insect on Vestpynten also runs the risk of getting blown out to sea when winds move towards Isfjorden (fig. 1).

#### **4.2.5 Hymenoptera**

In a way similar to Brachycera, Hymenoptera were caught at all sites, but were most abundant at Vestpynten and also responded to temperature and wind speed. CCA and linear regressions identified temperature variables as the most important predictors with positive relationships

with Hymenoptera aerial dispersal. Traps caught more hymenopterans during warmer periods. The zero-inflated poisson regression model also identified wind speed as a predictor with a negative effect on Hymenoptera dispersal. The likely explanation for this is the same as for Brachycera. The thoracic flight muscles need to be above a certain temperature threshold before take-off is possible (Pedgley 1982) and generally, warmer period means that on average, the time when ambient temperature exceeds the threshold values needed for take-off are extended and so hymenopterans are able to fly more. The cause of the negative effect of wind speed on Hymenoptera dispersal is also likely one shared with Brachycera. Flying during or into higher winds increases the chances of an insect to become removed from its favoured habitat or even carried out to sea or other inhospitable environments where risk of mortality is higher. To avoid this risk, hymenopterans likely spend less time in the air or fly closer to the ground when wind speeds increase.

#### **4.2.6 Other arthropods**

Catch numbers of Araneae and Aphidoidea were too low to confidently relate dispersal to weather, but our study shows that these arthropods are transported by winds on Svalbard. None of the aphids recovered from our traps were in a winged stage and so aerial dispersal of these must have been passive.

### **4.3 Problems with our study**

Many of the problems in the study stem from the fact that our sites are not entirely comparable. There is particularly one site, the site on Breinosa at 400 metres above sea level, which has a different climate from the other sites. Moving upwards in elevation some hundreds of metres on Svalbard may take you from a climate where snow and ice thaws every summer to a climate which is frozen the entire year. To achieve the same difference in average climate that you find from a 400 metres difference in elevation by moving only by latitude, you would have to travel comparatively far. In our analysis, when the relative catch of a taxa is greater on Breinosa compared to other sites, this can create or exaggerate trends in the data. As an example, let us say that most of one type of invertebrate is caught at Breinosa which also happens to have a very low average pressure. A scatterplot of invertebrate count vs. pressure is likely to show that invertebrate catch responds negatively to pressure and in a sense, this may be true because the invertebrate is mostly found in a low pressure

environment. However, if you produced a scatterplot using only data from the Breinosa site, you could find that more individuals are caught during the periods with the highest pressure and that the relationship between the variables is positive. However, the difference in climate between Breinosa and other sites from the study is so great that a relatively high pressure reading at Breinosa would be regarded as an extremely low pressure condition had it been recorded at any of the other sites. Instead of finding the truth in the results, one becomes mostly reliant on academic reasoning to explain why the variables behave the way they do.

Besides climate, other area effects and hidden variables also serve to make Breinosa less comparable to other sites in the study. It was the only site which had shallow freshwater streams running through it. Because catches seem to reflect the local fauna present around the traps, anything in the local environment which affects the abundance of invertebrates has importance to explaining catch success. When these variables are missing from our study, their effect may still be reflected in our weather variables. In our study, the problems connected with the Breinosa site apply to Collembola and Nematocera, both taxa that were relatively abundant on Breinosa compared to the other sites. Part of the problem of explaining Nematocera and Collembola dispersal at these sites could be rectified by leaving out other sites, but unfortunately, splitting Collembola and Nematocera datasets into two parts each, one from Breinosa and one from the other sites, would produce new datasets too small to be suitable for statistical analysis.

Climate variables are not independent and if an invertebrate responds to changes in one, it may respond to several more simply because of the way these variables react. This does not mean that the relationships are not true, but they may be caused by correlation rather than causation and so caution must be exerted when interpreting the results. In our study, such problems are most likely to affect Collembola.

Another possible source of error in our study relates to our trapping method. Our water traps may have been of interest to animals, for example reindeers looking for a drink or a bird looking for a place to take a bath. No animals were seen in the sites during fieldwork and no clear signs of tampering of traps were noticed. Also, because traps were secured to bags of rocks using strings tied to the top corners, there is a chance that some invertebrates may have crawled in. However, in addition to crawling up the plastic bag and the string, these invertebrates would also have to cross the barrier of Vaseline smeared along the lid of each

trap. We have no specific reason to believe events like these took place or have had an effect on our final results, but we cannot exclude the possibility.

Our traps may have actively attracted diptera, for example chironomid midges.

## **4.4 Suggestions for improvement**

Because our study uses the weather data from several study sites in the same statistical analyses, these study sites should have been at similar elevations so that changes in weather came from differences in local conditions and not fundamental differences in climate. A possible improvement could be not including the sites at Jansonhaugen and Breinosa in the study. Alternatively, invertebrates could be related to local climate only at the site they were caught, turning it into one study per site. Then, Breinosa could be interesting for looking at Collembola or Nematocera dispersal, the old northern lights could be an interesting place to study Acari dispersal and Vestpynten could be an interesting place to study Brachycera and Hymenoptera dispersal. However, in order to explain invertebrate catches by weather variables in one study per site, trapping efforts would have to be increased at each site in order to get enough data for statistical analysis. In such a case, the use of plastic boxes as traps is smart because it is a cheap and easy way of getting a large catch surface at the sites. However, the way the traps were secured could be improved. Instead of being secured to weights by strings which are possible to climb, weights could be secured to the bottom, for example by glueing lead weights to the underside of each box. Possibly, weights could also be put inside each trap and submerged in the water, but great care would have to be taken not to contaminate these weights if they are removed from the traps during the time the water is collected. Finally, sites should be visited more frequently in order to get more detailed data of the local weather changes at each site.

## **4.5 Conclusions**

Collembola aerial dispersal rates respond positively to relative humidity. The reason is hypothesized to be because in a more humid environment, Collembola are more active on surfaces where they may get caught by the wind. Generally, weather conditions which lead to increased relative humidity may also be expected to promote Collembola aerial dispersal.

During the summer of 2008, such conditions most often occurred during periods of low atmospheric pressure and wind speeds.

No significant relationships between Acari aerial dispersal rates and weather variables were found. Acari only responded with significance to the amount of days traps were out. Traps left out in the field are predicted to catch more Acari the longer they are left out before catches are collected. A likely explanation is that because Acari have higher tolerance to different weather conditions compared to Collembola (Hodkinson et al. 1996a), they remain active on surfaces where they can get caught by the wind during a wider range of weather conditions. However, we do not exclude the possibility that a relationships between Acari dispersal rates and weather do not exist. Explaining how Acari dispersal rates relate to weather requires further study.

Most nematocerans were caught at one site. This is thought to be because of the presence of water, both in streams and pools, at the site. The chironomid midges that make up the majority of our Nematocera catch has a freshwater larval stage and have been shown in other studies to have increased abundance with reduced distance from the pools they emerge from (Delettre and Morvan 2000). The likely significant effect from the presence of water at the site was hidden from our dataset and is thought to create errors in the results. For this reason, based on our results, we make no assumptions about the relationship between Nematocera dispersal and weather.

Brachycera and Hymenoptera aerial dispersal rates respond positively to increased temperatures. The reason for this is thought to be because the thoracic flight muscles of both Brachycera and Hymenoptera need to be above a certain temperature threshold before take-off is possible. During periods of days when conditions are relatively warm, Brachycera and Hymenoptera can spend more time flying than during periods when conditions are cold. Brachycera and Hymenoptera aerial dispersal rates also respond negatively to wind speed. The reason is thought to be because Brachycera spend less time flying or fly at lower altitudes in response to increasing winds in order to not get swept away from their preferred habitats.

# References

- Bergh, J. C. and C. W. McCoy. 1997. Aerial dispersal of citrus rust mite (Acari: Eriophyidae) from Florida citrus groves. *Environmental Entomology* **26**:256-264.
- Brandenburg, R. L. and G. G. Kennedy. 1982. Intercrop Relationships and Spider-Mite Dispersal in a Corn Peanut Agro-Ecosystem. *Entomologia Experimentalis et Applicata* **32**:269-276.
- Coulson, S., I. D. Hodkinson, A. Strathdee, J. S. Bale, W. Block, M. R. Worland, and N. R. Webb. 1993. Simulated Climate Change - the Interaction between Vegetation Type and Microhabitat Temperatures at Ny-Alesund, Svalbard. *Polar Biology* **13**:67-70.
- Coulson, S. J. 2000. A review of the terrestrial and freshwater invertebrate fauna of the High Arctic archipelago of Svalbard. *Norwegian Journal of Entomology* **47**:41-63.
- Coulson, S. J., I. D. Hodkinson, and N. R. Webb. 2003. Aerial dispersal of invertebrates over a high-Arctic glacier foreland: Midtre Lovenbreen, Svalbard. *Polar Biology* **26**:530-537.
- Coulson, S. J., I. D. Hodkinson, N. R. Webb, W. Block, J. S. Bale, A. T. Strathdee, M. R. Worland, and C. Wooley. 1996. Effects of experimental temperature elevation on high-arctic soil microarthropod populations. *Polar Biology* **16**:147-153.
- Coulson, S. J., I. D. Hodkinson, N. R. Webb, K. Mikkola, J. A. Harrison, and D. E. Pedgley. 2002. Aerial colonization of high Arctic islands by invertebrates: The diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species. *Diversity and Distributions* **8**:327-334.
- Delettre, Y. R. and N. Morvan. 2000. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology* **44**:399-411.
- Edwards, J. S. 1987. Arthropods of Alpine Aeolian Ecosystems. *Annual Review of Entomology* **32**:163-179.
- Elkinton, J. S. and A. M. Liebhold. 1990. Population-Dynamics of Gypsy-Moth in North-America. *Annual Review of Entomology* **35**:571-596.
- Frampton, G. K., P. J. Van den Brink, and S. D. Wratten. 2001. Diel activity patterns in an arable collembolan community. *Applied Soil Ecology* **17**:63-80.
- Gressitt, J. L. and Yoshimoto, C. M. 1974. Insect Dispersal Studies in Northern Alaska. *Pacific Insects* **16**:11-30.
- Hawes, T. C. 2008. Aeolian fallout on recently deglaciated terrain in the high Arctic. *Polar Biology* **31**:295-301.
- Hawes, T. C., M. R. Worland, P. Convey, and J. S. Bale. 2007. Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography. *Antarctic Science* **19**:3-10.
- Hertzberg, K. and H. P. Leinaas. 1998. Drought stress as a mortality factor in two pairs of sympatric species of *Collembola* at Spitsbergen, Svalbard. *Polar Biology* **19**:302-306.
- Hisdal, V. 1998. Svalbard : nature and history. Updated, and enl. edition. Norsk Polarinstitutt, Oslo, Norway.
- Hodkinson, I. D., S. J. Coulson, and N. R. Webb. 2004. Invertebrate community assembly along proglacial chronosequences in the high Arctic. *Journal of Animal Ecology* **73**:556-568.
- Hodkinson, I. D., S. J. Coulson, N. R. Webb, and W. Block. 1996a. Can high Arctic soil microarthropods survive elevated summer temperatures? *Functional Ecology* **10**:314-321.

- Hodkinson, I. D., S. J. Coulson, N. R. Webb, W. Block, A. T. Strathdee, J. S. Bale, and M. R. Worland. 1996b. Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *Oikos* **75**:241-248.
- Hodkinson, I. D., V. Healey, and S. Coulson. 1994. Moisture Relationships of the High Arctic Collembolan *Onychiurus-Arcticus*. *Physiological Entomology* **19**:109-114.
- Jeppson, L. R., H. H. Keifer, and E. W. Baker. 1975. Mites injurious to economic plants. University of California Press, Berkeley.
- Johnson, D. T. and B. A. Croft. 1981. Dispersal of *Amblyseius-Fallacis* (Acarina, Phytoseiidae) in an Apple Ecosystem. *Environmental Entomology* **10**:313-319.
- Jung, C. L. and B. A. Croft. 2001. Aerial dispersal of phytoseiid mites (Acari : Phytoseiidae): estimating falling speed and dispersal distance of adult females. *Oikos* **94**:182-190.
- Leinaas, H. P. 1999. Spredning og kolonisering. Betydning av habitatheterogenitet og populasjonsdynamikk. Bengtson, S.A., Mehlum, F. & Severinsen, T. (eds.) *Svalbardtundraens økologi. Terrestrisk økologisk forskningsprogram på Svalbard. Meddelelser 150. Norsk Polarinstitutt, Tromsø.*:175-180.
- Lods-Crozet, B., V. Lencioni, J. E. Brittain, L. Marziali, and B. Rossaro. 2007. Contrasting chironomid assemblages in two high Arctic streams on Svalbard. *Fundamental and Applied Limnology* **170**:211-222.
- Navarra, J. G. 1979. Atmosphere, weather, and climate : an introduction to meteorology. W.B. Saunders, Philadelphia.
- Pedgley, D. E. 1982. Windborne pests and diseases: meteorology of airborne organisms. Ellis Horwood Ltd & John Wiley & Sons, Chichester, New York etc.
- Ruel, J. C., D. Pin, and K. Cooper. 1998. Effect of topography on wind behaviour in a complex terrain. *Forestry* **71**:261-265.
- Shapiro, S. S. and M. B. Wilk. 1965. An Analysis of Variance Test for Normality (Complete Samples). *Biometrika* **52**:591-&.
- Svendsen, H., A. Beszczynska-Moller, J. O. Hagen, B. Lefauconnier, V. Tverberg, S. Gerland, J. B. Orbaek, K. Bischof, C. Papucci, M. Zajaczkowski, R. Azzolini, O. Bruland, C. Wiencke, J. G. Winther, and W. Dallmann. 2002. The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Research* **21**:133-166.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology (Washington D C)* **67**:1167-1179.
- Vanschoenwinkel, B., S. Gielen, M. Seaman, and L. Brendonck. 2008. Any way the wind blows - frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* **117**:125-134.
- Verhoef, H. A. and J. Witteveen. 1980. Water balance in Collembola and its relation to habitat selection; cuticular water loss and water uptake. *Journal of Insect Physiology* **26**:201-208.
- Weyman, G. S., K. D. Sunderland, and P. C. Jepson. 2002. A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland. *Ethology Ecology & Evolution* **14**:307-326.
- Zhao, S. and J. W. Amrine, Jr. 1997. Investigation of snowborne mites (Acari) and relevancy to dispersal. *International Journal of Acarology* **23**:209-213.