# Collection of data on microzooplankton (pelagic ciliates and heterotrophic dinoflagellates) rates: grazing, growth, metabolism in the lab and in the field.

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**Abstract**

We present a collection of data relating to microzooplankton physiological traits collected from the literature. We define microzooplankton as unicellular zooplankton (protozoans) within the 20-200 µm size class. The collected data mostly relates to grazing rates collected either in the field or through laboratory experiments. There is an equal number of grazing and growth rate measured through laboratory experiments and a smaller number of Gross Growth Efficiency (GGE), respiration and egestion values. Although the collected data showed inconsistencies in units, or gaps in knowledge of microzooplankton (*e.g.* effect of prey nutrient content, combined measurement of grazing and growth), they also contained information on microzooplankton functional response, and how some external factors affect them (*e.g.* prey concentration, prey offered, temperature) to be a base set for a meta-analysis of data or an indication of less frequently measured rates predator-prey combinations.

Link to the repository: http://doi.pangaea.de/10.1594/PANGAEA.820368 and http://doi.pangaea.de/10.1594/PANGAEA.826106 Note that the sum of all data sets differs from the present data compilations which provides harmonized units and temperature adjusted metabolic . Within the repository there is a link to the 'raw' dataset

## 1. Introduction

Microzooplankton is an important part of the food-web in regulating phytoplankton biomass as well as part of the microbial loop and a link to the higher trophic levels. It is defined as a diverse grouping of heterotrophic metazoans and protozoans (Sieburth et al., 1978), typically between 20 and 200 µm. However this definition includes the smaller life-stages of metazoans such as copepod nauplii and larvae of benthic organisms. We only consider the protozoan fraction of microzooplankton and will extend it to include nanozooplankton (less than 20µm) since organisms such as pelagic ciliates and heterotrophic dinoflagellates are found in both size class.

Ciliates and dinoflagellates tend to have similar biomass (Buitenhuis et al., 2010), but differences in sizes, feeding mode and prey size spectrum result in different grazing selectivity on phytoplankton communities: dinoflagellates consume diatoms, and ciliates primarily consume nanophytoplankton. Metabolic rates of similar-sized ciliates and dinoflagellates are also different with higher grazing and growth rate in ciliates than dinoflagellates (Strom and Morello 1998).

This work presents a collection of data for the marine system that was collected to improve representation of the "microzooplankton" functional group in ecosystem model (Buitenhuis et al., 2011). It contains field and laboratory measurements of grazing, laboratory measurements of growth (response to prey concentration and, or type), egestion rate, respiration and gross growth efficiency.

## 2. Data source and metadata

### 2.1 Data collection

From the existing literature, we synthesized all data that we could find on marine microzooplankton functional and numerical response. The aim of this data collection was to obtain data to parameterize microzooplankton for a marine ecosystem model (Buitenhuis et al., 2011), and collection was stopped in 2008. Due to the aim and timing of the data collection, there is no freshwater data and more recent work are not included, other sources (e.g. non-English literature) are missing but none were purposefully ignored at the time. We did not include autotrophic dinoflagellates in the database, but mixotrophic organisms may have been included. This is due to the large uncertainty about which taxa are mixotrophic, heterotrophic or symbiont bearing.

Field data on microzooplankton grazing are mostly comprised of grazing rate using the dilution technique with a 24h incubation period (Landry 1982). As such what is measured is the protozoan community grazing. Laboratory grazing and growth data are focused on pelagic ciliates and heterotrophic dinoflagellates. The experiments measured grazing or growth as a function of prey concentration or at saturating prey concentration (maximal rate).

Note that throughout this manuscript “experiment” means a laboratory experiment that resulted in the measurement of the growth or grazing rate as a function of prey concentration in a controlled setting: predator species, prey species, temperature and light

intensity. When considering every single data point available (each measured rate for a defined predator-prey pair and a certain prey concentration) there is a total of 1485 data points for the ciliates and 801 data points for the dinoflagellates in the raw data linked to the data repository. Experiments that measured growth and grazing simultaneously are counting as 1 data point. The number of experiments and data points collected is available in Table 1, which resumed the data repository.

## 2.2 Metadata

*Laboratory experiments*

The raw data referred to in the worked dataset have two sets of metadata. The first set of metadata, available for all experiments, is the experimental conditions. Experimental conditions are temperature, light intensity, light:dark cycle and a short description of what the experiment measured: grazing or growth rate as a function of: (i) prey concentration, (ii) prey type, and (iii) temperature. The other set of ancillary data is available for both predator and prey. They include cell dimensions, cell volume, cell ESD and cell carbon content if measured or available from other sources. If the value is from an external source, the source is given in the database. Predator concentration (if measured) and prey concentration is given in different units by each author. Within the database they are homogenized to: (i) cell $L^{-1}$, (ii) pgC $L^{-1}$, and (iii) biovolume: $\mu m^3$ $L^{-1}$. Origin of the predator / prey species is given with latitude and longitude, general location or strain identification, and date at which it was isolated.

The metadata for the dataset from the linked repository contain cell volume ($\mu m^3$), cell carbon content (pgC), estimated spherical diameter (ESD, µm) and original reference.

*Field grazing*

The metadata for the field studies include in all cases the location (ocean basin, station, coordinates), depth of the sampled water and temperature, and the method used to measure grazing. In some cases nutrient concentration (all forms of N, and P) and POC were measured. Chlorophyll concentration (µg Chla $L^{-1}$) was measured and used to derive the phytoplankton biomass (µg C $L^{-1}$); lastly, phytoplankton growth and grazing mortality were measured. Bacterial abundance (cell $L^{-1}$) and biomass (µg C $L^{-1}$) was measured along with bacterial growth rate and grazing mortality. Duration and type of experiment used to determine the grazing rate are also given.

*Other processes*

Microzooplankton respiration, excretion and gross growth efficiency have also been compiled from the literature. However, the amount of data available for those is much smaller (<100 data points). The data have been entered into the database with any available metadata and without any processing.

## 2.3 Data processing

The raw data (linked dataset) were collected either by obtaining the value directly from a table provided by the author or from the text. Values available as a figure (rate as a function of concentration) were extracted using the Image J software from the NIH

(imagej.nih.gov/ij). If no carbon content or carbon to volume relationship were provided by the author, the relationships for volume to carbon transformation from Menden-Deuer and Lessard (2000) were used. Rates and concentration were homogenized to units of day-1 and pgC $L^{-1}$, respectively. Data from the raw dataset were fitted to a Michaelis Menten to obtain values for maximal rates. The maximal rates obtained from fitting the data were corrected for temperature using a $Q_{10}$ calculated from collected data that included effect of temperature on the rates; these are the rates presented in the main datasets.

## 3. Data description

### 3.1 Laboratory growth / grazing

Table 1 contains a summary of the number of collected data.

*Pelagic ciliates*

For the pelagic ciliates we collected 31 papers, totaling 342 experiments. The collected data represent15 ciliate genera, the most abundant being *Strombidium sp.* (15 experiments), *Tintinnopsis sp.* (14 experiments) and *Favela sp.* (9 experiments), other genera were used in fewer than 5 experiments. The experiments used a total of 43 different prey genera, with the most abundantly used (more than 10 experiments) being: *Heterocapsa sp.* (28 experiments), *Thalassiossira sp.* (22 experiments), *Isochrysis sp.* (19 experiments), *Pavlova sp.* (18 experiments), *Gymnodinium sp.* (18 experiments) and *Pfiesteria sp.* (14 experiments). Two studies did not use specific prey species, one used

natural assemblages of plankton (60 experiments all from Rassoulzadegan, 1982) and the other used bacteria (4 experiments in Rivier et al., 1985), and the remaining studies used latex beads instead of living prey with a total of 49 experiments.

The ciliates ranged in size (based on the Estimated Spherical Diameter, ESD, Fig. 1; Table 2 for average, standard deviation and median) from 10.0 – 97.6 µm and a carbon content of 131.4 – 41,756.5 pgC cell$^{-1}$. The offered prey covered a size range of 0.4 – 79 µ), and a carbon content of 0.05 – 4,280 pgC cell$^{-1}$. The prey to predator size ratio (ESD ratio) ranged from 0.01 to 3.95.

*Heterotrophic dinoflagellates*

For heterotrophic dinoflagellates we collected a total of 26 papers, totaling 157 experiments. The collected data covered 21 dinoflagellate genera, with the most commonly used being *Protoperidinium sp.* and *Gyrodinium sp.* (12 experiments each), and *Prorocentrum sp.* (9 experiments), other genera were used in fewer than 5 experiments. The prey offered to the dinoflagellates covered 33 genera, the most commonly used being: *Synechococcus sp.* (19 experiment, all from Jeong et al., 2005), *Heterocapsa triquerta* (13 experiments), *Prorocentrum sp*. (12 experiments), and *Dytillium brightwelli* (10 experiments). It is noteworthy that 40 experiments used diatoms, 4 used fish blood cells and two more offered toxic algae as food.

The dinoflagellates used ranged in size from 5.8 – 81.0 µm (Fig. 2; Table 2 for average, standard deviation and median) and a carbon content of 24.4 – 22,421.0 pgC cell$^{-1}$. The offered prey species covered a size range of 1 – 211.9 µm, and a carbon

content of 0.2 – 92,768.8 pgC $cell^{-1}$. The prey to predator size ratio (ESD ratio) ranged from 0.03 to 6.2.

### 3.2 Field grazing

A total of 115 studies were collected for a total of 2548 data points. Out of the 2548 data points not all of them measured the same thing. Community grazing on phytoplankton (phytoplankton grazing mortality, µg C $L^{-1}$), was measured for 1234 of the data points, with only 39 data points for grazing mortality of bacteria (µg C $L^{-1}$).

Out of the 115 studies, 49 looked at the grazing of one type of microzooplankton or the community composition. These provide additional data for dinoflagellates grazing rate (22 data in cell $predator^{-1}$ $day^{-1}$ and 3 in µg C $predator^{-1}$ $day^{-1}$); heterotrophic flagellates, ciliates or even nauplii. The measured grazing rate cover a wide range of the chlorophyll *a* concentration: maximum value 33 µg chl $L^{-1}$, but focuses on low concentrations: average of 1.34 ± 2.55 µg chl $L^{-1}$, with a median of 0.45 µg chl $L^{-1}$ (Fig. 3).

### 3.3 Other processes

Data for microzooplankton respiration are provided by 4 studies for a total of 137 data points. The experiments are conducted with either starved or feeding organisms, for a temperature range of 17-30 ºC. The experiments cover four broad taxa: ciliates (86 data points), amoebae (30 data points), and flagellates (21 data points).

Data for microzooplankton excretion had already been compiled (Nagata, 2000) from 9 studies for a total of 16 data points. Of the 16 measurement, 10 are of *Paraphysomonas imperforata* grazing on bacteria (10) or diatoms (2).

Data for microzooplankton gross growth efficiency can be derived from the laboratory grazing and growth measurement for the experiments that measured both at the same time NUMBERS

## 4. Data caveats and discussion

From this collection of data it appears that there is no consensus on the units used to express grazing or prey concentration. It has either been expressed as the number of prey cell, amount of carbon or the prey biovolume ingested. It is understood by the author that this reflect what could be done at the time of the experiment, also if the prey species is known it is possible to convert between units, relying on additional information available in the literature (e.g. estimated spherical diameter, cell volume to cell carbon conversion). However, those are, often, generalizations around one broad taxonomic level (e.g. Prymnesophytes, diatoms; Menden-Deuer and Lessard, 2000) and will introduce some error; as such additional measurements would be a useful addition to data for broader use.

Another point that comes out of this is that although grazing is widely measured, other processes are often ignored. As such values for metabolic processes are left to be derived from the grazing rate. This is problematic when it comes to model

parameterization: repartition of ingested carbon, and other nutrients, is left to what can be deduced. One way to proceed is to express all processes as a fraction of grazing; they should then add up to 1. The sum of respiration (flow to inorganic nutrients), egestion (flow to dissolved organic matter), growth (into body mass/somatic growth) and unassimilated food (flow to particulate organic carbon as excreted material) should equal grazing. To obtain a better picture of microzooplankton processes as well as the fluxes that are mediated through it, it would be interesting if coordinated measurement of other processes along with grazing were to be considered in the future (Caron et al., 1986).

The available data are a starting point for investigating predator prey size ratio or prey type (e.g. specific species, food preference) effect on grazing and/or growth rate. Hanssen et al. (1994) established predator:prey size ratio of 8:1 for oligotrich ciliates with 3 data points and a predator:prey size ratio of 1:1 for heterotrophic dinoflagellates with one data point. The data presented here are for the most part within this range but outside of it as well and could contribute to revisiting optimal predator:prey size ratio. Similarly because of the number of grazing and growth experiment there is a chance to look at the coupling between both and variations of gross growth efficiency (Montagnes and Fenton, 2012).

Finally, the data presented here have been useful in parameterizing the microzooplankton in the Dynamic Green Ocean Model PlankTOM5 (Buitenhuis et al., 2010). We hope it will also prove helpful in designing future experiments and know where to start to fill in the knowledge gaps.

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## Tables

**Table 1:** Number of compiled studies or experiments and resulting number of data points for the different rates collected in this manuscript.

| Organism and rate | Experiments/studies | Data points |
|---|---|---|
| Pelagic Ciliates laboratory grazing and growth | 342 | 1845 |
| Heterotrophic Dinoflagellates laboratory grazing and growth | 157 | 801 |
| Microzooplankton field grazing | 115 | 2548 |
| Microzooplankton respiration | 4 | 137 |
| Microzooplankton excretion | 9 | 16 |
| Microzooplankton gross growth efficicency | 199 | 199 |

**Table 2:** Average, standard deviation and median of the ESD (µm) and carbon content (pgC $cell^{-1}$) found in the laboratory experiments. Values are for predator and prey, plus the prey to predator size ratio.

| | ESD (µm) | | | Carbon content (pgC $cell^{-1}$) | | |
|---|---|---|---|---|---|---|
| | average | std | median | average | std | median |
| ciliate | 45.50 | 20.30 | 45.00 | 8,723.30 | 9,412.60 | 5,844.60 |
| ciliate prey | 10.00 | 14.30 | 6.90 | 161.50 | 469.40 | 37.40 |
| prey:predator size ratio | 0.29 | 0.50 | 0.15 | - | - | - |
| dinoflagellate | 26.80 | 13.10 | 25.30 | 1,994.10 | 3,004.00 | 1,103.10 |
| dinoflagellate prey | 17.20 | 25.70 | 11.50 | 1,971.00 | 11,044.30 | 95.60 |
| prey:predator size ratio | 0.68 | 0.82 | 0.50 | - | - | - |

**Figure legends**

**Figure 1**: Ciliate ESD as a function of prey ESD from laboratory experiments (ESD in µm)

**Figure 2**: Dinoflagellate ESD as a function of prey ESD from laboratory experiments

**Figure 3**: Measured specific grazing rate as a function of chlorophyll a concentration, field data (ESD in µm).

**Figure 4**: Data on (A) gross growth efficiency from Straile (1997), downward sloping line is ciliate linear regression (GGE = 0.68 − 0.022T, n = 132, r2 = 0.36); upward sloping line is dinoflagellate and flagellate linear regression (GGE = 0.046 + 0.014T, n = 173, r2 = 0.18), (B) excretion as the fraction of grazing that is converted to DOC (dis for Dissolved Organic Carbon), (C) respiration as the respiration of starved micro-zooplankton (Fenchel and Finlay, 1983). Adapted from Buitenhuis et al., 2010. Crosses are field measurements, circles are ciliates, triangles are dinoflagellates, plus signs are flagellates, and squares are amoeba.

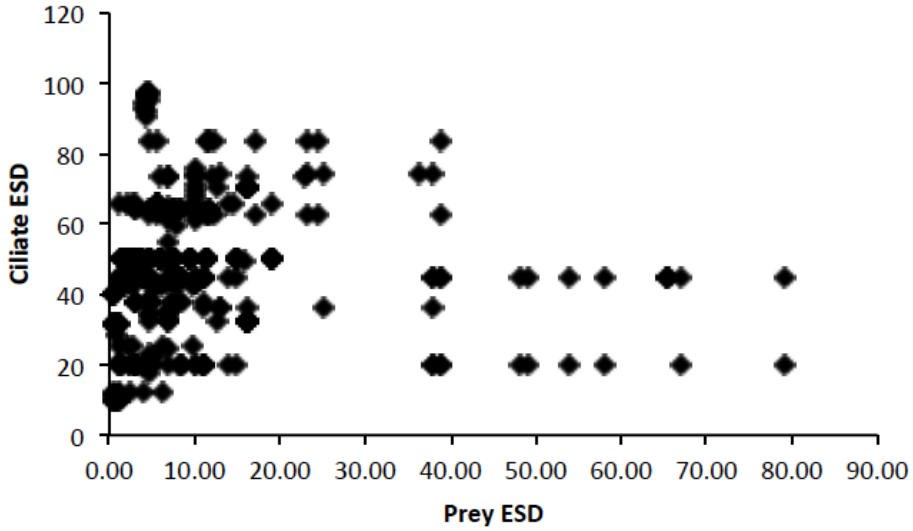



Figure 1

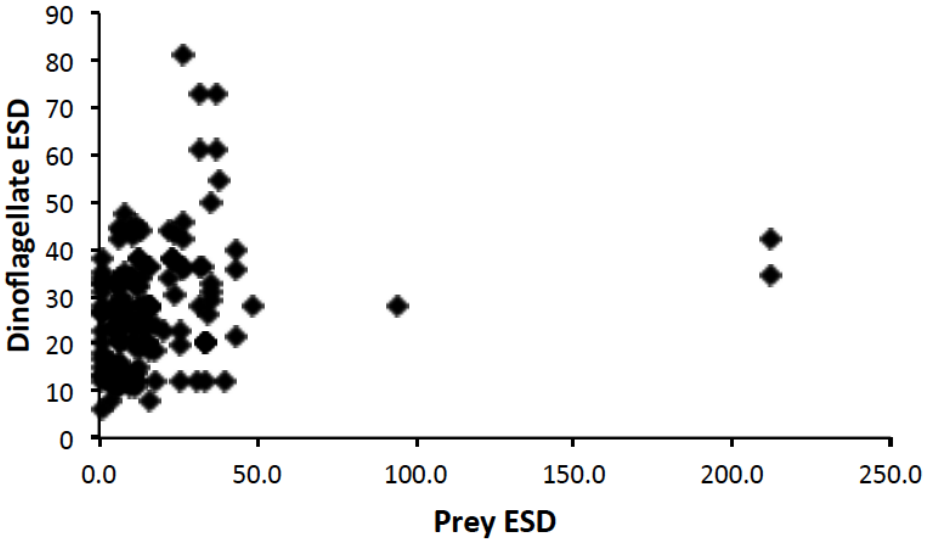



Figure 2

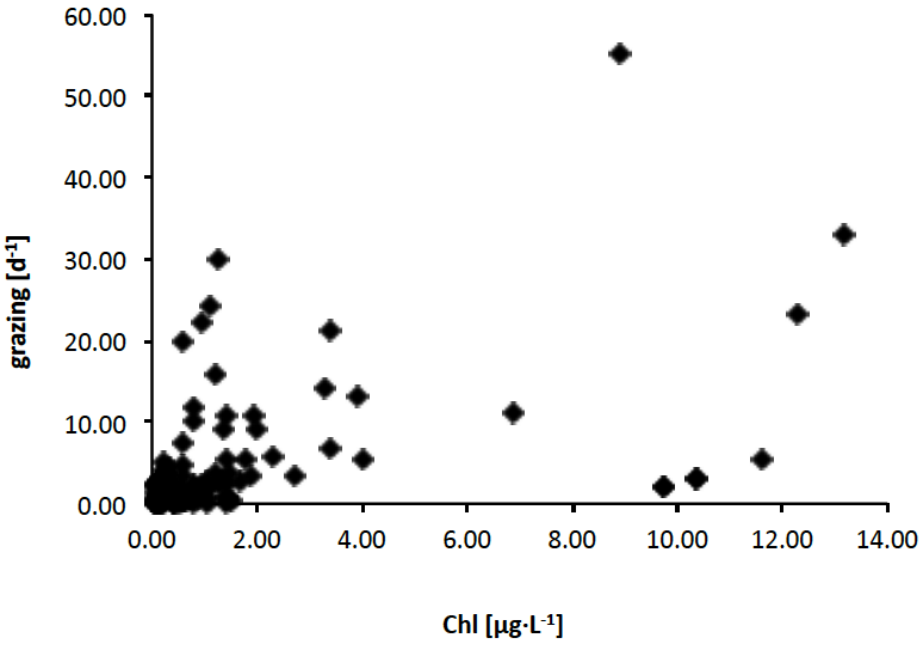
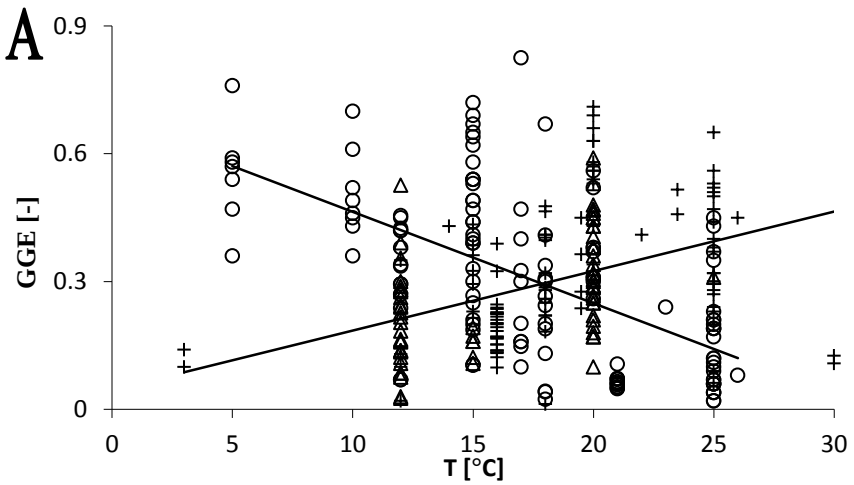

60.00
50.00
40.00
30.00
20.00
10.00
0.00
grazing [d-1]
0.00
2.00
4.00
6.00
8.00
10.00
12.00
14.00
Chl [µg·L-1]

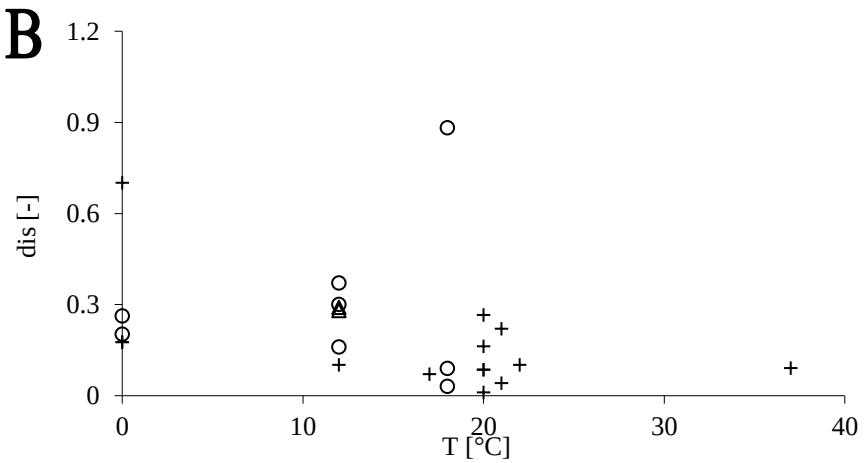
Figure 3

1




2

3

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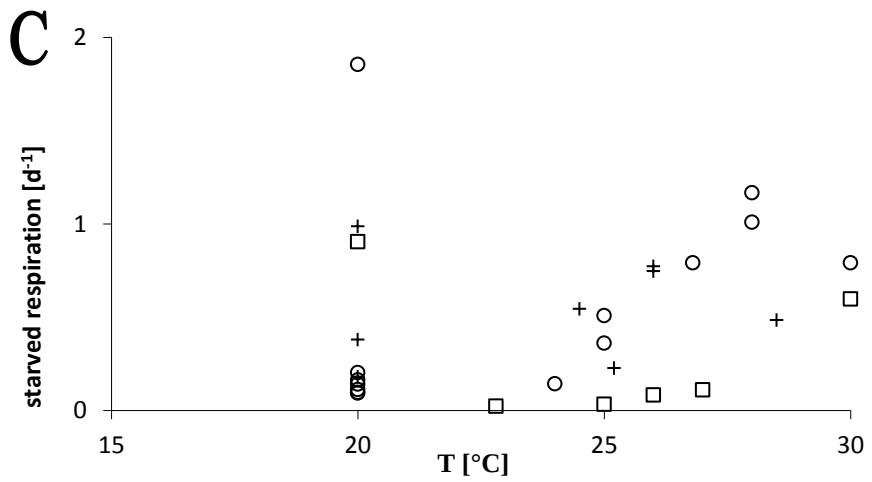


Figure 4