Earth Syst. Sci. Data Discuss., 7, 149–167, 2014
www.earth-syst-sci-data-discuss.net/7/149/2014/
doi:10.5194/essdd-7-149-2014

Open Access Earth System Science Data Discussions

Microzooplankton functional responses in the lab and in the field

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Received: 31 January 2014 – Accepted: 21 March 2014 – Published: 10 April 2014

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Published by Copernicus Publications.

Abstract

We present a collection of data relating to microzooplankton physiological traits collected from the literature. We define microzooplankton as unicellular zooplankton (protozoans). 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).

Link to the repository: doi:10.1594/PANGAEA.820368 and doi: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 can be defined either taxonomically as a diverse grouping of heterotrophic protists, or operationally as a size class, typically < 200 µm. The difference between the taxonomic and operational definitions is that the latter includes the smaller life-stages of metazoans such as copepod nauplii. The protists can be divided into two size fractions. The larger than 20 µm protistan fraction mostly consists of pelagic ciliates (ciliates) and heterotrophic dinoflagellates (dinoflagellates), and the smaller fraction mostly consists of heterotrophic nanoflagellates (HNF). In this paper microzooplankton is defined in the taxonomic sense.

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Ciliates, dinoflagellates and HNF tend to have similar biomass (Buitenhuis et al., 2010), implying that HNF dominate microzooplankton numerically. Ciliates are filter feeders, sieving the surrounding water to find and capture their prey and are known to have an optimal prey size roughly one tenth of their own diameter (Heinbokel, 1978; Jonsson, 1986; Hansen et al., 1994). Heterotrophic dinoflagellates are raptorial feeders: they actively swim around in search of prey items that are either engulfed or digested externally (palium and peduncle feeding; Jakobsen, 1999). The variety of feeding modes found in dinoflagellates allows this group to feed on a wide range of prey and particle sizes up to five times larger than their own size (Hansen et al., 1994). Heterotrophic nanoflagellates as a class includes both filter feeding and raptorial feeding individuals (Boenigk and Arndt, 2000a, b). The differences in sizes, feeding mode and prey size spectrum results in different grazing selectivity on phytoplankton communities, with dinoflagellates consuming diatoms, ciliates primarily nanophytoplankton and HNF picoplankton and small nanophytoplankton. Metabolic rates of similar-sized ciliates and dinoflagellates are also different with higher grazing and growth rate in ciliates than dinoflagellates (Strom, 1998).

The differences in traits and grazing selectivity between microzooplankton's three dominant groups indicate a variety of impacts from microzooplankton on their environment (e.g. export, primary production, carbon cycle). The impact will depend on the composition of the microzooplankton community, the composition of the phytoplankton community and other environmental factor. To advance understanding of microzooplankton, its role in the ecosystem and its representation in models, we present here a collection of data on microzooplankton processes. 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.

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2 Data source and metadata

2.1 Data collection

From the existing literature, we synthesized all data that we could find on microzooplankton. Some sources might be missing but none were purposefully ignored. 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 24 h incubation period (Landry, 1982). 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 grazing rate).

Note that throughout this manuscript "experiment" means a laboratory experiment that resulted in the measurement of the maximal rate (growth or grazing) in a controlled setting: predator species, prey species, amount of prey, 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, counting experiments that measured growth and grazing simultaneously as 1 data point. The number of experiments and data points collected is available in Table 1.

2.2 Metadata

2.2.1 Laboratory experiments

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

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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.

2.2.2 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 ($\mu g\,Chl\,a\,L^{-1}$) was measured and used to derive the phytoplankton biomass ($\mu g\,C\,L^{-1}$), lastly, phytoplankton growth and grazing mortality were measured. Bacterial abundance (cell L^{-1}) and biomass ($\mu g\,C\,L^{-1}$) was measured along with bacterial growth rate and grazing mortality. Duration and type of experiment used to determine the grazing rate are also given.

2.2.3 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.

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3 Data description

3.1 Laboratory growth/grazing

3.1.1 Pelagic ciliates

For the pelagic ciliates we collected 31 papers, totaling 342 experiments. The collected data represent 15 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) from 10.0–97.6 µm (average ESD of 45.5 ± 20.3 µm, median of 45.0 µm) and a carbon content of 131.4–41 756.5 pg C cell^{-1} (average of 8,723.3 ± 9412.6 pg C cell^{-1}, median of 5844.6 pg C cell^{-1}). The offered prey covered a size range of 0.4–79 µm (average ESD of 10.0 ± 14.3 µm, median ESD of 6.9 µm), and a carbon content of 0.05–4280 pg C cell^{-1} (average of 161.5 ± 469.4 pg C cell^{-1}, median carbon content of 37.4 pg C cell^{-1}). The prey to predator size ratio (ESD ratio) ranged from 0.01 to 3.95 (average of 0.29 ± 0.5, with a median size ratio of 0.15).

3.1.2 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

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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 (average ESD of 26.8 ± 13.1 µm, median ESD of 25.3 µm, Fig. 2) and a carbon content of 24.4–22 421.0 $\mathrm{pg\,C\,cell^{-1}}$ (average of 1994.1 ± 3004.0 $\mathrm{pg\,C\,cell^{-1}}$, median of 1103.1 $\mathrm{pg\,C\,cell^{-1}}$). The offered prey species covered a size range of 1–211.9 µm (average ESD of 17.2 ± 25.7 µm, median ESD of 11.5 µm), and a carbon content of 0.2–92 768.8 $\mathrm{pg\,C\,cell^{-1}}$ (average of 1971.0 ± 11 044.3 $\mathrm{pg\,C\,cell^{-1}}$, median carbon content of 95.6 $\mathrm{pg\,C\,cell^{-1}}$). The prey to predator size ratio (ESD ratio) ranged from 0.03 to 6.2 (average of 0.68 ± 0.82, with a median size ratio of 0.5).

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, $\mathrm{\mu g\,C\,L^{-1}}$), was measured for 1234 of the data points, with only 39 data points for grazing mortality of bacteria ($\mathrm{\mu g\,C\,L^{-1}}$).

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 $\mathrm{predator^{-1}\,day^{-1}}$ and 3 in $\mathrm{\mu g\,C\,predator^{-1}\,day^{-1}}$); heterotrophic flagellates, ciliates or even nauplii. The measured grazing rate cover a wide range of the chlorophyll *a* concentration: maximum value 33 $\mathrm{\mu g\,chl\,L^{-1}}$, but focuses on low concentrations: average of 1.34 ± 2.55 $\mathrm{\mu g\,chl\,L^{-1}}$, with a median of 0.45 $\mathrm{\mu g\,chl\,L^{-1}}$ (Fig. 3).

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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 °C. The experiments cover four broad taxa: ciliates (86 data points), amoebae (30 data points), 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 had already been compile as well (Straile, 1997), from 74 studies for ciliates, 62 for dinoflagellates and 63 for nanoflagellates, for a total of 199 data points.

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. 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) and will introduce some error. However, not converting means that data cannot be compared and a mine of useful information is then lost to the broader community.

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. 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 bodymass/somatic

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growth or eggs) and unassimilated food (flow to particulate organic carbon as fecal pellets or a result of sloppy feeding) should equal grazing. Another 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 more complete data from the database would be useful to look at diverse aspect of grazing like the effect of prey nutrient content on the grazing response of microzooplankton (i.e. prey selection, Mitra and Flynn, 2006) or a possible interference of microzooplankton with self, for example: access to prey when microzooplankton biomass is superior to that of phytoplankton (Ardity and Ginzburg, 1989), and intra-class predation.

Finally, although there are gaps in the microzooplankton rates covered, 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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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

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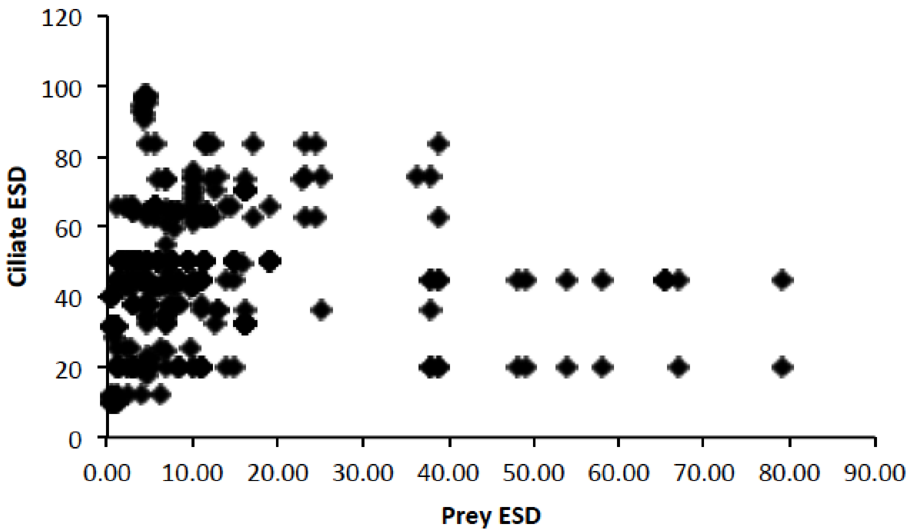

Fig. 1. Ciliate ESD as a function of prey ESD from laboratory experiments.

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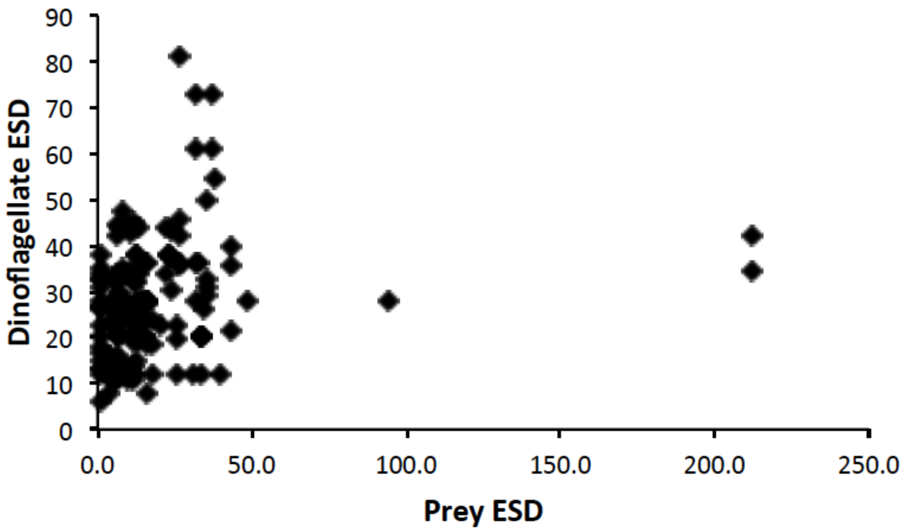

Fig. 2. Dinoflagellate ESD as a function of prey ESD from laboratory experiments.

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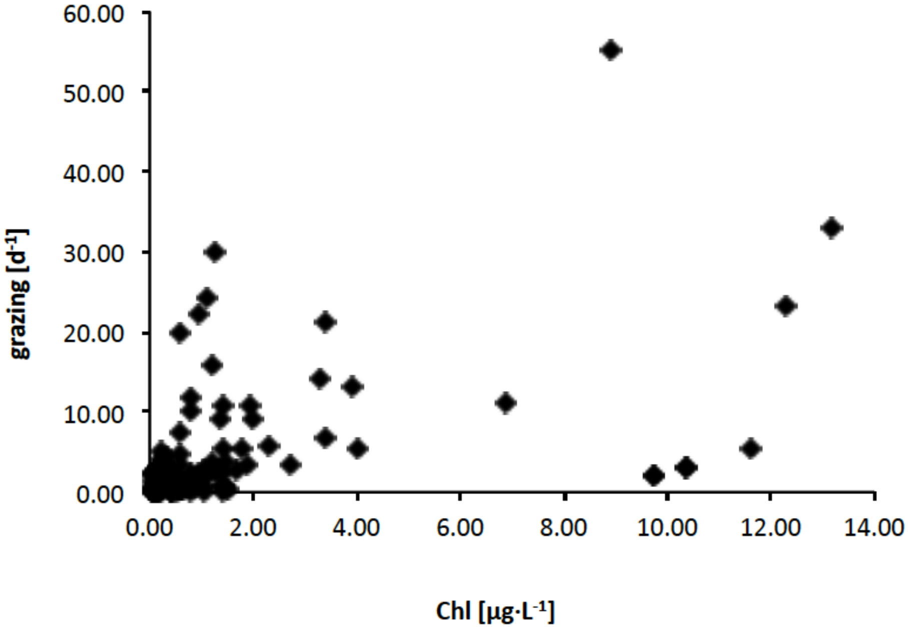

Fig. 3. Measured specific grazing rate as a function of chlorophyll *a* concentration, field data.

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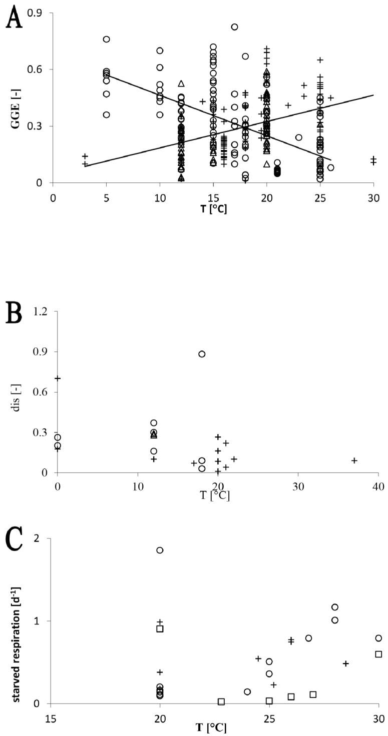

Fig. 4. Data on **(A)** gross growth efficiency from Straile (1997), downward sloping line is ciliate linear regression (GGE = 0.68 – 0.022 T, n = 132, r^2 = 0.36); upward sloping line is dinoflagellate and flagellate linear regression (GGE = 0.046 + 0.014 T, n = 173, r^2 = 0.18), **(B)** excretion as 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.

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