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Trophic role and top-down control of a subarctic protozooplankton community

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Abstract:

Plankton succession was investigated in the subarctic Godthåbsfjord, Western Greenland, from March to August 2010. The trophic role of protozooplankton (ciliates and heterotrophic dinoflagellates) was evaluated with emphasis on their seasonal succession and as prey for the copepod community. The integrated protozooplankton biomass ranged between 0.1 and 4.0 g C m^{-2}, and was dominated by ciliates. Over the 6 mo study period, maximum potential ingestion rates of the protozooplankton ranged from 0.02 to 1.2 g C m^{-2} d^{-1}, corresponding to 30 to 194% of primary production d^{-1} or 0.5 to 37% of phytoplankton biomass d^{-1}. The highest copepod biomass (24 g C m^{-2}) occurred in spring, with *Metridia longa* alone contributing up to 92% of the biomass. A grazing experiment with *M. longa* feeding on a natural plankton assemblage confirmed that this species cleared cells in the size range 10 to 60 µm with an average clearance rate of 2.4 ml µg C^{-1} d^{-1}. The copepod community, dominated by the genera *Calanus, Metridia, Pseudocalanus, Oithona, Microsetella* and *Triconia/Oncaea,* accounted for 72 to 93% of the copepod biomass in the spring. After the large calanoid copepod species left the surface layer, the protozooplankton increased numerically and were the most important grazers for some weeks until a late summer copepod community, dominated by cyclopoids *Oithona* spp., controlled the protist community. Our study indicated that protozooplankton succession is regulated by copepod grazing during most of the season, and that these protists provide an essential source of nutrition for the copepod populations.

Keywords: Protozooplankton ; Subarctic ; Grazing ; *Metridia longa*

1. Introduction

Greenlandic fjords are highly valuable ecosystems for the commercial as well as cultural fishing and hunting and support a rich and diverse wildlife (Hamilton et al. 2000). Climate models for the Arctic predict significant increases in temperatures, decline in the sea ice cover and acceleration of glacial melting (Stroeve et al. 2007, Holland et al. 2008, Comiso et al. 2008, Motyka et al. 2011). The Greenlandic fjords are major outlets of glacial runoff and changes in the climate will hereby affect the hydrography and possibly food web structures within these ecosystems (Mortensen et al. 2011).

The Godthåbsfjord is a subarctic fjord system located next to Nuuk, the Capital of Greenland. It is one of the largest fjord systems in Greenland harbouring large populations of e.g. capelin and Atlantic cod (Bergstrøm 2006, Storr-Paulsen et al. 2004, Smidt 1979). The copepod community is dominated by *Pseudocalanus* spp, *Microsetalla* sp., *Oithona* spp. and *Metridia longa* (Arendt et al. 2010 and 2012, Tang et al. 2011), in contrast to most other Arctic regions where copepods of the genus *Calanus* dominate (Digby 1953, Nielsen and Hansen 1995, Rysgaard et al. 1999, Seuthe et al. 2011).

Especially in the inner parts of the Godthåbsfjord the large calanoid copepod *Metridia longa* dominates the copepod community (Arendt et al. 2010, Tang et al. 2011). *M. longa* was previously not recognized as an important component in the Arctic food web (e.g. Madsen et al. 2001) since sampling often is conducted during daytime when *M. longa* is absent from the upper water column (Hays 1995, Falkenhaug et al. 1997, Daase et al. 2008). However, recent studies show that *M. longa* is highly abundant during the productive season in the Godthåbsfjord (Arendt et al. 2010 and 2012, S. Kjellerup unpublished) where its high lipid content (Hopkins et al. 1984) makes it a high quality prey item for planktivores (Pedersen and Fossheim 2008). *M. longa* is considered an omnivore; feeding preferable on protozooplankton and zooplankton in the size range 5-300 µm (Haq 1967), even when phytoplankton within this size range is available (Campbell et al. 2009).

We investigated the seasonal plankton dynamics in a side branch of the Godthåbsfjord, Kapisigdlit Fjord, with emphasis on the role of protozooplankton in the food web and the interaction between the protozooplankton and the copepod communities. The latter was evaluated from maximum potential production and clearance rates given in Hansen et al. (1997) and Møller et al. (2006). Estimates of *M. longa* maximum potential clearance rates were supported by a grazing experiment with *M. longa* feeding on a natural plankton assemblage.

2. Materials and Methods

2.1. Locality and sampling

Sampling was conducted on 15 occasions from 24 March to 5 August, 2010, in the fjord branch Kapisigdlit in the inner part of the Godthåbsfjord system, West Greenland (Fig. 1), from the vessel Lille Masik, except 16-18 June, where sampling was conducted from R/V Dana (National Institute for Aquatic Resources, Denmark). Sampling was conducted in early evening at Station K4 located 64°25'N, 50°22'W (Fig. 1).

Vertical profiles of water temperature, salinity and density were obtained from the surface to ca. 10 m above bottom using a CTD (SBE 19 plus or 911 plus, SeaCat, and a SBE 25 SM, MicroCat). CTDs were calibrated against each other, and salinity samples that were collected on 24 May and 6 July 2010 and analysed on a Portosal salinometer. Water samples were collected at 1, 10, 20,

50, 75, 100, 150 and 250 m depth using a Niskin bottle. Inorganic nutrient samples (dissolved phosphate, nitrate, nitrite, ammonium and silicate) were immediately frozen (-20°C) for later analysis on a Skalar autoanalyser following the procedures of Hansen and Koroleff (1999). The precision (analytical reproducibility) of the nutrient analyses was 0.06, 0.1, and 0.2 µM for phosphate, nitrate, and silicate, respectively. Water for Chlorophyll *a* (chl *a*) was stored cold and dark in 10 l containers for 1-12 h until it was processed. One exception was 3 April 2010, where the water was stored ca. 36 h because the water unintentionally froze onboard and had to defreeze before filtration.

2.2. Phytoplankton

Chl *a* concentration was determined from triplicate subsamples of 100-500 ml seawater and size fractionated on Whatman GF/F filters (0.7 µm pore-size, total phytoplankton biomass) and 10 µm mesh filters (from 1, 10 20, 50 and 100 m). Filters were extracted in 96 % ethanol for 12-24 h (Jespersen and Christoffersen 1987) and analyzed immediately after or stored at -20° C for a maximum of 2 months. Chl *a* was measured on a TD-700 Turner fluorometer calibrated against a chl *a* standard before and after acidification (Yentsch and Menzel 1963) and converted into µg C using a conversion factor of 42.7 (Juul-Pedersen et al. 2006).

Primary production was measured on 6 occasions using the C^{14} incubation method (Stemann-Nielsen 1958). Water samples from 5, 10, 20, 30 and 40 m was incubated at *in situ* depths for ca. 2 hours in Winkler glass bottles (2 light and 1 dark bottles at each depth) on a free-drifting array. After recovery the samples were kept completely dark until filtration on Whatman GF/C filters. The filters were then added 100 µM 1M HCl and left to fumigate for ca. 12 hours to remove any remaining C^{14} on the filter. Scintillation liquid (PerkinElmer Ultima Gold) was added and the sample was mixed and left for ca. 24 hours before analyses on a TriCarb 2800 TR Liquid scintillation analyzer (PerkinElmer, USA). *In situ* dissolved inorganic carbon (DIC) concentrations measured with a CM5012 CO2 Coulometer according to Rysgaard & Glud (2004) was applied for the calculation of primary production. The dark bottle value from each depth was subtracted from the light bottle value in order to correct for uptake of C^{14} in dark. *In situ* incoming irradiance, as photosynthetically active radiation (PAR; supplied by ASIAQ, Greenland), during the deployment vs. the entire day was used to calculate the daily primary production. Primary production was integrated vertically from 0-45 m covering the euphotic zone.

2.3. Protozooplankton

Biomass, abundance and taxonomic composition of protozooplankton was determined at 5 depths; 1, 10, 20, 50/60 and 100 m. Water samples of 250-300 ml were collected with a Niskin bottle at each depth and gently tapped through a silicon tube into brown glass bottles and fixed in acidic Lugol's solution (final concentration of 2%). Samples were kept cool and dark until analyses (maximum of 6 months). Depending on the cell concentration 50 to 100 ml sub-samples were allowed to settle for 24 h in sedimentation chambers. All or a minimum of 300 cells were identified and counted using an inverted microscope (Nikon K18). Protozooplankton depth profiles were determined 9 times during the investigated period.

Protozooplankton were identified to genus level when possible. Ciliates were all categorized as heterotrohic/mixotrophic. The dinoflagellates were dominated by the large heterotrophic *Gyrodinium spirale* (mean: 46 % of the dinoflagellates biomass, range 0-98 %) and the small heterotrophic *Gyrodinium glaucum* (mean: 22 % of the dinoflagellates biomass, range: 8-78 %). In

general all dinoflagellates > 10 µm are classified as heterotrophic/mixotrophic (Hansen 2011). Cell volumes were calculated using appropriate geometric shapes without including the membranelles. To compensate for cell shrinkage due to Lugol's solution preservation cell volumes were increased by a factor of 1.3 (Stoecker et al. 1994). The bio-volumes (V) were converted to carbon (pg C) using the volume-to-carbon conversion factors given in Table 1.

During enumeration ciliates and dinoflagellates were divided into groups covering 10-µm ranges of equatorial spherical diameter (ESD) starting with 10-20 µm. ESD and cell volume are related by:

$\pi/6 \times \mathrm{ESD}^3 = \text{cell volume}$.

Rates of protozooplankton maximum potential clearance rates were calculated according to the equation in Hansen et al. (1997) for ciliates:

$$\mathrm{Log}(C_{max}) = 1.491 - 0.23\mathrm{Log}(P_{vol}) \quad (1)$$

and for heterotrophic dinoflagellates:

$$\mathrm{Log}(C_{max}) = 0.851 - 0.23\ \mathrm{Log}(P_{vol}) \quad (2)$$

where C_{max} is the maximum potential clearance rate and P_{vol} is the cell volume in μm^3. Maximum potential clearance rate was normalized to *in situ* temperatures (ranging between 0.5 to 13 °C) by using a Q_{10} factor of 2.8 (reviewed in Hansen et al. 1997). Maximum potential ingestion rate, *I* (µg C $cell^{-1}$ d^{-1}) was calculated from size specific maximum potential clearance rates and the *in situ* chl *a* concentration.

$$I = C_{max} \times d \quad (3)$$

where *d* (µg C l^{-1}) is the phytoplankton density. Ciliates were assumed to graze on the chl *a* fraction <10 µm, while heterotrophic dinoflagellates were assumed to graze the chl *a* fraction >10 µm (Jakobsen and Hansen 1997). Protozooplankton production (µg C l^{-1} d^{-1} or g C m^{-2} d^{-1}) of ciliates and dinoflagellates were estimated from the maximum potential ingestion rates using an average gross growth efficiency of 0.33 (Hansen et al. 1997/2000).

2.4. Copepod biomass

Copepods were collected in five depth strata (0-50, 50-100, 100-150, 150-200, 200-235 m) with a multinet (50-µm mesh size, Multinet, Hydrobios type mini). The nets were hauled with a speed of

0.2-0.3 m s^{-1} and samples were immediately preserved in buffered formalin (4% final concentration). Sampling was carried out around 18:00 local time. Samples containing high numbers of copepods were split into subsamples. In each sample/subsample all nauplii and copepodite development stages were identified down to species or genus level and length was measured of up to 10 individuals of each stage. Biomass of the different copepod species were calculated based on measurements of prosome length, and length/weight (L/W) relationships from the literature (table 2).

2.5. *Metridia longa* grazing experiment

Seawater was collected on 28 July 2010 from 20 m with a 30 l Niskin bottle and transferred gently *via* a silicon tube into a 25 l dark carboy. The carboy was stirred gently, nutrients added (15µM NH_4Cl and 1µM Na_2HPO_4) and seawater was inverse filtered *via* a silicon tube through a 200 µm mesh to remove mesozooplankton and filled into 42 transparent 600 ml polycarbonate bottles.

M. longa for the experiment was collected using a 200-µm WP2 net. One actively-swimming adult female *M. longa* was added to 28 polycarbonate experimental bottles (600 ml). Fourteen additional bottles without copepods were used as control bottles. To ensure that copepods on average cleared < 30 % of the prey, half of the experimental and control bottles were incubated for 12 h and the other half for 24 h. Bottles were incubated in darkness at 5 °C (*in situ* temperature was 3.2 °C) and rotated by hand every 6 h. Dark incubation was chosen since *M. longa in situ* undergo dial vertical migrations and feed during the night (Hays 1995). As soon as the experiment was terminated triplicate sub-samples were taken from the bottles for determination of chl *a*. For protozooplankton analysis 100 ml subsamples were fixed in acidic Lugol's solution in a final concentration of 2 %.

Metridia longa clearance rate, *F*, (ml µg C^{-1} d^{-1}) was calculated from Frost (1972) when prey growth rates differ significantly from the controls (t-test, $p < 0.05$). Clearance rate on protozooplankton was calculated for four size classes of ciliates (7-15µm, 15-30 µm, 30-40 µm and 40-60 µm), one size class of dinoflagellates (25-50 µm) and two size classes of nanoflagellates (3-4 µm and 5-6 µm, respectively), whereas clearance rate on phytoplankton was calculated using chl *a* as a proxy. Clearance rates were converted into *in situ* temperatures by using a Q_{10} factor of 2.8 (Hansen et al. 1997/2000).

2.6. Copepod community grazing

Clearance capacity of the copepod community was estimated from maximum specific clearance rate assuming that the copepod population was not food saturated. Maximum specific clearance rate (F) of *M. longa* was estimated according to Hansen et al. (1997/2000):

$$Log\ (F) \times 10^5 = Log\ (1.5753) - 0.23\ Log\ (V) \qquad (7)$$

where *V* is the copepod body volume in μm^3. Since *M. longa* undertake pronounced dial vertical migration and only visit the surface during night, *M. longa* maximum potential clearance capacity is only realized in the upper 50 m 6 h per day i.e. around midnight (Kjellerup unpublished).

Maximum potential clearance was converted into *in situ* temperatures in the upper 50 m of the water column using a Q_{10} factor of 2.8 (Hansen et al. 1997/2000).

The maximum potential clearance rates of *Calanus* spp. and other copepods (i.e. *Pseudocalanus*, *Oithona*, *Centropages* and *Microcalanus*) were estimated according to Møller et al. (2006):

2.7. Protozooplankton

$$\text{Log}(F) = 1.16 - 0.45\ \text{Log}(W),\ r^2 = 0.73 \qquad (8)$$

where *W* is the copepod biomass (µg C). Maximum potential clearance rates of *Calanus* spp. and other copepods were estimated assuming that the copepod communities were distributed evenly throughout the water column. Maximum potential clearance rates were converted into *in situ* temperatures using a Q10 factor of 2.8 (Hansen et al. 1997/2000). From March until break-up of Kapisigdlit River around 20 June 2010, Q_{10} was calculated in the 0-100 m depth stratum. Hereafter *Calanus* spp. and other copepods were distributed below the warm and fresh surface water and Q_{10} was calculated in the 20-100 m depth stratum. The small copepods *Microsetella* spp. and *Oncaea* spp. were not included in the grazing estimates since they both have morphologies and feeding strategies suited for solid substrate such as marine snow (Koski et al. 2007).

3. Results

3.1. Hydrography

Sampling was initiated in March when the water column was well-mixed with cold, saline, nutrient-rich water throughout the euphotic zone (Fig. 2, Table 3). The chl *a* concentration was low (0.5-1 µg l^{-1}) and evenly distributed in the upper 40 m (Fig. 2C). From late April a weak halocline was established (Fig. 2B) and additional heat was trapped in the surface layer (Fig. 2A). The stratification stimulated phytoplankton growth which then quickly depleted the nitrate to below 0.5 µM in association with the peak of the first phytoplankton bloom of 3 µg chl *a* l^{-1} (Fig. 2C).

From May, melt water was added to the surface layer as runoff from land and culminated with the seasonal pulse of fresh water following the break-up of ice in the Kapisigdlit River around 20 June 2010. Hereafter the surface salinity rapidly decreased from 31 to 16 by the beginning of August. The melt water established a strong halocline, strengthened by a thermocline due to warming of the freshwater surface plume to above 13 ºC on the last sampling day (5 August 2010). After the depletion of nitrate above the pycnocline, a subsurface bloom developed with a peak value of 12 µg chl *a* l^{-1} on 26 June 2010 (Fig. 2).

3.2. Nutrients

High concentrations of nutrients (i.e. phosphorus, nitrate and silicate) were measured in the upper 100 m of the water column at the initiation of the investigation (data not shown). During the first part of the investigation the average nitrate concentration in the upper 50 m stratum decreased from 6.8 ± 0.3 µM to 0.5 ± 0.3 µM as a result of increased stratification and the developing phytoplankton bloom (Fig. 2 C). The overall phosphorous and silicate distributions (Table 3) and succession mirrored that illustrated by nitrate (Fig. 2C), but were not fully depleted in the euphotic

zone. In association with the breakup of the ice in the Kapisigdlit River, a freshwater plume overlaid the fjord water, characterized by a very high concentration of silicate (Table 3).

Comparison of the major nutrients species (Fig. 3 A-C) suggest nitrate limitation of the primary producers, since nitrate concentration in the upper 50 m became depleted relative to the Redfield ratios with respect to phosphorus (Fig. 3A) and silicate (Fig. 3B) .

3.3. Phytoplankton

The integrated phytoplankton biomass averaged 3.0 ± 2.4g C m^{-2} over the study period with peak values of 3.5 and 11.4 g C m^{-2} during the spring and summer blooms, respectively (Fig. 4). The phytoplankton spring bloom was initially composed of small phytoplankton cells (< 10 µm) which progressed into a phase dominated by larger cells (> 10 µm). Within a few weeks, nitrate was depleted in the photic zone, and the total phytoplankton biomass and relative proportion of large phytoplankton cells decreased. As the Kapisigdlit River broke-up in mid-June a freshwater plume resulted in a temporary upwelling of nutrients into the photic zone (Fig. 2) developing a summer bloom and the relative proportion of large cells increased. Nutrients became once again depleted in the stratified water column and the relative proportion of small cells increased (Fig. 4).

Average integrated primary production (PP) for the investigated period was 0.11 g C m^{-2} d^{-1} (n = 6) with a maximum of 0.21 g C m^{-2} d^{-1} in early spring (Fig. 4). The phytoplankton community was dominated by chain-forming diatoms (mainly *Thalasiosira* spp.) during the two blooms. In the non-bloom periods the phytoplankton biomass was mostly composed of small (< 10 µm) unidentified nanoflagellates, primarily cryptophytes and solitary haptophytes (probably *Phaeocystis*).

3.4. Protozooplankton

At the onset of the investigation, the abundance of protozooplankton was low (<10^3 cells l^{-1}), but throughout June and July a diverse protozooplankton community developed in the upper 50 m with cell concentrations as high as 3 ×10^4 cells l^{-1}(Fig. 5 A-B). Ciliates dominated the protozooplankton community (Fig. 5A), while dinoflagellates were less abundant (Fig. 5B).The protozooplankton biomass mirrored the phytoplankton biomass with maximum biomass associated with the chl *a* max at a depth of 19 ± 3 m (mean ± SD). Protozooplankton biomass peaked on July 6 with 155 µg C l^{-1} (Fig. 5 C-D).

Eleven genera of ciliates and seven genera of dinoflagellates were identified. The main contributors to the protozooplankton biomass were *Strombidium* spp. and *Gyrodinium spirale* during spring, while *Mesodinium* sp., *Strobilidium* spp., *Strombidium* spp., *Laboea strobila* and *G. spirale* dominated during the summer (Fig. 6). Numerically, small (< 20 µm) ciliates dominated the protozooplankton community (Fig. 6).

The integrated biomass of protozooplankton ranged between 0.1 and 4.0 g C m^{-2} (Fig. 7A, 7B and 8A). Initially, and by the termination of the investigated period, the protozooplankton community was composed of small ciliates and dinoflagellates. However, during the bloom period, the relative amount of large cells increased. Thus, from June 45-98% of the integrated protozooplankton biomass was composed of large specimens (>40 µm), mainly ciliates (Fig. 7A).

The estimated protozooplankton production ranged between 0.01 and 0.42 g C m^{-2} d^{-1} (Fig. 7C and 7D). For ciliates the seasonal variation mirrored the integrated biomass with small ciliates being the

most productive during spring and large ciliates being most productive during the summer (Fig. 7C).

Assuming that ciliates only feed on phytoplankton <10 µm and dinoflagellates only feed on phytoplankton >10 µm (Hansen et al. 1994), the protozooplankton maximum potential ingestion rates ranged between 0.01 and 1.2 g C m^{-2} d^{-1} corresponding to 26 to 196 % of the primary production d^{-1} (data not shown) or 0.5 to 50 % of phytoplankton biomass d^{-1} (Fig. 7E and 7F). The highest maximum potential ingestion rates were achieved in the summer after the disappearance of *Metridia longa*.

3.5. Copepod succession

The copepod community was dominated by the genera *Calanus, Metridia,Oithona, Microsetella*, *Oncaea* and *Pseudocalanus. Metridia longa* dominated the copepod biomass during spring accounting for 72-93 % of the copepod biomass. The integrated biomass of copepods showed a maximum of 24 g C m^{-2} in early March (Fig. 8B) but decreased after June 3 where the community changed towards dominance of smaller species such as *Pseudocalanus* spp., *Microsetella norvegica* and *Oithona similis*. The copepod biomass remained low (< 6 g C m^{-2}) throughout the rest of the study period.

A pairwise correlation between the integrated protozooplankton biomass and the grazing part of the copepod biomass (i.e. *Acartia* spp. *Calanus* spp., *Metridia longa*, *Microcalanus*, *Oithona* spp. and *Pseudocalanus* spp.) revealed a significant relationship between the two zooplankton groups, with the protozooplankton biomass being inversely proportional to the copepod biomass (r^2 = 0.89, P < 0.01, Fig. 9). A similar trend was found between chl a and copepod biomass (r2 = 0.22, P = 0.08, Fig. 9). No significant correlation was found between protozooplankton biomass and chl a.

3.6. Grazing impact by *Metridia longa*

Since *Metridia longa* dominated the copepod biomass this species was used in a grazing experiment. The grazing experiment was initiated with a phytoplankton biomass of 22 µg C l^{-1}. Phytoplankton cells in the small size fraction (0.7-10 µm) contributed 95 % of the total phytoplankton biomass. *M. longa* clearance rate on the large chl *a* fraction (>10 µm) was estimated to 2.1 ± 0.5 ml µg C^{-1} d^{-1} (mean ± SE, n = 10), while there was negative clearance (-1.5 ± 0.6 ml µg C^{-1} d^{-1}, mean ± SE, n = 23) on the small chl *a* fraction (< 10 µm). The lower threshold of clearance was corroborated from the Lugol's sample counts, where no significant clearance was found on particles in the size range 3-6 µm (Fig. 10, t-test, p > 0.05). We cannot conclude whether *M. longa* in fact prey on these small sized prey items or if the non-significant clearance rates on small sized particles are due to a bottle generated cascade effect caused by removal of protozooplankton in the experimental bottles. This may have caused a significant underestimation of the grazing rates (Nejstgaard et al. 1997, 2001). On a global average copepod grazing on phytoplankton is underestimated by 20-30 % in these kinds of grazing experiment (Saiz and Calbet 2011). The protozooplankton concentration in the experimental bottles was 21 ± 5 ×10^3 l^{-1} corresponding to an average biomass of 14 ± 2 µg C l^{-1}. The protozooplankton community was dominated by *Mesodinium* spp., *Strombidium* spp., *Gyrodinium spirale*, *Laboea strobila* and *Strobilidium oviformis*. *M. longa* cleared cells in the size range of 10 to 60 µm with an average clearance rate of 2.4 ± 0.2 ml µg C-1 d-1 (mean ± SE, n = 26) (Fig. 10A). While clearance was positively correlated to prey size (r2=0.90, P=0.06) no clear relationship was found between biomass of the prey size classes and the clearance rate (Fig. 10B).

3.7. Copepod community grazing

The maximum potential grazing rates of the copepod community was highest from March to late May where the copepod community cleared 16 ± 7 % of the water column (WC) per day. *M. longa* alone accounted for >90 % of the maximum potential copepod community clearance (Fig. 11A). *Microsetella* and *Oncea* are excluded from the grazing estimates, since these are assumed not to feed on phytoplankton and protozooplankton but rather graze on surfaces of aggregates (Koski et al. 2007).

As the *M. longa* population disappeared from the water column, the maximum potential clearance capacity was reduced and stayed low (7 ± 2 % WC d^{-1}) throughout the summer period (Fig. 11A). Generally our maximum potential grazing estimates suggest that *M. longa* was able to control the protozooplankton community during spring, grazing >100 % of the protozooplankton production per day (Fig. 11B). From June to August the predation pressure was reduced and there was an intense build-up of protozooplankton biomass in response to the reduction in *M. longa* grazing pressure.

4. Discussion

4.1. Hydrography and plankton characteristics

Fjords are important elements of the coastal zone of Greenland. They are the first parts of the marine environment to be impacted by increased melt water from land and are therefore good proxies for how the open marine environments will respond. In this sense, the freshwater-impacted fjord branch Kapisigdlit represents an ideal test site to generate knowledge on the potential impact of increased freshwater input and water-column stratification on the pelagic community.

The Kapisidglit Fjord represents a seasonally oligotrophic stratified subarctic ecosystem controlled by nitrate during the productive season. The fjord shows strong seasonality in chl *a* concentrations, but is characterized by lower concentrations than reported from other Sub-arctic and Arctic regions, where the surface chl *a* generally exceeds 1.5 µg l^{-1} during the productive season (Pabi et al. 2008). The freshwater runoff in the Kapisigdlit Fjord creates a more stratified water column preventing mixing of nutrients up in the euphotic zone, which cause the low chl *a* concentration, the low primary production rates and the high proportion of nanoflagellates and protozooplankton.

Few attempts have been made to investigate the role of protozooplankton in subarctic and Arctic ecosystems, and most have focused on the high-productive regions dominated by diatoms and *Calanus* (Verity et al. 2002, Sherr and Sherr 2007, Seuthe et al. 2011). This study documents that Sub-arctic fjords may support rich and diverse protozooplankton communities and that abundances are comparable to those found in temperate waters (Sherr and Sherr 2007, Saiz and Calbet 2011).

Compared to existing data from Arctic and Sub-arctic regions, the protozooplankton biomass in the Godthåbsfjord (including Kapisigdlit Fjord) is remarkably high (Poulsen and Reuss 2002, Arendt et al. 2010, this study). Maximum integrated protozooplankton biomasses in coastal Arctic and Sub-arctic waters such as Kongsfjorden (Svalbard), Disko Bay (West Greenland), Young Sound (North East Greenland), Fyllas Bank (off West Greenland), the Barents Sea and the Sub-arctic Pacific Ocean have been reported in the range 0.2 to 1.1 g C m^{-2} (Rysgaard and Nielsen 1999, Levinsen et al. 2000, Rat'kova and Wassmann 2002, Strom et al. 1993, Seuthe et al. 2011). In comparison, the maximum integrated protozooplankton biomass in the Kapisigdlit Fjord was 4.0 g C m^{-2}.

In contrast to studies at Fyllas Bank, Kongsfjorden, Disko Bay and Young Sound, where dinoflagellates dominate the protozooplankton (Poulsen and Reuss 2002, Levinsen and Nielsen

2002, Sherr et al. 2009, Seuthe et al. 2011), ciliates contributed with 82 % of the total protozooplankton biomass in our study. A similar community structure has been observed in the Barents Sea (Rat'kova and Wassmann 2002) and in the Sub-arctic Pacific Ocean (Strom et al. 1993). The difference in the relative composition of the protozooplankton community can be explained by the different feeding strategies of ciliates and dinoflagellates. While ciliates generally prefer small particles (~2-10 µm), heterotrophic dinoflagellates feed on diatoms and other large particles (>10 µm) (Hansen et al. 1994). The Kapisigdlit Fjord represents a seasonally stratified and oligotrophic ecosystem supporting a phytoplankton community of small flagellates and accordingly ciliates as the dominant protozooplankton grazers. Ciliates feeding on nanoflagellates could not be distinguished from potential predatory ciliates feeding on other ciliates and dinoflagellates. However, known predatory ciliates like *Didinium* spp. or *Favella ehrenbergii* (Berger 1980, Stoecker et al. 1981) were rare in the samples and thus predatory ciliates were not considered important for the trophic role of the protozooplankton community.

The estimated maximum potential grazing impact of protozooplankton on phytoplankton was highly variable, but generally exceeding 100 % of the primary production during the summer months. This high grazing impact of protozooplankton is corroborated by Calbet et al. (2011) who, based on dilution experiments, estimated grazing rates corresponding to 128 % of the primary production consumed per day in June. In comparison, grazing rates estimated from dilution experiments in other regions of the Arctic seas have been in the range of 26 to 77 % of the primary production per day (Verity et al. 2002, Sherr et al. 2009). Although the maximum potential grazing impact may be slightly overestimated due to inclusion of mixotrophic species like *Mesodinium rubrum, Laboea strobila* and *Strombidium cornicum*, the estimate is within a realistic range and emphasizes the need to consider protozooplankton as key grazers.

4.2. Protozooplankton as prey for copepods

It is well documented in the literature that *Calanus* can exploit protozooplankton (Ohman and Runge 1994, Levinsen et al 2000, Turner et al. 2001), whereas knowledge about *Metridia* feeding biology is restricted to a few studies presenting that *Metridia* feed on various prey items including diatoms, nauplii and copepod eggs (Haq 1967, Sell et al. 2001, Campbell et al. 2009, Kjellerup and Kiørboe 2011). In contrast to typical suspension-feeding copepods, e.g. *Calanus*, which generate a feeding current in which they capture prey, *M. longa* feed by cruising through the water and capture prey by remote detection (Kjellerup and Kiørboe 2011). The cruising behavior of *Metridia* may be an advantage in environments in which prey concentrations are low or when the prey tries to escape the feeding current like e.g. ciliates as *Mesodinium rubrum* (Jonsson and Tiselius 1990, Fenchel and Hansen 2006). Haq (1967) demonstrated that *M. longa* was able to feed on prey in the size range 5-300 µm with clearance rates in the range 3-7 ml ind^{-1} day^{-1}. Our study support that particles <60 µm are efficiently captured by adult *M. longa* females, but in comparison to Haq (1967) average clearance rate was higher; 222 ± 36 ml ind^{-1} day^{-1} (mean ± SE, n=26) for protozooplankton in the size range 10-60 µm. The estimated grazing obtained from the grazing experiment are close to maximum potential clearance rates estimated from empirical relations in Hansen et al. (1997/2000) and Møller et al. (2006) (Fig. 12). The low clearance rates presented in Haq (1967) could be explained by the limited variability in offered prey since *M. longa* was only exposed to phytoplankton cells, small flagellates and *Artemia* nauplii. Our data suggest that *M. longa* has a high affinity for protozooplankton prey, which is in agreement with Haq (1967) who demonstrated that *M. longa* fed more rapidly on animal prey than on phytoplankton. Due to the size composition of the plankton community and the possible cascading effects within the phytoplankton community in the razing experiment, we did not find upper and lower prey size thresholds for *M. longa*. However, relative optimal size range for copepods is surprisingly constant

between species suggesting that adult copepods of similar size as *M. longa* has optimal prey size range of ~10-70 µm (Berggren et al. 1988, Hansen et al. 1994, Levinsen et al. 2000).

Since the *in situ* size composition of the phytoplankton in the Kapisigdlit Fjord was dominated by small cells (<10 µm) we presume that only a small fraction of the phytoplankton community is available to adult *M. longa* and that this species to a large extent, dependent on preying on alternative prey items such as microzooplankton. During the study period ciliates accounted for 55 % (10-81 %) of the carbon available for the copepods and dinoflagellates 10 % (2-25 %) assuming that copepods primarily feed on phytoplankton and protozooplankton > 10 µm. This proportion is within the same magnitude as found in global oligotrophic ecosystems (< 50 µg C l^{-1}), where ciliates and dinoflagellates on average account for 43 % and 19 % of the copepod carbon consumption, respectively (Saiz and Calbet 2011). Although *M. longa* has been shown to be capable of feeding on nauplii (Haq 1967, Kjellerup and Kiørboe 2012), nauplii only contributed with 11 % (1-40 %) of the microzooplankton biomass (calculated as the sum of ciliate-, dinoflagellates- and nauplii biomass). Prey preference and clearance rate will likely vary depending on the copepod community composition and prey availability. However, throughout the study period adult females and copepodites in the CV stage made up 78 ± 9 % (55-89%) of the entire *M. longa* biomass (i.e. all copepod stages including nauplii, copepodites and males), rendering that the rates estimated from the grazing experiment are within a realistic range. Thus, the present study indicate that protozooplankton, especially ciliates, are an essential source of food for the copepod community in Sub-arctic oligotrophic systems, such as the Kapisigdlit Fjord.

4.3. Correcting grazing impact to *in situ* temperature using Q_{10}

The *in situ* temperature throughout the study period ranged between 0.5 and 13 °C. Literature Q_{10} values for maximum potential clearance, ingestion and production rates of protozooplankton and copepods (reviewed in Hansen et al. 1997) range between 1.5 and 4.0 (average 2.8) within the temperature range 5-25 °C. Since there are no consistent differences in Q_{10} between temperatures a universal Q_{10} of 2.8 was applied to all temperatures when estimating maximum grazing potential. By using Q_{10} within the realistic range of 1.5 to 4.0 the overall conclusions of the study would be unchanged. E.g. using a Q_{10} of 4.0 at temperatures < 5 °C maximum potential clearance, ingestion and production rates for protozooplankton would have been 28 % lower than when using a Q_{10} of 2.8 for all temperatures.

4.4. Regulation of protozooplankton

The late summer peak of protozooplankton observed in the Kapisigdlit Fjord is a result of the disappearance of the large copepods which reduces the grazing pressure on the protozooplankton community. A similar seasonal succession has been observed in Disko Bay (Levinsen and Nielsen 2002), where a “regulation window” is created by the phytoplankton spring bloom. During the spring bloom *Calanus* becomes food saturated and thereby decreases the grazing pressure on the protozooplankton. In Disko Bay, a second “window” is created when the adult *Calanus* leave the surface layer in the late summer. In the Godthåbsfjord the “regulation window” is established as the predation pressure from *Metridia longa* is reduced when leaving the surface layer. In the Kapisigdlit Fjord the “regulation window” stays “open” a few weeks during the summer period until a high grazing pressure is reestablished by a late summer community of small copepods; mainly *Oithona* spp.(Zamora-Terol et al. in press) (Fig. 8 & 11). In high Arctic regions such as Young Sound, “regulation windows” are usually absent due to the very short open water period. In these systems, copepods are able to consume most of the primary production meaning that copepods control both

the phytoplankton and protozooplankton during the entire productive season (Rysgaard et al. 1999, Nielsen et al. 2007).

Climate changes are probably the largest ecological challenge facing the Arctic marine environment in the future, and knowledge about Sub-arctic marine ecosystems provides an important tool to understand and predict the impact of changes at higher latitudes. In some areas of the Arctic, increased temperatures may reduce the sea-ice cover and expand the productive season (Tremblay and Gagnon 2009, Slagstad et al. 2011) allowing a more complex plankton succession to develop (Rysgaard et al 1999). In some areas, intensified precipitation and glacial melting may strengthen the water column stratification favoring small-sized phytoplankton populations (Ardyna et al. 2011) and position ciliates as key grazers. According to this scenario, the zooplankton community will change from dominance of copepods towards a more bimodal grazer succession with a peak of large calanoids copepods in the spring succeeded by a late summer peak of protozooplankton and small copepod spp. as illustrated from Disko Bay (Levinsen and Nielsen 2002) and this present study.

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References

Ardyna M, Gosselin M, Michel C, Poulin M and Tremblay J (2011) Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: Contrasting oligotrophic and eutrophic regions. Mar Ecol Prog Ser 442: 37-57

Arendt KE, Juul-Pedersen T, Mortensen J, Blicher ME and Rysgaard S (2012) A 5-year study of seasonal patterns in mesozooplankton community structure in a sub-Arctic fjord reveals dominance of *Microsetella norvegica* (Crustacea, Copepoda). J Plankton Res 35 (1): 105-120

Arendt KE, Nielsen TG, Rysgaard S and Tönnesson K (2010) Differences in plankton community structure along the Godthabsfjord, from the Greenland Ice Sheet to offshore waters. Mar Ecol Prog Ser 401: 49-62

Berger J (1980) Feeding-behavior of *Didinium nasutum* on *Paramecium bursaria* with normal or apochlorotic zoochlorellae. J Gen Microbiol 118:397-404

Berggreen U, Hansen B and Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development - Implications for determination of copepod production. Mar Biol 99: 341-352

Bergstrøm B and Vilhjálmsson H (2006) Cruise report and preliminary results of the acoustic/pelagic trawl survey off West Greenland for capelin and polar cod. Greenland Institute of Natural Resources

Calbet A, Riisgaard K, Saiz E, Zamora S, Stedmon C and Nielsen TG (2011) Phytoplankton growth and microzooplankton grazing along a sub-Arctic fjord (Godthabsfjord, west Greenland). Mar Ecol Prog Ser 442: 11-22.

Campbell RG, Sherr EB, Ashjian CJ, Plourde S, Sherr BF, Hill V and Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. J Deep-Sea Research 56: 1274-1289

Comiso JC, Parkinson CL, Gersten R and Stock L (2008) Accelerated decline in the Arctic sea ice cover. Geophys Res Lett 35: L01703

Daase M, Eiane K, Aksnes DL and Vogedes D (2008) Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations. Mar Biol Res 4(3): 193-207

Digby PSB (1953) Plankton Production in Scoresby Sound, East Greenland. J Anim Ecol 22:289-322

Falkenhaug T, Tande KS and Semenova T (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. Mar Ecol Prog Ser 149: 105-119

Fenchel T, Hansen PJ (2006) Motile behaviour of the bloom-forming ciliate *Mesodinium rubrum.* Mar Biol Res 2(1): 33-40

Frost BW (1972) Effects of size and concentration of food particles on feeding behavior of marine planktonic copepod *Calanus pacificus*. Limnol Oceanogr 17: 805-815.

Hamilton L, Lyster P and Otterstad O (2000) Social change, ecology and climate in 20th-century Greenland. Clim Change 47: 193-211

Hansen B, Bjørnsen PK, Hansen PJ (1994) The size ratio between planktonic predators and their prey. Limnol Oceanogr 39:395-403

Hansen PJ, Bjørnsen PK, Hansen BW (1997) Zooplankton grazing and growth: Scaling within the 2-2,000-µmm body size range. Limnol Oceanogr 42:687-704

Hansen PJ, Bjørnsen PK and Hansen BW (2000) Zooplankton grazing and growth: Scaling within the 2-2,000-µm body size range. Limnol Oceanogr 45: 1891-1891.
Hansen PJ (2011) The role of photosynthesis and food uptake for the growth of marine mixotrophic dinoflagellates. J Eukaryot Microbiol 58(3): 203–214

Haq SM (1967) Nutritional physiology of *Metridia lucens* and *M. longa* from Gulf of Maine. Limnol Oceanogr 12: 40-51

Hays GC (1995) Ontogenetic and seasonal variation in the diel vertical migration of the copepods *Metridia lucens* and *Metridia longa*. Limnol Oceanogr 40: 1461-1465

Hirche HJ, Mumm N (1992) Distribution of dominant copepods in the Nansen Basin, Arctic-Ocean, in summer. Deep-Sea Res Part a - Oceanographic Research Papers 39(2A): 485-505

Holland DM, Thomas RH, De Young B, Ribergaard MH and Lyberth B (2008) Acceleration of Jakobshavn Isbræ triggered by warm subsurface ocean waters. Nature Geoscience 1: 659-664

Hopkins CCE, Tande KS, Grønvik S and Sargent JR (1984) Ecological investigations of the zooplankton community of Balsfjorden, Northern Norway - an analysis of growth and overwintering tactics in relation to niche and environment in *Metridia longa* (Lubbock), *Calanus finmarchicus* (Gunnerus), *Thysanoessa inermis* (Krøyer) and *Thysanoessa raschi* (M Sars). J Exp Mar Biol Ecol 82: 77-99

Hygum BH, Rey C, Hansen BW (2000) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. Mar Biol 136(6): 1075-1085

Jakobsen HH and Hansen PJ (1997) Prey size selection, grazing and growth response of the small heterotrophic dinoflagellate *Gymnodinium* sp. and the ciliate *Balanion comatum* - a comparative study. Mar Ecol Prog Ser 158: 75-86

Jespersen AM and Christoffersen K (1987) Measurements of chlorophyll-a from phytoplankton using ethanol as extraction solvent. Archiv für Hydrobiologie 109: 445-454.

Jonsson PR and Tiselius P (1990) Feeding-behavior, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. Mar Ecol Prog Ser 60:35-44
Juul-Pedersen T, Nielsen TG, Michel C, Møller EF, Tiselius P, Thor P, Olesen M, Selander E and Gooding S (2006) Sedimentation following the spring bloom in Disko Bay, West Greenland, with special emphasis on the role of copepods. Mar Ecol Prog Ser 314: 239-255

Kjellerup S, Kiørboe T (2012) Prey detection in a cruising copepod. Biological letters 8(3): 438-441

Koski M, Møller EF, Maar M and Visser AW (2007) The fate of discarded appendicularian houses: degradation by the copepod, *Microsetella norvegica*, and other agents. J Plankton Res 29: 641-654

Levinsen H and Nielsen TG (2002) The trophic role of marine pelagic ciliates and heterotrophic dinoflagellates in arctic and temperate coastal ecosystems: A cross-latitude comparison. Limnol Oceanogr 47: 427-439

Levinsen H, Turner JT, Nielsen TG and Hansen BW (2000) On the trophic coupling between protists and copepods in arctic marine ecosystems. Mar Ecol Prog Ser 204: 65-77

Madsen SD, Nielsen TG and Hansen BW (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Biol 139: 75-93

Menden-Deuer S and Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol Oceanogr 45: 569-579

Møller EF, Nielsen TG and Richardson K (2006) The zooplankton community in the Greenland Sea: Composition and role in carbon turnover. Deep-Sea Res Part I 53: 76-93

Mortensen J, Lennert K, Bendtsen J and Rysgaard S (2011) Heat sources for glacial melt in a sub-Arctic fjord (Godthåbsfjord) in contact with the Greenland Ice Sheet. J Geophys res 116: C01013

Motyka RJ, Truffer M, Fahnestock M, Mortensen J, Rysgaard S and Howat I (2011) Submarine melting of the 1985 Jakobshavn Isbræ floating tongue and the triggering of the current retreat. J geophys Res 116: F01007

Nejstgaard JC, Gismervik I and Solberg PT (1997) Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi*. Mar Ecol Prog Ser 147: 197-217

Nejstgaard JC, Naustvoll JL and Sazhin A (2001) Correcting for underestimation of microzooplankton grazing in bottle incubation experiments with mesozooplankton. Mar Ecol Prog Ser 221: 59-75

Nielsen TG and Hansen B (1995) Plankton Community structure and carbon cycling on the Western coast of Greenland during and after the sedimentation of a diatom bloom. Mar Ecol Prog Ser 125: 239-257

Ohman MD and Runge JA (1994) Sustained fecundity when phytoplankton resources are in short supply - Omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. Limnol Oceanogr 39: 21-36

Pabi S, van Dijken GL and Arrigo KR (2008) Primary production in the Arctic Ocean, 1998-2006. JGeophys Res 113: C08005

Poulsen LK and Reuss N (2002) The plankton community on Sukkertop and Fylla Banks off West Greenland during a spring bloom and post-bloom period: Hydrography, phytoplankton and protozooplankton. Ophelia 56: 69-85

Putt M and Stoecker DK (1989) An experimentally determined carbon - volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. Limnol Oceanogr 34: 1097-1103

Rat'kova TN and Wassmann P (2002) Seasonal variation and spatial distribution of phyto- and protozooplankton in the central Barents Sea. J Mar Syst 38: 47-75

Rysgaard S, Nielsen TG and Hansen BW (1999) Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 179: 13-25

Saiz E and Calbet A (2011) Copepod feeding in the ocean: scaling patterns, composition of their diet and the bias of estimates due to microzooplankton grazing during incubations. Hydrobiologia 666: 181-196

Sell AF, van Keuren D and Madin LP (2001) Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. Limnol Oceanogr 46: 953-959

Seuthe L, Iversen KR and Narcy F (2011) Microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard): II. Ciliates and dinoflagellates. Polar Biol 34: 751-766

Sherr EB and Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar Ecol Prog Ser 352: 187-197

Sherr EB, Sherr BF and Hartz AJ (2009) Microzooplankton grazing impact in the Western Arctic Ocean. Deep-Sea Res Part I 56: 1264-1273

Slagstad, D, Ellingsen IH and Wassmann P (2011) Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: An experimental simulation approach. Prog Oceanogr 90:117-131

Smidt ELB (1979) Annual cycles of primary production and of zooplankton at Southwest Greenland. Greenland bioscience 1: 1-56

Steemann Nielsen E (1958) A survey of recent Danish measurements of the organic productivity in the sea. Rapp P-v Reun Cons Perm int Explor Mer 144:92-95

Stoecker DK, Gifford DJ and Putt M (1994) Preservation of marine planktonic ciliates - losses and cell shrinkage during fixation. Mar Ecol Prog Ser 110: 293-299

Storr-Paulsen M, Wieland K, Hovgard H and Ratz HJ (2004) Stock structure of Atlantic cod (*Gadus morhua*) in West Greenland waters: implications of transport and migration. ICES J Mar Sci 61: 972-982

Stoecker D, Guillard RRL, Kavee RM (1981) Selective predation by *Favella ehrenbergii* (tintinnia) on and among dinoflagellates. Biol Bull 160:136-145

Stroeve J, Holland MM, Meier W, Scambos T and Serreze M (2007) Arctic sea ice decline: faster than forecast. Geophys Res Lett 34

Strom SL, Postel JR and Booth BC (1993) Abundance, variability, and potential grazing impact of planktonic ciliates in the open sub-Arctic Pacific Ocean. Prog Oceanogr 32: 185-203

Tang KW, Nielsen TG, Munk P, Mortensen J, Møller EF, Arendt KE, Tönnesson K and Juul-Pedersen T (2011) Metazooplankton community structure, feeding rate estimates, and hydrography in a meltwater-influenced Greenlandic fjord. Mar Ecol Prog Ser 434: 77-90

Thor P, Nielsen TG, Tiselius P, Juul-Pedersen T, Michel C, Møller EF, Dahl K, Selander E, Gooding S (2005) Post-spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. J Plank Res 27(4): 341-356

Tremblay J and Gagnon J (2009) The effects of irradiance and nutrient supply on the productivity of Arctic waters: a perspective on climate change. NATO Science for Peace and Security Series-C: Environmental Security, pp. 73–93.

Turner J, Levinsen H, Nielsen TG and Hansen BW (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Mar Ecol Prog Ser 221: 209-219

Verity PG, Wassmann P, Frischer ME, Howard-Jones MH and Allen AE (2002) Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. J Mar Syst 38: 109-123

Yentsch CS and Menzel DW (1963) A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res 10: 221-231

Zamora-Terol, S. Nielsen TG & Saiz E (in press) Plankton community structure and role of *Oithona similis* on the western coast of Greenland during the winter-spring transition . Mar Ecol Prog Ser

Tables

Table 1. Volume (V) to carbon (pg C $cell^{-1}$) conversion factors used for heterotrophic protists.

Aloricate ciliates	Log (pg C $cell^{-1}$) = -0.639 + 0.984 Log (V)	Putt and Stoecker 1989, modified by Menden-Deuer and Lessard 2000
Loricate ciliates	Log (pg C $cell^{-1}$) = -0.168 + 0.841 Log (V)	Verity and Langdon 1984, Menden-Deuer and Lessard 2000
Dinoflagellates	Log (pg C $cell^{-1}$) = -0.353 + 0.864 Log (V)	Menden-Deuer and Lessard 2000

Table 2. Length (L) to carbon (mg C) conversion factors used for copepod nauplii (N1-N6) and copepodites (C1-C6).

Taxon	a	b	Reference	Stage	Remarks
Acartia spp.[1]	1.11×10^{-11}	2.92	Berggreen et al. 1988	C1-C6	Modified by Thor et al. 2005, L, µm
Calanus finmarchicus[1]	4.8×10^{-3}	3.5687	Madsen et al. 2001	C1-C6	L, mm
Calanus glacialis[1]	4.8×10^{-3}	3.5687	Madsen et al. 2001	C1-C6	L, mm
Calanus hyperboreus[1]	1.4×10^{-3}	3.3899	Hirche and Mumm 1992	C1-C6	L, mm
Centropages spp. [2]	1.78×10^{-2}	2.45	Klein Breteler et al. 1982	C1-C6	Modified by Hay et al. 1991, L, mm
Centropages spp. [2]	1.45×10^{-2}	2.24	Klein Breteler et al. 1982	N1-N6	Modified by Hay et al. 1999, L, mm
Metridia spp.[1]	6.05×10^{-3}	3.0167	Hirche and Mumm 1992	C1-C6	L, mm
Microcalanus spp.[1]	9.47×10^{-10}	2.16	Sabatini and Kiørboe 1994	C1-C6	Regression made on *Oithona* sp., L, µm
Microsetella spp.[1]	2.65×10^{-9}	1.95	Uye et al. 2002	N1-C6	L, µm
Oithona spp.[1]	9.47×10^{-10}	2.16	Sabatini and Kiørboe 1994	C1-C6	L, µm
Oithona spp. [1]	5.545×10^{-11}	2.71	Sabatini and Kiørboe 1994	N1-N6	L, µm
Oncaea spp.[1]	2.51×10^{-11}	2.9	Satapoomin 1999	C1-C6	Modified by Thor et al. 2005, L, µm
Paraeuchaeta spp.[3]	3.1107	1.8633	K. Tönnesson unpublished	N1-C6	L, mm
Pseudocalanus spp.[1]	6.12×10^{-11}	2.7302	Klein Breteler et al. 1982	C1-C6	Modified by Thor et al. 2005, L, µm
Calanus and Metridia nauplii[1]	4.29×10^{-9}	2.05	Hygum et al. 2000	N1-N6	L, µm
Acartia spp. Microcalanus pp. Oncaea spp. Paracalanus Pseudocalanus spp.[1]	3.18×10^{-12}	3.31	Berggreen et al.1988	N1-N6	L, µm

[1] Calculated from the following equation: $a\times L^b$

[2] Calculated from the following equation: $a\times L^b$, multiplied with 0.45 to convert into carbon.

[3] Calculated ash free dry weight from the following equation: 10^(a×Log(L)-b), multiplied with 0.45 to convert into carbon.

Table 3. Average concentrations (µM) of nutrients ± SE, in the freshwater plume (1-5 m depth) after the break-up of ice in the Kapisigdlit river (June 20), and the average nutrient concentration in 50 m strata . n = number of samples, BD = below detection level.

Strata (n)	NO_3	SiO	PO_4	NO_2	NH_3
Plume, (20)	BD	5.09±0.36	0.038±0.003	BD	0.20±0.002
0-50, (47)	1.70±0.05	2.07±0.03	0.22±0.01	0.03±0.001	1.12±0.02
50-100, (30)	4.67±0.10	3.15±0.07	0.47±0.01	0.129±0.003	1.28±0.03
100-150, (16)	5.92±1.50	5.92±0.99	0.56±0.08	0.18±0.08	1.36±0.50
150-200, (17)	7.21±1.25	4.43±0.98	0.65±0.08	0.24±0.05	2.02±1.16
>200 m, (18)	11.47±1.23	7.31±0.58	0.94±0.14	0.05±0.03	0.68±0.39

Figures

Fig. 1. Map of the study area showing the location of the sampled station.

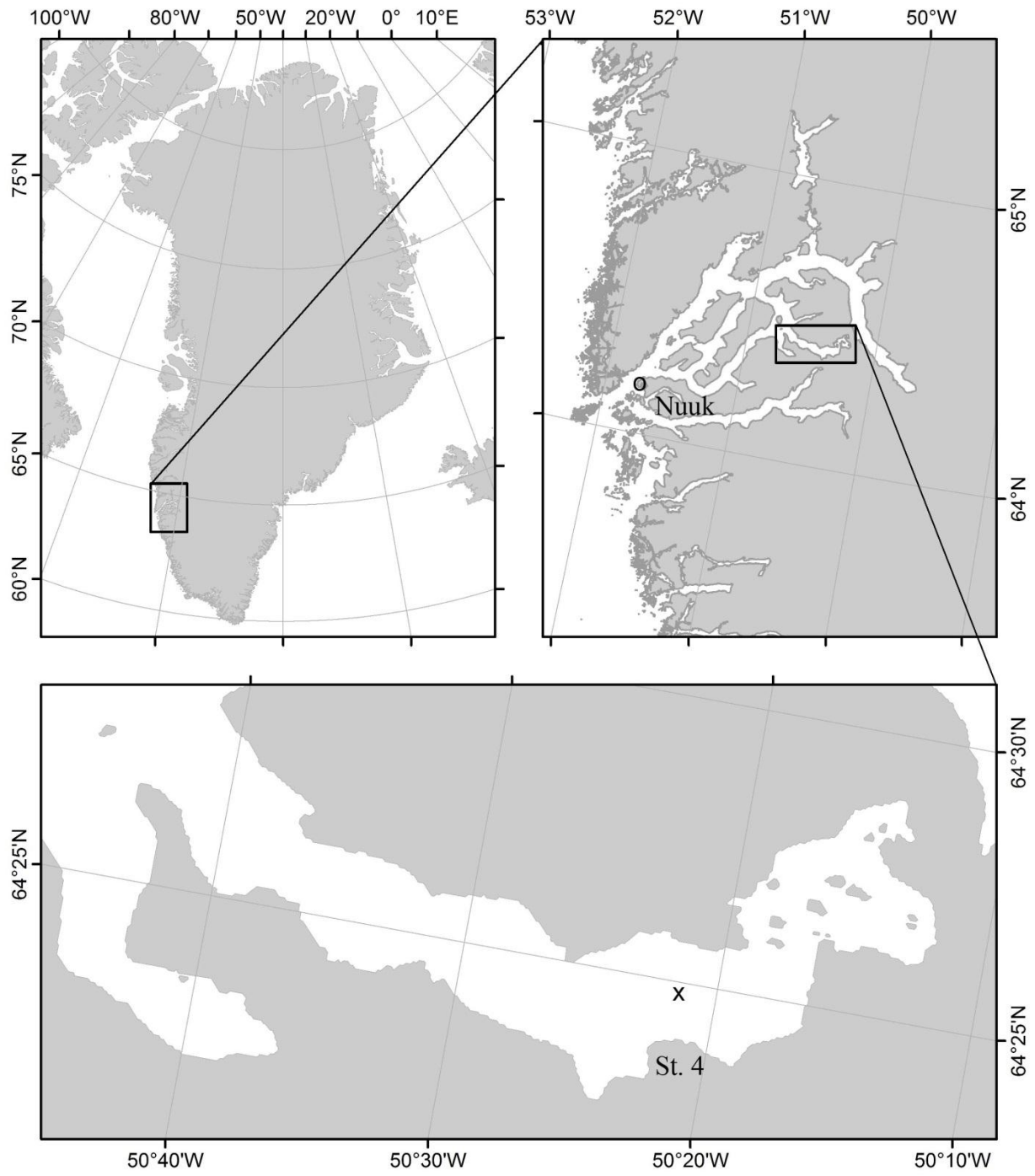


Fig. 2. Water column characteristics over the investigation period. (A) Temperature (ºC), B) salinity and C) density (kg m^{-3}) overlaid chlorophyll *a* (chl *a*) concentrations (µg l^{-1}) and concentration of the limiting nutrient nitrate (µm), displayed as red isolines. Points represent sampling depths. The vertical black line indicates break-up of the ice in the fjord.

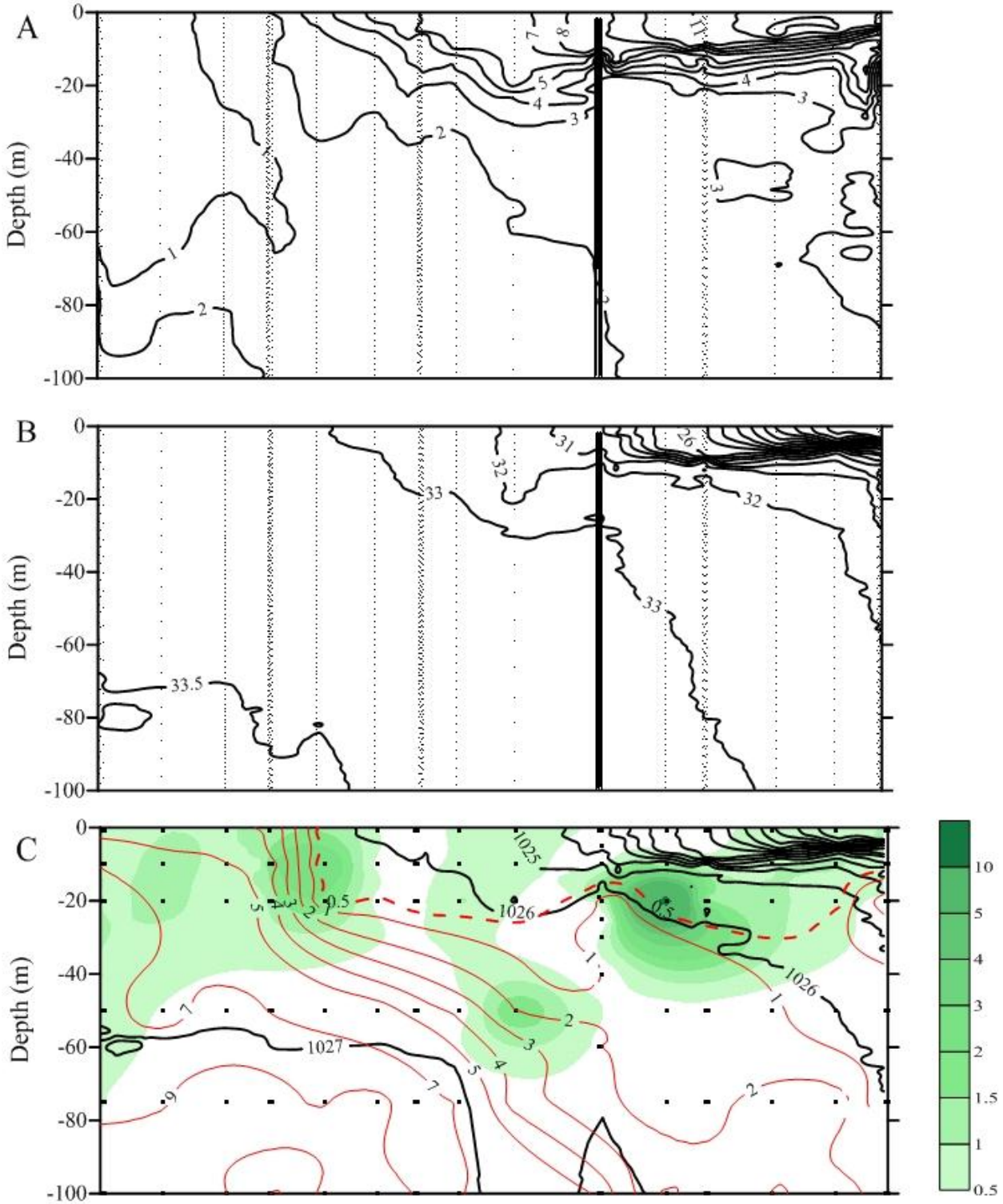
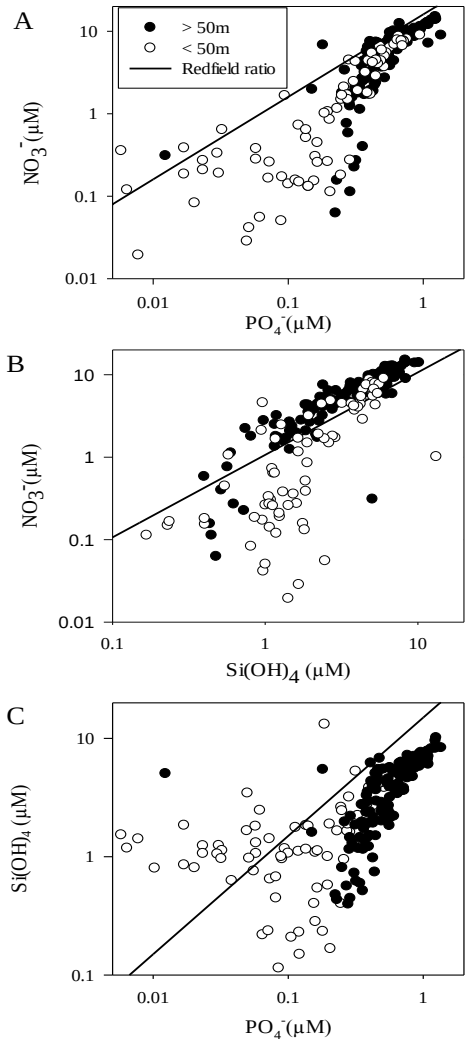


Fig. 3. Relationship between (A) phosphorous and nitrate, (B) silicate and nitrate and (C) phosphorous and silicate. ●: Samples taken below the photic zone i.e. deeper that 50 m. ○: Surface samples taken above 50 m. Data from the freshwater plume after the breakup of the river is not included, but shown in Table 3. Lines indicate the Redfield ratios of the nutrients in consideration to the Redfield plots.



3

Fig. 4. Seasonal succession in phytoplankton. Bars: integrated biomass, phytoplankton (g C m^{-2}). ●: Integrated primary production, PP (g C m^{-2} d^{-1}). Integration depth: 250 m for phytoplankton and 45 m for PP.

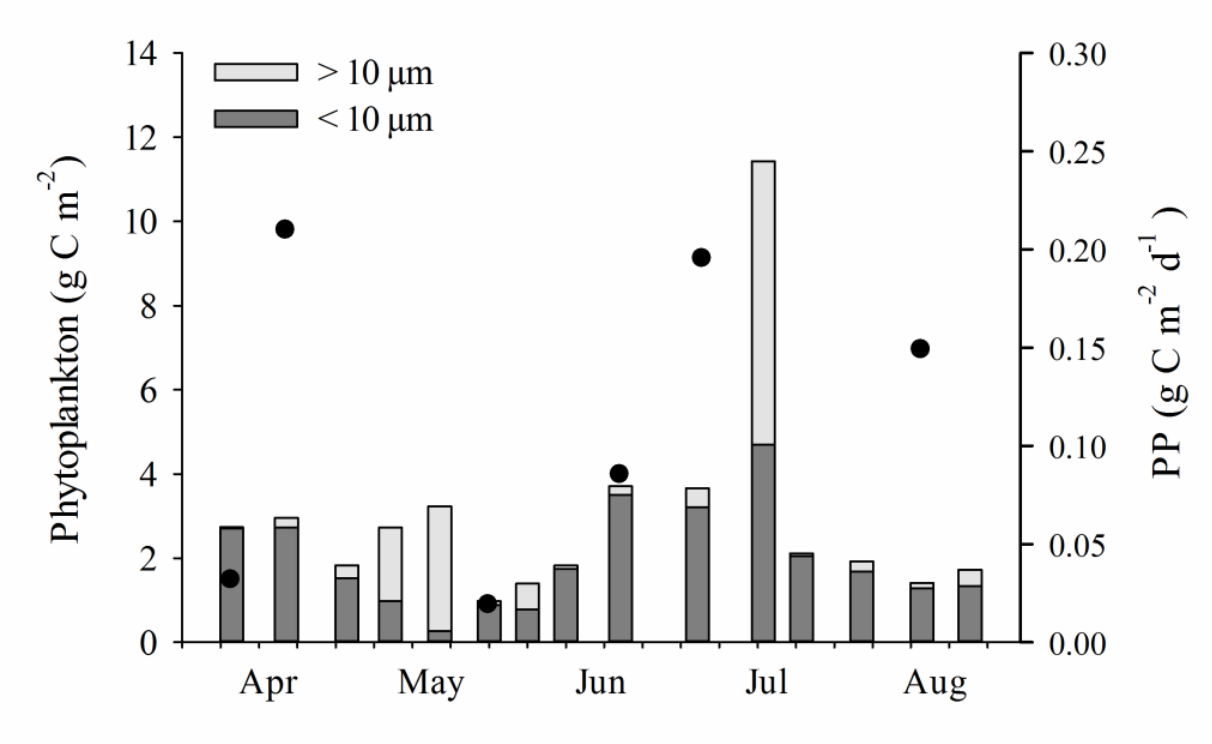


Fig. 5. Seasonal development in the abundance (cells l^{-1}) of (A) ciliates and (B) heterotrophic dinoflagellates superimposed on the chl *a* concentration (green shading) and seasonal succession in the biomass (µg C l^{-1}) of C) ciliates and D) heterotrophic dinoflagellates. ●: sampling depths.

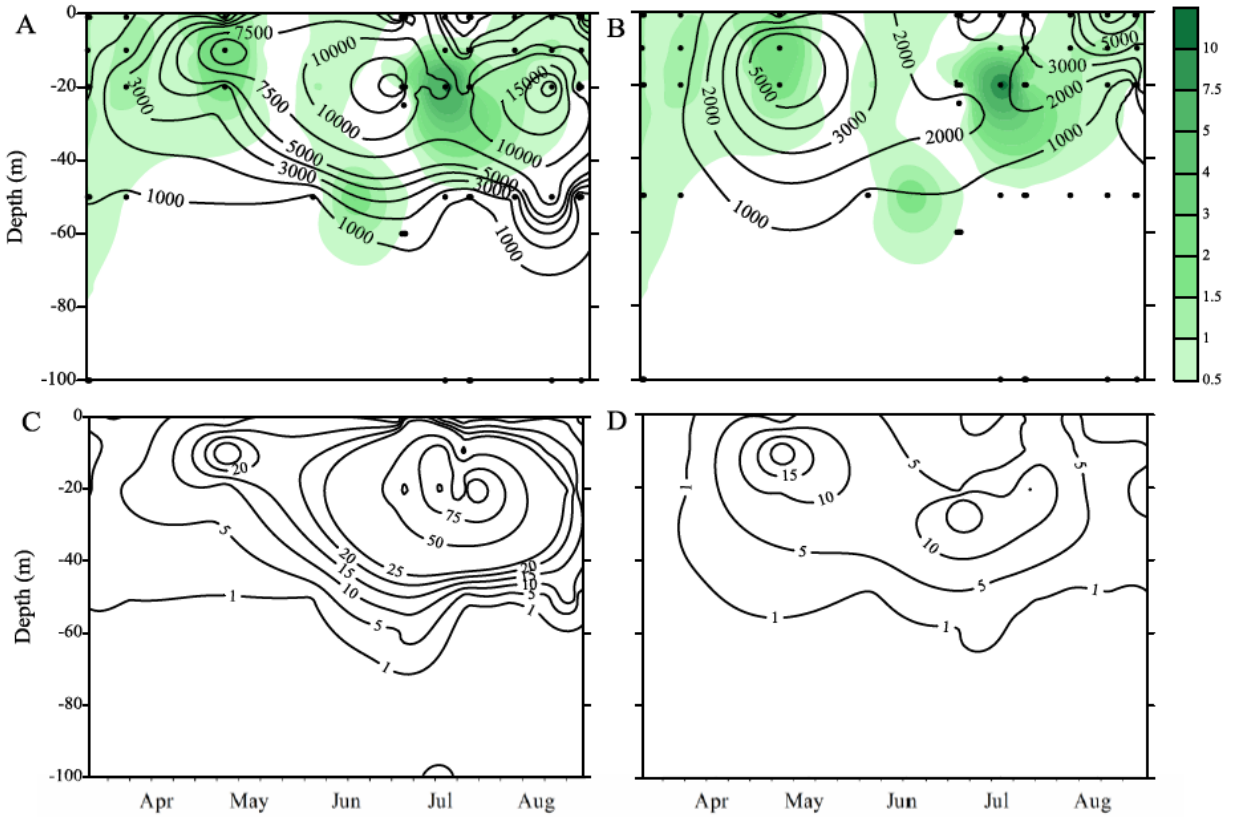


Fig. 6. Seasonal development in selected protozooplankton specimens. Bars: Integrated biomass (g C m^{-2}). ●: abundance (cells l^{-1}). Integration depth: 100 m. Note different y-axis.

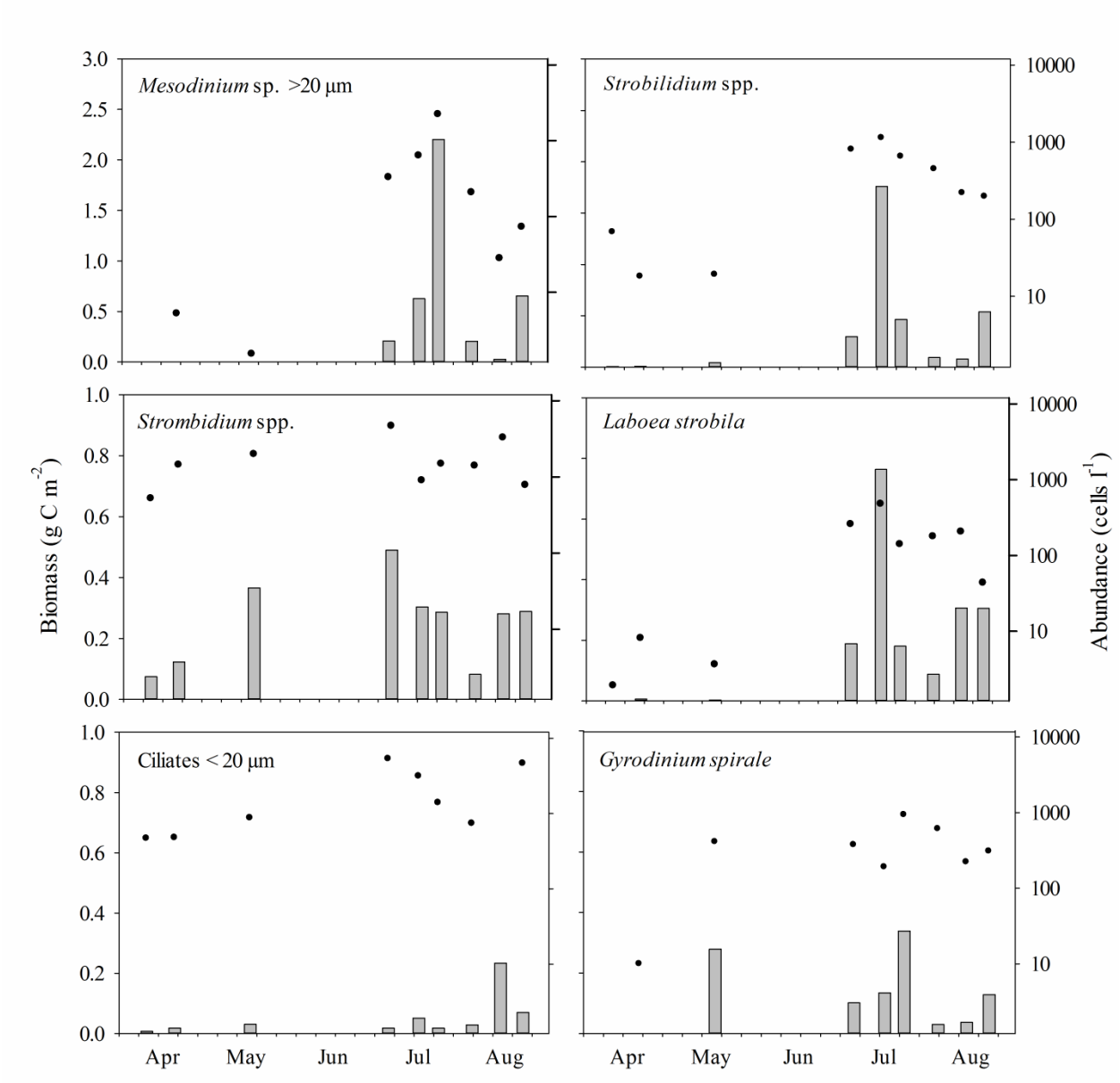


Fig.7. (A-B) Integrated biomass (g C m^{-2}), (C-D) estimated production (g C m^{-2} d^{-1}) calculated from (E-F) estimated maximal potential ingestion rates (g C m^{-2} d^{-1}) of ciliates (*left panel*) and heterotrophic dinoflagellates (*right panel*). The color codes represent the fraction of each protozooplankton size class. Size is given in equatorial spherical diameter (ESD). (E-F) ●: phytoplankton biomass ingested per day (% d^{-1}). Integration depth: 100 m. Note different y-axis.

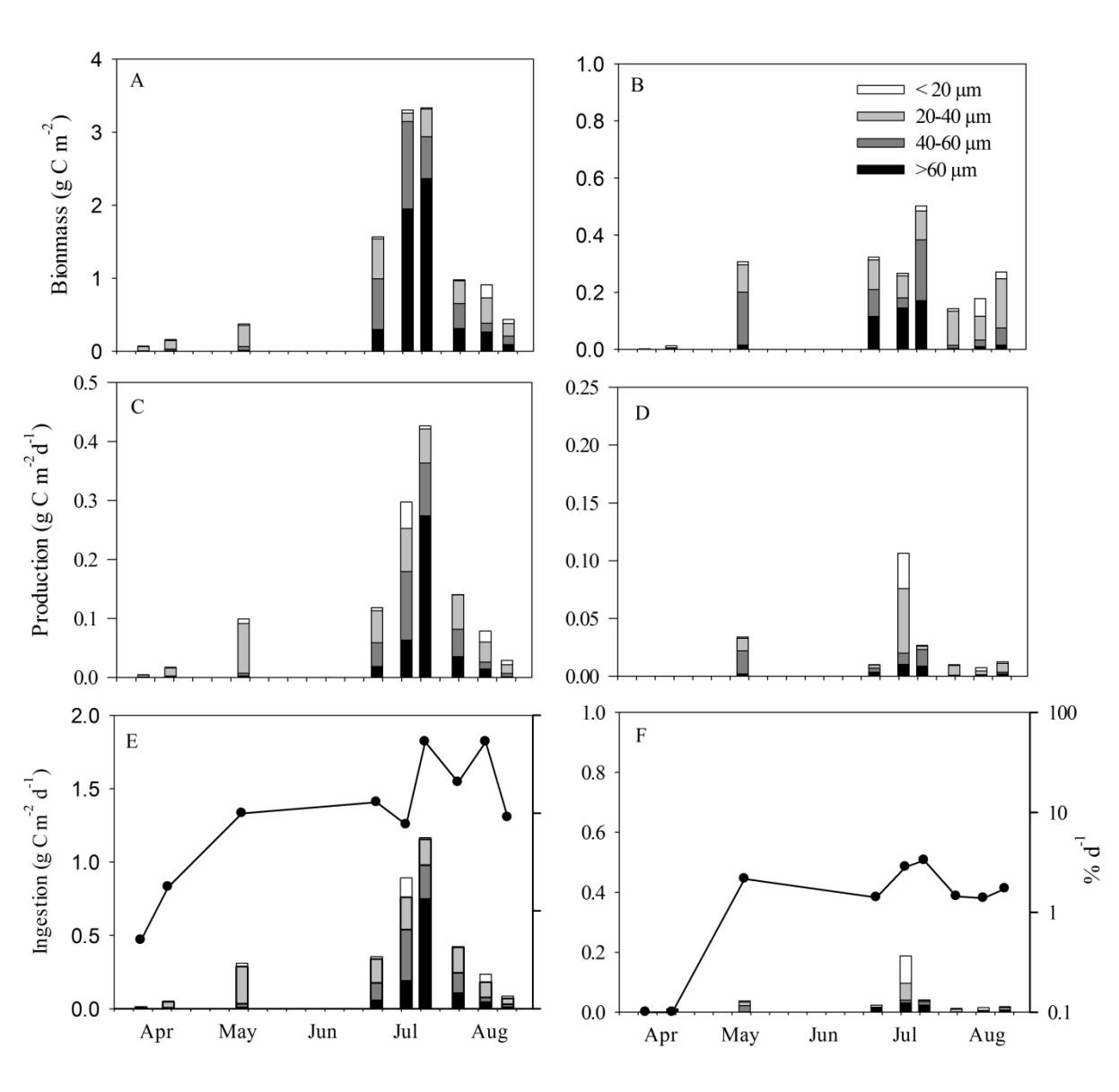


Fig.8. (A) Integrated protozooplankton biomass (g C m^{-2}), (B) integrated copepod biomass (g C m^{-2}). Integration depth: 100 m for protozooplankton and 250 m for copepod biomass.

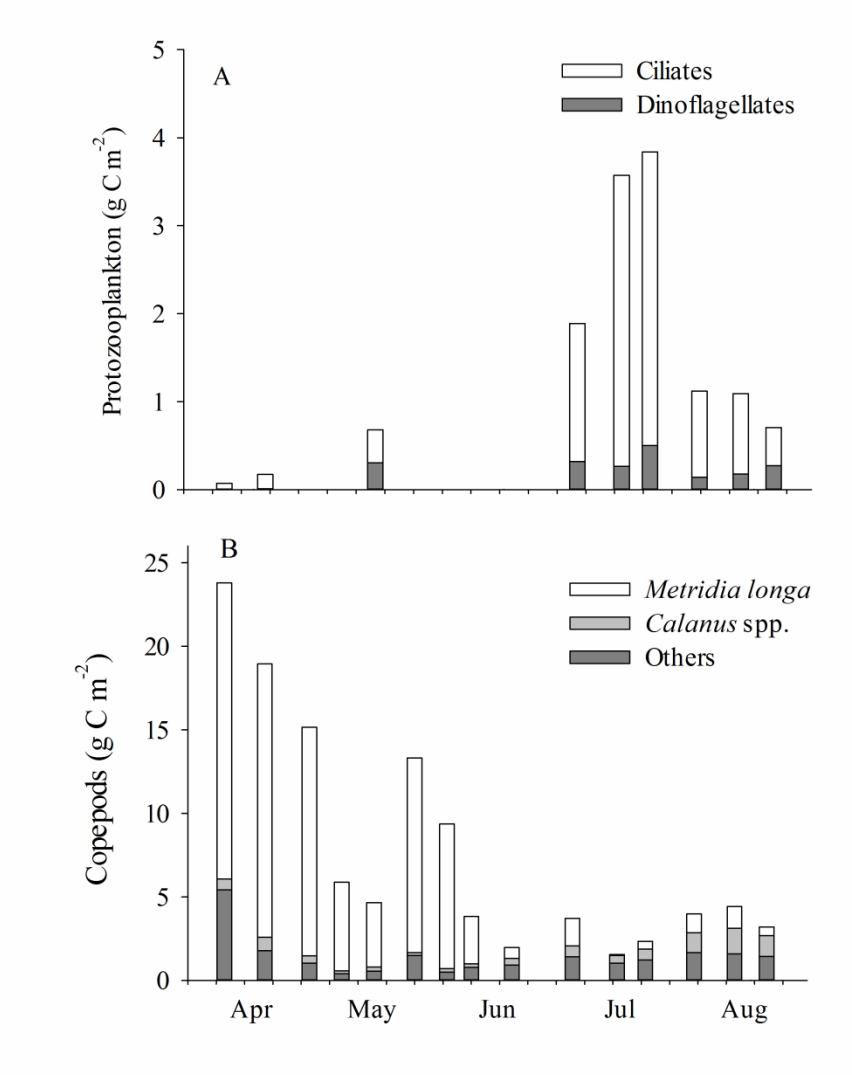


Fig. 9. Relationship between integrated copepod biomass and integrated phytoplankton and protozooplankton biomass. White dots indicate regression between copepods and phytoplankton, r^2 = 0.22, P = 0.08. Black dots indicate regression between copepods and protozooplankton, r^2 = 0.89, P < 0.01.

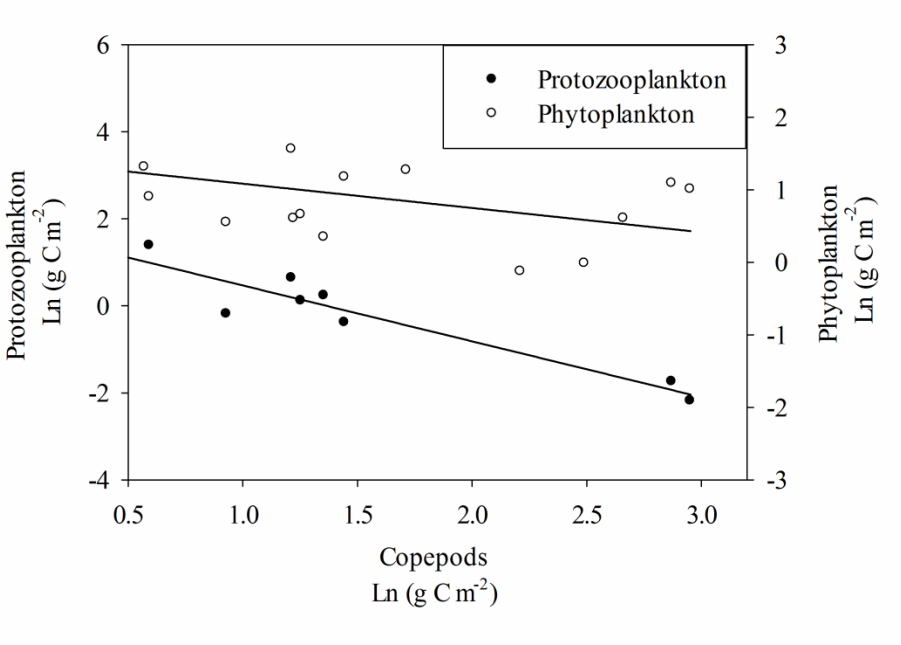


Fig. 10. *Metridia longa* specific clearance rate (ml µg C^{-1} d^{-1}) at 3˚C of different size classes (A) and biomass classes (B) of ciliates, dinoflagellates, nanoflagellates and phytoplankton.
Error bars indicate mean ±SE (n ≥ 14).

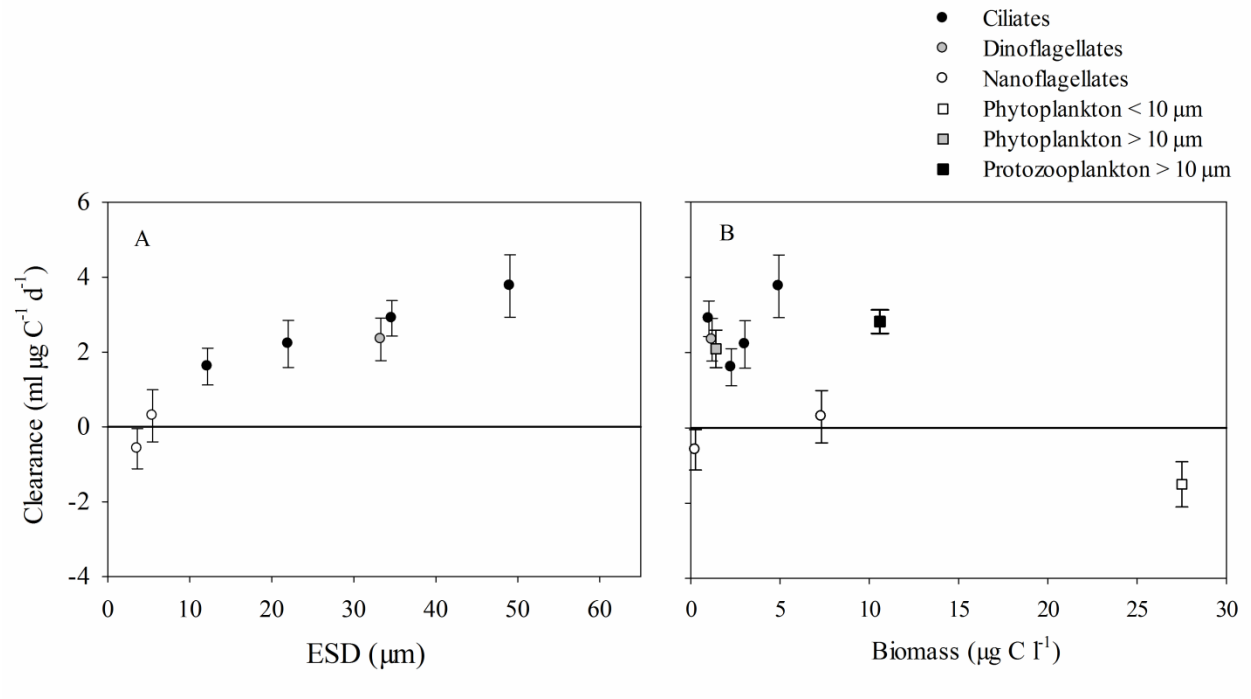


Fig. 11. Seasonal development in copepod grazing impact. (A) Water column (WC) cleared by the copepod community (% d^{-1}). (B) Bars: Integrated protozooplankton production (g C m^{-2} d^{-1}) and ●: fraction of protozooplankton production cleared by the copepod community (% d^{-1}).

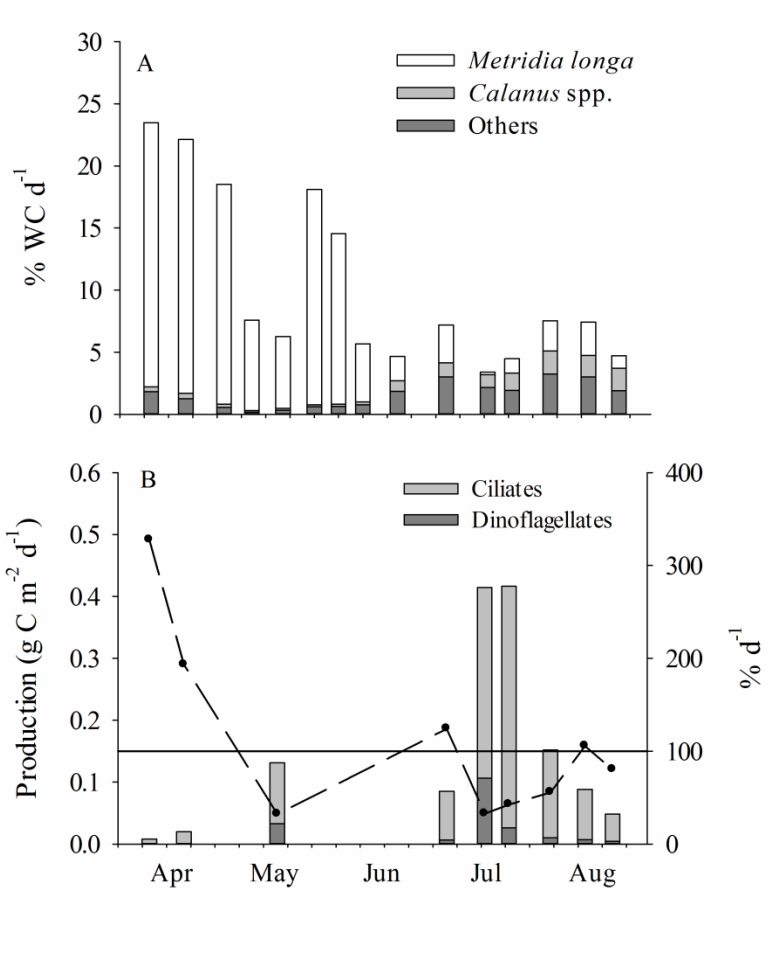


Fig. 12. Water column (WC) cleared by *Metridia longa* (% d^{-1}). Values are estimated using maximum potential clearance rates from Hansen et al. (1997) and Møller et al. (2006) or by using the average clearance rate generated from the grazing experiment with *M. longa* (present study).