The production and fate of picoplankton and protozoa in the pelagic food web of Napoleon Gulf, Lake Victoria, East Africa

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Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of this thesis, including any required final revisions, as accepted by my examiners.
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Abstract

The importance of the microbial food web and how it interplays with the classical food chain has gained considerable attention in temperate lakes. However its role in carbon transfer from pico- and nanoplankton to zooplankton and planktivores is relatively unknown in tropical lakes. Sampling of the microbial food web and experiments to estimate the growth rate and fate of its components were performed in Lake Victoria, East Africa, during the mixing season (May to August) 2002. Bacterioplankton and ciliate densities in Napoleon Gulf ranged from 6.2 to 14.9 cells x 10^{6}·mL^{-1} and 51.9 to 75.2 cells·mL^{-1}, respectively. Flagellate abundance was high, ranging from 70.4 to 127.9 cells x 10^{3}·mL^{-1}. Small flagellates, tentatively called Choanoflagellida, dominated the flagellate community by abundance and biomass. Bacterial growth rates were low, yet high abundance and cell size resulted in high bacterial production representing 24 to 38% of phytoplankton production. Protozoan growth rates and production are similar to values reported for other African lakes and the Laurentian Great Lakes. Protozoa were the dominant grazers of bacteria with grazing pressure switching from protozoa > 5 μm in June to protozoa < 5 μm (presumably flagellates) in July. In July, grazing on flagellates was from predators < 40 μm, probably ciliates, while the ciliate community was grazed by > 40-μm plankton. Given that plankton of Lake Victoria is dominated by colonial cyanobacteria and raptorial zooplankton, protozoa could be an important pathway in the pelagic food web of Lake Victoria, East Africa.

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Dedication

To two special Shaws in my life; Sylvia Eileen Jackson and Robert James Shaw. Thank you for your love, stories and times shared.

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Introduction

Understanding pelagic food webs is a major focus of freshwater research and is crucial for the management of lakes from several perspectives, including production of fish, bioaccumulation of contaminants, and control of phytoplankton and bacterioplankton. In the last couple of decades, particular attention has been paid to the importance of the microbial food web and how it interplays with the classical food chain. Although many aspects of the microbial food web, such as its role in biogeochemical cycling, are generally well accepted, its role in supporting production at higher trophic levels is still in need of further exploration. Most studies on the microbial loop are on temperate systems, whereas research on the different trophic groups of the microbial loop is generally scarce for tropical regions. In this thesis I examine the role of the microbial food web in Napoleon Gulf, Lake Victoria.

The Microbial Food Web

Bacterioplankton

The bacterioplankton community is the base of the microbial loop, and can be divided into four main functional groups based on their sources for carbon, energy and electrons. The majority of pelagic bacterioplankton are heterotrophic, utilizing reduced complex molecules as their carbon source. These organic molecules can be autochthonous in origin, eg. from phytoplankton, or allochthonous, from the terrestrial plants in the drainage basin. Heterotrophs gain electrons from organic compounds. The remaining bacterial community is composed of lithoautotrophs, which obtain carbon by reducing CO_2 and gain electrons from inorganic substances. Organoheterotrophs and lithoautotrophs can be further divided into phototrophs, which obtain energy from light, and chemotrophs which oxidize organic or inorganic compounds for their source of

energy. While species generally belong to one of the four functional groups, some display mixotrophic abilities, switching their metabolic pattern in response to environmental changes (Prescott et al. 2002; Perry et al. 2002).

Heterotrophic bacteria contribute production to the base of pelagic food webs along with phytoplankton, with their relative importance to the overall productivity of the food chain decreasing along a trophic gradient from oligotrophic to eutrophic systems (Cole and Caraco 1993). This is because the relative importance of allochthonous carbon from the drainage basin should decline as autochthonous production within the lake increases. However, in lakes dominated by inedible phytoplankton, such as cyanobacteria, heterotrophic bacteria can be important for carbon transfer to zooplankton communities (Christoffersen et al. 1993) unable to graze most of the algal community.

The mechanisms controlling bacterial abundance, biomass and production are not completely understood. Controversy exists as to whether bottom-up or top-down factors regulate bacterial activity. Support for bottom-up control has come from studies demonstrating that nutrients such as phosphorous can limit bacterial abundance and production (e.g. Pace and Cole 1996). In two oligotrophic lakes, Chrzanowski et al. (1995) found that bacterial growth was limited by phosphate, whereas abundance was controlled by grazers. In contrast, Adrian et al. (2001) observed that in a high-nutrient lake bottom up factors exerted weak effects on bacterial production, which was regulated by top-down control.

Grazing on bacteria by protozoa appears to be a major factor regulating bacterioplankton. Both heterotrophic flagellates and ciliates are important grazers on bacteria; however, the dominant grazer has been shown to differ in systems of differing trophic status and bacterial abundance. In oligotrophic lakes and oceans heterotrophic flagellates are the dominant grazers; in contrast, ciliates

have been observed as the principal grazers of the bacterial community in eutrophic lakes (Christoffersen et al. 1990). In systems where bacterial densities exceed 5×10^6 mL^{-1}, most ciliates are bacterivorous and are important predators of bacteria. Grazing control is dominated by flagellates in lakes where bacterial numbers are below this level. In these oligotrophic and mesotrophic systems, ciliates are lower in abundance and most taxa are consumers of small phytoplankton (Beaver and Crisman 1989). Metazoans, Cladocera and Rotifera, also directly ingest bacterioplankton, and in some cases are more important grazers than protozoa (Pace and Cole 1996).

Protozoa

The flagellate community consists of varying trophic modes, including autotrophs, mixotrophs and heterotrophs. The ciliate community can be an assemblage of both mixotrophic and heterotrophic species (Foissner et al. 1999). In contrast to mixotrophic flagellates, which are autotrophic forms capable of phagotrophy, mixotrophic ciliates contain an autotrophic endosymbiont. These endosymbionts may be green algae of the genus *Chlorella* (zoochlorellae) or chloroplasts retained from their prey. They can be permanent or temporary; in the latter case the functional plastids must be continuously replaced (Foissner et al. 1999). Many small bacterivorous ciliates (< 30 μm) are specialized for retaining picoplankton-sized (0.2 – 2.0 μm) cells. Larger ciliates are generally inefficient grazers of particles < 1 μm and thus tend to be algivorous, consuming larger particles (Beaver and Crisman 1989), or predacious on other protozoa. Eutrophic lakes are usually dominated by small bacterivorous ciliates; however, abundance of both small and large ciliates increases with increasing trophic state.

Due to overlap in the size ranges of prey items, nanoflagellates (2 – 20 μm), nanociliates, microzooplankton (20 – 200 μm) and mesozooplankton

(0.2 – 20 mm) are potential competitors for the same food resources (Sanders et al. 1994; Beaver and Crisman 1989). In addition to competing with micro- and mesozooplankton for bacterioplankton prey, heterotrophic flagellates are also grazed significantly by these communities. Although rotifers have minor impacts on bacterioplankton, both ciliates and rotifers are dominant grazers on the nanoflagellate community (Jurgens et al. 1996), often exerting more grazing pressure than their crustacean counterparts (Sanders et al. 1994). Observation of ciliates within food vacuoles of predatory ciliates indicates that ciliates can receive predation pressure from within the ciliate community (Yasindi 2001).

Trophic Link

Both ciliates and flagellates receive grazing pressure from metazoa, thereby acting as an important link for carbon flux from the pico- and nanoplankton size fractions to zooplankton (Bennett et al. 1990; Beaver and Crisman 1989; Adrian et al. 2001). They can also increase the nutritional value of poor quality food for higher trophic levels (Tang et al. 2001), such as zooplankton, which may be affected by poor food quality resulting in decreased growth rates (Branstrator et al. 1996). This nutritional improvement due to grazing on intermediate prey can increase egg production, growth rates and yields of higher predators such as ciliates and zooplankton, compared to grazing strictly on poor quality algal cells (Tang et al. 2001).

Cladocera, Copepoda and Rotifera all consume ciliates and flagellates; however, there is debate as to which are more effective as consumers, with inconsistencies between studies. These inconsistencies may be a result of differences in predator feeding mechanisms among taxa. In a study by Burns and Schallenberg (2001), calanoid copepods had higher ingestion rates on protozoa than did cladocerans, with relative ingestion rates on ciliates increasing with

increasing lake productivity. This trend is consistent with the feeding behaviour of copepods and cladocerans. Copepods are wholly (cyclopoids) or partially (calanoids) selective raptorial feeders, capable of selecting and ingesting ciliates from amongst other particles. Ingestion rates on ciliates are therefore relatively independent of the presence of algae. In contrast, suspension-feeding cladocerans filter food particles from the water. When algal concentrations are high, such as in eutrophic lakes, excess items clog their filtering apparatus. These particles, including ciliates, are cleared unselectively so ciliates may actually sustain lower predation with increasing phytoplankton abundance (Burns and Schallenberg 2001).

Predation on ciliates can be size-selective, with copepods often selecting large-bodied ciliates. Some ciliate species display behaviours used in predator avoidance. Thus the size distribution and species composition of the ciliate community are both important when analyzing predation efficiency and are possible explanations for discrepancies within the literature. Rotifers are similar to Cladocera in their feeding mechanisms, typically being suspension feeders grazing particles between 1 – 20 μm; however, some genera such as *Synchaeta*, *Polyarthra* and *Asplanchna*, exhibit specialized feeding mechanisms to capture specific food items, such as protozoa (Ruttner-Kolisko 1974; Gilbert and Bogdan 1984; Bogdan and Gilbert 1987; Gilbert and Jack 1993; Walz 1993; Moss 1997). Gilbert and Jack (1993) found that *Synchaeta pectinata* fed more efficiently on the ciliate *Strobilidium gyrans* compared to the algae *Cryptomonas phaesolus*, which was believed to be its favoured food.

Fish larvae also utilize ciliates as food items, with first feeding larvae preferentially selecting them over copepod nauplii (Stoecker and Govoni 1984; Hunt von Herbin and Gallager 2000). This selection is based on a variety of factors including slower swimming speed of the protozoa in comparison to the

nauplii (Hunt von Herbin and Gallager 2000), and potentially mouth gape size (Nagano et al. 2000). Development of larval feeding structures, visibility, and speed could be factors contributing to the switch from ciliates to copepod nauplii in the diet of larvae as they mature (Hunt von Herbin and Gallager 2000). Ciliates enhance the survival of larvae at a critical life stage where starvation often causes mortality within the first few weeks post hatching (Nagano et al. 2000). Fish larvae also selectively target particular genera within the ciliate community, which can increase the survival rate of the fish larvae. Ciliates of different trophic levels, i.e. algivores and bacterivores, could have different nutritional values, resulting in different survival rates of fish larvae feeding selectively on ciliates of different trophic levels. Improved quantification techniques for ciliates have proven that, in addition to loricate ciliate species, aloricate ciliates are consumed indicating that ciliates may be even more important in fish larvae diets than previously believed (Nagano et al. 2000). These results show a direct link between the microbial food web through protozoa to the fish community.

Virioplankton

Within the last couple of decades, detection methods for viruses in plankton have improved and indicate that their abundance in natural waters exceeds those of the bacterioplankton (Wommack and Colwell 2000). Studies on the mortality of bacteria induced by virioplankton indicate that viral activity could be an important top-down control on bacterioplankton populations, matching and even exceeding that of grazing induced mortality (Weinbauer and Hofle 1998; Fuhrman 2000). Viral lysis of phytoplankton and bacterioplankton releases fragments and organic matter. Subsequent uptake of this material can result in a bacterial-viral loop, altering the flux of carbon through the food web

and potentially decreasing the production passed to higher trophic groups (Fuhrman 2000).

Virioplankton may also be an important nutrient source to upper trophic levels via heterotrophic nanoflagellates. In a study by Gonzalez and Suttle (1993) the ingestion and digestion of viruses by heterotrophic flagellates was indicated by the disappearance of both fluorescently labeled-viruses and 50-nm sized microspheres from flagellate food vacuoles. Although the results indicated that viruses may be a significant nutrient source for flagellates, grazing losses exerted by the nanoflagellate community on the virioplankton was deemed minor (Gonzalez and Suttle 1993). The implications of viral activity on higher trophic levels are relatively unknown.

Carbon Efficiency Transfer

The efficiency of carbon transfer through the food web depends on the number of trophic levels. Flow of carbon to top predators will be reduced as trophic links increase, independent of whether the original food source was autotrophic or heterotrophic, with losses largely due to increased respiration (Sanders et al. 1994). Effects of zooplankton predation are species-specific resulting in changes in trophic level interactions both seasonally and with depth within the same system (Adrian et al. 2001). A variety of physical and chemical factors, including oxygen, temperature and light, affect community structure which in turn alters the pathways and efficiency of carbon flow through the food web.

Lake Victoria

Located in East Africa, Lake Victoria is the largest tropical lake in the world (Table 1, Figure 1) and is a highly productive ecosystem. With the total fish catch in 2000 reaching 220 thousand metric tonnes, it holds the largest

freshwater fishery in Africa (Balirwa et al. 2003). Affected by eutrophication and introduced species, dramatic changes have occurred in its food web and in water quality. Concern over these changes has resulted in intensive research activity by the three surrounding countries, Uganda, Kenya and Tanzania, in cooperation with international partners. Biological research has concentrated on the composition, interactions and changes of the phytoplankton and fish communities. Research has focused on invaders and species which have economic impacts, such as the water hyacinth, Nile perch and cyanobacteria. Invertebrates, such as freshwater prawns and crustacean zooplankton, have also received attention, however not to the same extent. Relatively little is known about the heterotrophic microbes at the base of this food web. In lakes dominated by inedible phytoplankton and raptorial zooplankton, such as Lake Victoria, bacteria and protozoa could be an important food source for zooplankton and planktivores. Quantification of the microbial food web components, their interactions, and their connection to zooplankton production is therefore fundamental to the understanding of the pelagic food web of this important lake. In order to help fill this gap, I examined the microbial component of Lake Victoria's food web at a nearshore station in Napoleon Gulf.

With a convoluted shoreline, Napoleon Gulf consists of numerous bays and receives water flowing from the main lake through to the outlet of the White Nile**.** The centre of the Gulf currently reaches a maximum depth of 20.5 m (Silsbe 2004). The Gulf is sheltered, experiencing low wind stress. Mugidde (2001) reported well developed oxyclines occurring between 9 and 20m, leading to deep water hypoxia from January through December. However, between June and August declines in oxygen at lower depths are only temporary with diurnal mixing replenishing oxygen levels throughout the water column (Mugidde 2001; Ramlal et al. 2001). Oxygen levels range from 0.04 – 10.6 $mg \cdot L^{-1}$ from July to

August, with lower values occurring at depth (Mugidde 2001; Ramlal et al. 2001). Water column temperatures ranged from approximately 24˚C to 28˚C, with little temporal variation (Mugidde 2001; Ramlal et al. 2001; Campbell 2001). The Gulf is eutrophic, with chlorophyll *a* values typically ranging from 8 – 54 $\mu g \cdot L^{-1}$ (Ramlal et al. 2001; Campbell et al. 2003). Average chlorophyll *a* values are around 30 $\mu g \cdot L^{-1}$, however peaks exceeding 150 $\mu g \cdot L^{-1}$ between September and November have been recorded (Mugidde 2001; Mugidde et al. 2003). Due to this high phytoplankton biomass, the secchi depth is shallow, about 1 m (Campbell et al. 2003; Mugidde et al. 2003).

Food Web of Lake Victoria

Both biomass and relative species abundance of phytoplankton varies seasonally in Napoleon Gulf, with cyanoprokaryotes dominating the algal biomass for most of the year (Kling et al. 2001; Mugidde 2001). Diatoms (Bacillariophyta) dominated the algal community in Napoleon Gulf in August and September 1995 in terms of biomass, with *Nitzschia aciculatis* as the dominant species (Ramlal et al. 2001). Cyanoprokaryotes comprised most of the remaining algal biomass. Chlorophytes, cryptophytes and dinoflagellates were also represented, yet were a much smaller fraction of the overall biomass. The annual variation in phytoplankton biomass is largely caused by cyanoprokaryotes, which are lower in biomass during the mixing period (June-August) and during sustained thermal stratification (January-April), yet exhibit high concentrations of biomass at the onset of stratification (September-December). In 1998, cyanoprokaryote biomass ranged from 3.8 – 9.0 $mg \cdot L^{-1}$ during the low seasonal periods, but reached 135.5 $mg \cdot L^{-1}$ in October (Mugidde 2001). At a nearshore station in Pilkington Bay, located at the northern end of Lake Victoria just southeast of Napoleon Gulf, cyanoprokaryotes comprised 70% of the

phytoplankton community by biomass in November, with *Cylindrospermopsis africana* as the prominent species. Phytoplankton biomass was higher at Pilkington Bay with values ranging from 3.7 - 3.9 $mg \cdot L^{-1}$ (live weight) compared to Napoleon Gulf with values between 1.6 - 2.4 $mg \cdot L^{-1}$ (Ramlal et al. 2001).

A recent study by Yasindi and Taylor (2003) of Napoleon Gulf and Bugaia (an offshore site) found *Strombidium*, *Strobilidium* and *Halteria* to dominate the planktonic ciliate community in terms of abundance, with total ciliate abundance ranging from 0.5 to 63 $ciliates \cdot mL^{-1}$. Average biomass was 35.7 $\mu g\ C \cdot L^{-1}$, with *Linostomella*, *Frontonia*, *Vorticella* and *Strombidium* being the dominant genera by biomass. A large fraction of the ciliates were herbivorous; 63% by biomass. Bacterivores were also an important guild contributing 22% of the biomass. Metazoan zooplankton consumed most of the ciliate production at Winam Gulf, Kenya, during a single grazing experiment (Yasindi 2001). In September, 1995, protozoan biomass was only 0.03% of the phytoplankton biomass in Napoleon Gulf (Ramlal et al. 2001).

Taxonomic composition of the crustacean zooplankton has been well documented for both inshore and offshore sites (Lehman 1996; Mwebaza-Ndawula 1994). Cyclopoid copepods are the most abundant crustacean zooplankton both inshore and offshore, followed by calanoid copepods. Cladocera are present both inshore and offshore; however, their abundance is quite low in comparison to copepods. Although diversity of rotifers is high within the pelagic food web, they are relatively scarce in terms of numbers and biomass (Mwebaza-Ndawula, Fisheries Resources Research Institute, Jinja, Uganda, personal communication). Copepods formed over 99% of the zooplankton community in Napoleon Gulf by abundance; with nauplii and copepodites contributing 82.8% of the total. Cyclopoid adults were the next dominant group forming of 17.1% of the total. While calanoid adults were

present their numerical contribution to the zooplankton community was not substantial (Mwebaza-Ndawula 1994). In another inshore station, Pilkington Bay, a similar pattern was found with cyclopoids dominating the community at 94%. Although calanoids and cladocerans were present; their numbers were low, contributing 5% and less than 1% to the total zooplankton community. Crustacean zooplankton (Cladocera and Copepoda) abundance was 636550 individuals·m^{-2} with a total dry weight of 1353 mg·m^{-2} (Branstrator et al. 1996). Grazing experiments from Pilkington Bay and Bugaia indicate that zooplankton are not capable of controlling phytoplankton production (Lehman and Branstrator 1993). Seasonal peaks are also observed for the zooplankton community, tending to occur between April and August (Branstrator et al. 1996). The presence of a large daphnid, *Daphnia magna*, offshore at Bugaia (Jonna and Lehman 2002) may indicate that fish predation has an affect on the structure of the zooplankton community in Lake Victoria (Branstrator et al. 1996). The appearance of this large bodied cladoceran could be related to the decline of haplochromines following the introduction of Nile perch (*Lates niloticus*) to the lake in the 1960's. The collapse of the haplochromines may have reduced the level of planktivory in offshore regions, allowing for the persistence of a large-bodied zooplankton (Branstrator et al. 1996).

Other pelagic invertebrates are also present in Napoleon Gulf. The abundance of the freshwater prawn, *Caridina nilotica*, varies temporally, ranging from 2 – 3231 individuals·m^{-2}. Diel vertical migrations have been recorded for the offshore site Bugaia and a nearby inshore site, Buvuma Channel, with low abundances at the surface during the day (Mbahinzireki et al. 1998). *Chaoborus* and acarid mites are present, yet at low densities compared to the crustacean zooplankton (Mwebaza-Ndawula 1994).

Nile perch is the top trophic predator in Napoleon Gulf, consuming fish and larger invertebrates such as *Caridina* (Campbell 2001). Stable isotope analyses by Campbell (2001) indicate that piscivory increases as Nile perch mature, with their diet becoming less reliant on invertebrates. The analyses also indicate that zooplanktivorous fish contribute little to the diet of Nile perch. *Rastrineobola argentea*, a small cyprind, and *Yssichromis laparograma*, a haplochromine, feed primarily on zooplankton but are not regular components in the diet of Nile perch. However, these small zooplanktivores are both commercially and locally harvested for human use, including consumption (Wanink et al. 1998). Lungfish (*Protopterus aethiopicus*), which are becoming an important basis for the fishery in some parts of the lake, also consume small zooplanktivorous fish in addition to *Caridina*, mollusks and gastropods (Campbell 2001). Introduced in the 1950's, Nile tilapia (*Oreochromis niloticus*) feeds on a variety of flora and fauna, with benthic detritus a major component of its diet (Balirwa 1998, Campbell 2001). *O. niloticus* is thought to have competitively excluded many of the native tilapiine species. Due to its importance as a food item for a variety of fish species, the detritivore *Caridina nilotica* is considered to be a key species within the food web of Lake Victoria (Campbell 2001).

Until recently, bacterioplankton, nanoflagellates, microflagellates and ciliates within the pelagic food web of Napoleon Gulf, and Lake Victoria as a whole, were relatively unexplored. The purpose of this thesis is to determine the abundance, biovolume, biomass and community composition of the bacterioplankton, flagellates and ciliates in Napoleon Gulf. The production and fate of each component was estimated in order to test the following four hypotheses:

1) Bacterial production in the plankton of Napoleon Gulf is a large fraction of phytoplankton production.

2) Bacterivorous ciliates are the dominant grazers of the bacterioplankton, consuming most of the bacterial production.

3) Herbivorous ciliates are significant contributors to the grazing of edible phytoplankton (defined as single cells).

4) Ciliate production is regulated by grazing from the crustacean zooplankton, as opposed to food limitation.

Materials and Methods

Sample Site and Collection

Located between the Eastern and Western African rift valleys, Lake Victoria is the largest tropical lake by surface area. Sampling occurred at an inshore sample site (00°24′N, 033°14′E; site depth = 14 m) in Napoleon Gulf of Lake Victoria, Uganda. Napoleon Gulf serves as the outlet for the lake, draining into the River Nile. Physical parameters and chlorophyll *a* samples were taken weekly, mid morning (9:30 – 11:00 am) from May to August, 2002. On May 30, June 20 and July 11, 2002 discrete depths were sampled for bacterioplankton (2, 5 and 10 m), protozoa (2 and 5 m) and chlorophyll *a* (0, 2, 5 and 10 m) using a Van Dorn sampler. Samples were collected in duplicate, except chlorophyll *a*, which was taken in triplicate.

Sample Fixation

Bacterioplankton and flagellate samples of 8 - 20 mL were fixed with 1% formalin buffered with saturated sodium borate, filtered through a 0.2 μm acrodisc and kept at 4°C until enumeration (Sherr and Sherr 1993). Lugol's Iodine solution (1%, Edmondson 1959) was used to preserve samples for protozoa (250 mL). These samples were then settled in graduated cylinders for at least 30 hours. The top section was then suctioned off and discarded. The remaining concentrated sample (approximately 20 mL) at the bottom was transferred to a clear glass scintillation vial with a Teflon*-fluorocarbon-resin-lined-lid. Samples were stored in the dark at room temperature.

Bacterioplankton Enumeration and Biomass Estimation

Following dispersion of clumps by vortexing, subsamples between 0.25 mL and 0.5 mL were added to individual filter wells. Each subsample was stained on a 0.2 μm black polycarbonate filter (backed by a 0.45 μm mixed cellulose ester

membrane) for approximately 5 minutes with DAPI (4', 6-diamidino-2-phenylindole) at a final concentration of 0.57 $\mu g \cdot mL^{-1}$. Using a Zeiss Axioscop 2 microscope, random fields were photographed at 1000x with a Q imaging Qicam digital camera. A Northern Eclipse Imaging System was used to enumerate and measure at least 300 cells per sample to determine abundance per mL and biovolume. This method did not differentiate autotrophic picoplankton from heterotrophic bacteria. Abundance of photoautotrophic picoplankton were examined unstained under blue light excitation and were found to be 5.4% of total picoplankton on May 16, 2002. The number of photoautotrophic picoplankton is neligible relative to the heterotrophic picoplankton, however the number of chemoautotrophs is unknown. Hochstadter (2000) found a similar percentage (10%) of picoplankton to be autotrophic picoplankton in mesotrophic Lake Constance, and regarded plankton between 0.2 – 2.0 μm as bacteria. The term picoplankton in this thesis includes both auto- and heterotrophic picoplankton, but is mainly heterotrophic bacteria. To estimate biovolume, cell measurements were entered into a formula which equates cells to straight rods with hemispherical ends (Bratbak 1993). Average carbon content per cell ($fg\ C \cdot cell^{-1}$) was determined by multiplying average biovolume (μm^3) per cell by a carbon conversion factor of 200 $fg\ C \cdot \mu m^{-3}$ (Bratbak 1993). This carbon conversion factor was recommended as a conservative value if a carbon conversion factor was not determined within a particular study. The conversion factor recommended by Bratbak (1993) is lower than a carbon conversion factor (250 $fg\ C \cdot \mu m^{-3}$) determined using the average seasonal picoplankton biovolume in this study (0.37 μm^3) and the allometric conversion formula for DAPI stained cells by Posch et al. (2001). Total biomass ($mg\ C \cdot L^{-1}$) was determined by multiplying average carbon content per cell by picoplankton abundance.

Enumeration and Identification of Protozoa

Flagellates were enumerated both via epifluorescence and phase microscopy with an inverted microscope. Choanoflagellates were not seen in Lugol's Iodine preserved samples, however they were observed when formalin fixed samples were stained with DAPI and viewed using epifluorescence. Due to the high density of particles, mainly algae, relative to the abundance of flagellates I was unable to count the whole flagellate community using epifluorescence. Therefore the remaining flagellate community was enumerated via an inverted microscope.

Protozoan samples preserved in Lugols Iodine were topped up to 22 mL using 1% Lugols solution, then 1 mL of each sample was settled in Ütermohl settling chambers with the addition of 1% Lugols solution for a total volume of 50 mL. Settling occurred for at least 12 hours prior to examination of the settling chamber. Protozoa were identified based on descriptions in Foissner et al. (1999) and Lee et al. (2000); classifications followed Lee et al. (2000). Random fields of view were scanned using an Axiovert 35 Zeiss Inverted microscope until at least 100 flagellates were enumerated. Flagellates were categorized into Choanoflagellida, Cryptomonadida, Gymnodiniales, Prymensiida and 'other heterotrophic flagellates'. The latter two were further divided into groups based on size (< 5 and > 5 μm). Ciliates were counted to the genus level and, when possible, were differentiated further within a genus by either size or distinguishable characteristics. Transects were scanned at 200x to count the larger ciliate genera, while smaller cells were enumerated at 400x using the Axiovert 35 Zeiss Inverted microscope.

Estimation of Protozoan Biovolume and Biomass

Pictures of protozoa were taken with a Q imaging Qicam digital camera and measured using Northern Eclipse Imaging System. At least 10 cells were measured in each replicate from duplicate samples taken at 2 m on May 30, June 20 and July 11, 2002 (range: 11-63 ciliates, 14-34 flagellates). If cells measured were less than 10 in the individual replicates, replicates were combined for that sampling date. If the combined number of cells in the duplicates for the date was less than 10 cells, then measurements for the three sample dates were combined. Linear dimensions were entered into appropriate geometric formulae used by the Roff and Hopcroft (1986) microbiota image analysis system to determine biovolume (Tables 2 and 3). Abundance was multiplied by average biovolume to obtain total biovolume. Biomass ($\mu g\ C \cdot L^{-1}$) was calculated from total biovolume using a conversion factor of 190 fg $C \cdot \mu m^{-3}$ (Putt and Stoecker 1989). This value is similar to the conversion factor I used for picoplankton and within the range (121 to 864 fg $C \cdot \mu m^{-3}$) of carbon:biovolume conversion factors reported by Pelegri et al. (1999) for a bacterium and four species of protozoa.

Chlorophyll *a*

Samples were placed in carboys and protected from exposure to light during transport to the laboratory. They were then filtered (250 mL) through 47 mm GF/F filters, and the filters were placed in scintillation vials. Whole lake water from 2 m (56 – 80 mL) was also filtered through 25 mm 2.0 μm polycarbonate filters. Average chlorophyll determined from material collected on 2.0 μm polycarbonate filters was subtracted from average chlorophyll obtained from the GF/F filter to estimate the amount of chlorophyll between 0.7 μm and 2.0 μm. Chlorophyll from each filter was extracted in 10 mL of 90% methanol

overnight. Following the measurement of chlorophyll *a* using a spectrophotometer (665 nm), chlorophyll was degraded to phaeophytin with the addition of 1-2 drops of 1 M HCl to each sample. Phaeophytin was read at a wavelength of 750 nm five minutes following the addition. In this report chlorophyll *a* refers to chlorophyll *a* plus phaeophytin calculated according to Lorenzen (1967). Chlorophyll *a* values, uncorrected for phaeophytin, were also calculated, based on Talling and Driver (1963).

Physical Parameters

Temperature, fluorescence (as an indicator of chlorophyll *a*), conductivity and dissolved oxygen were measured throughout the water column using a Seabird CTD with additional sensors each sampling date. Water transparency was measured using a secchi disk. These secchi depth measurements were used to estimate the euphotic depth (0.5% of surface irradiance) using a relationship between secchi depth and the vertical attenuation coefficient of photosynthetically active radiation in Lake Victoria found by Silsbe (2004).

Grazing Experiments

Whole water samples collected using a Van Dorn sampler from 2 m depth on May 30, June 20 and July 11, 2002 were used to conduct the experiments outlined below. The size fraction and dilution experiments were performed in duplicate. Bacteria and protozoa were enumerated as described above.

Size Fraction Experiments

Size fraction experiments were performed to estimate grazing rates of different size-classes of predators on the bacterioplankton by creating incubations with different size-fractions removed. Whole water samples were filtered through 40-µm Nitex mesh, and 5-µm and 1-µm polycarbonate membranes. Replicate 1-L carboys (platypus bags) were filled with 500 mL of the

5 μm and 1 μm filtrate, whereas 2-L carboys were filled with 1 L of the 40-μm filtrate and unfiltered whole water. Carboys were incubated for 48 h in a water filled cooler maintained between 21 and 26°C in the light protected by a double layer of black fibre glass window screen.

Subsamples for bacterioplankton were taken in either 6 and 12 h intervals for 48 h and fixed with borate-buffered formalin at a concentration of 1%. Bacterial growth rates (μ) were estimated as the regression slope of the natural logarithms of bacterial density in the 1-μm filtrate against time.

Protozoa were preserved using Lugol's Iodine solution at time zero and 24 hours. Protozoan rates of population change (μ) were determined in the whole lake water (μ_{WLW}) and the < 40-μm filtrate ($\mu_{<40\mu m}$) incubations from the formula:

$$\mu = (\ln N_t - \ln N_0)/t$$

where N_0 and N_t are initial and final cell densities in each of the incubations and t is the duration of the experiment. When rates of population change are greater in the < 40-μm filtrate ($\mu_{<40\mu m}$) incubations compared to the whole lake water (μ_{WLW}) rates of change, I assumed that the protozoa are receiving predation pressure from organisms > 40 μm. That is, with the absence of > 40-μm predators in the < 40-μm filtrate incubations, the protozoa are relieved from grazing pressure and exhibit a higher rate of population change. Predation rate from organisms > 40 μm was estimated by subtracting μ_{WLW} from $\mu_{<40\mu m}$. In some cases, $\mu_{<40\mu m}$ and μ_{WLW} were lower than the estimated predation rate by predators > 40 μm. In this case I assumed that the true population growth rate of the protozoan population was at least equal to predation rate by predators > 40 μm and selected that predation rate as the rate of population growth. However, if $\mu_{<40\mu m}$ is less than μ_{WLW} it could indicate predation pressure on the protozoan community from predators < 40 μm, which are controlled in the whole lake water incubations by predators > 40 μm. If predation on protozoa occurs in both the < 40-μm and

WLW treatments, their growth rates and predation rates will be underestimated regardless of which method is used.

Predator Dilution Experiments

Modified from the Landry and Hassett (1982) dilution technique, these predator dilution experiments are based on the assumption that the growth rate of the prey will remain constant, while the rate of encounter between prey and predator will decrease if lakewater is diluted. The change in abundance ($N_t - N_0$) is plotted against dilution. The slope of this regression reveals the grazing rate of the predators, while the y-intercept provides the rate of population change of the prey in the absence of predators. GF/F filtrate was used to dilute the whole lake water. Replicate 2L carboys were filled with one liter of whole lake water, 65%, 50% and 25 % whole lake water. Incubation of carboys and subsampling of bacterioplankton and protozoa occurred as outlined in the size fraction experiment.

Productivity

Production estimates for picoplankton, flagellates and ciliates were calculated by multiplying rates of population change (selected from the size fraction and predator dilution experiments; see above) by biomass.

An empirical model developed by Silsbe (2004) was used to estimate gross phytoplankton production on each grazing experiment date from corresponding chlorophyll *a* concentrations within the euphotic zone. Photosynthetic-irradiance parameters, chlorophyll and the vertical attenuation of irradiance are significantly related to each other, and in Lake Victoria, chlorophyll alone explains 75% of the variance of measured phytoplankton production (Fee 1990, Silsbe 2004).

Statistical Analysis

Statistical analyses were performed using SPSS 12.0 for Windows.

Results

Limnological parameters and chlorophyll *a*

There was little vertical structure during my sampling season; in general, temperature changed less than one degree Celsius with depth (Figure 2). Surface temperatures cooled slightly from May to July. Oxygen varied less than 2 $mg \cdot L^{-1}$ with depth on the three grazing experiment dates, indicating that the water column was mixing (Figure 3). Average oxygen for the sampling season was 6.4 $mg \cdot L^{-1}$. Secchi depth ranged from 0.6 m (May 30) to 1.4 m (June 20), with a seasonal average of 1.1 m (Figure 4). The euphotic zone was the shallowest in May, first grazing experiment date, at 2.2 m and reached 5.7 m in August. The euphotic zones on the other grazing experiment dates, were 5.2 m in June and 3.6 m in July (Figure 4). Chlorophyll *a*, measured as fluorescence, was higher in the upper 4 m, decreasing with depth on all three grazing experiment dates (Figure 4). However, a deep chlorophyll maximum occurred around 9 m on June 20, the second grazing experiment date. Two other deep chlorophyll maxima occurred during the sampling season between 12 and 14 m depths (Figure 4). Chlorophyll *a*, measured by spectrophotometry, was similar to the range measured by fluorometry (Figure 4); ranging from 13.9 to 35.2 $\mu g \cdot L^{-1}$ during the sampling season (Table 4). At 2 m, chlorophyll *a* was similar on the three grazing experiment dates. Chlorophyll *a* in the 0.7 to 2.0 μm size fraction (picophytoplankton) contributed little to total chlorophyll *a* for most of the sampling season. However, on May 30, approximately 50 percent of total chlorophyll *a* was in the picoplankton size range (Table 4).

Picoplankton abundance, biovolume and biomass

Picoplankton abundance ranged from 6.2 to 14.9 cells x $10^6 \cdot mL^{-1}$ during the three grazing experiment dates, with biomass ranging from 0.4 to

1.2 mg $C \cdot L^{-1}$. Both picoplankton abundance and biomass were higher in May compared to June and July (Figure 5). Abundance peaked at 2 m and then generally decreased with depth in May and June, whereas abundance was relatively consistent throughout the water column in July (Figure 5a). In May and July, biomass was greatest at 1 m depth and decreased with depth, whereas in June biomass peaked at 2 m (Figure 5b). There was no temporal difference in picoplankton mean biovolume and cell carbon content, however there was a decrease with depth in July (Figure 6). Picoplankton mean biovolume for the water column ranged from 0.31 to 0.44 μm^3 on the three grazing experiment dates, with a seasonal average of 0.37 μm^3.

Flagellate abundance, biovolume, biomass and community composition

Abundance of flagellates was consistently higher at 5 m compared to 2 m on all three grazing experiment dates (Figure 7), however the difference was not quite significant (repeated measures ANOVA, P= 0.077). Abundance ranged from 70.4 to 127.9 cells x $10^3 \cdot mL^{-1}$, with abundance significantly different among dates (repeated measures ANOVA, P = 0.022). I used a simple one-way ANOVA and *a posteriori* test to determine that this was due to lower abundance in June than on the other two dates.

Small colonial cone-shaped flagellates with a straight single flagellum extending from the apical end were tentatively called Choanoflagellida (Figure 8). These flagellates were not seen in samples preserved with Lugol's Iodine, yet were present in samples preserved with formalin; this may indicate that lysis of the cells occurred in the Lugol's Iodine samples. They were observed singly and in colonies consisting of up to 8, yet colonies generally consisted of 2-3 individuals. Lengths measured from individuals sampled at 2 m on the three grazing dates ranged from 1.6 to 3.9 μm, with an average of 2.7 μm. The range in

diameters was 1.0 to 1.8 μm, with an average of 1.3 μm. Collars typically associated with Choanoflagellida were not observed in DAPI stained samples (epifluorescence microscope; 1000x) or in either formalin-preserved samples or formalin-preserved samples with the addition of Lugol's Iodine (inverted phase microscope; 1000x). However, the cells were so small that our inability to see collars does not necessarily indicate that they were not present.

Choanoflagellida dominated flagellate abundance at both depths in May, June and July, consisting of at least 98% of total flagellate abundance (Tables 5, 6 and 7). 'Other heterotrophic nanoflagellates' was the second most abundant group of flagellates. Abundance of Cryptomonadida and Gymnodiniales were approximately two times lower at 5 m compared to 2 m (Tables 5 and 6).

The biovolume ($\mu m^3 \cdot cell^{-1}$) of Choanoflagellida was extremely small in comparison to the other flagellates, with Cryptomonadida and Gymnodiniales having the largest biovolumes (Table 8).

The biomass of flagellates ranged from 28.6 to 59.9 $\mu g\ C \cdot L^{-1}$ during the three grazing experiment dates (Figure 9). Biomass followed a similar trend to abundance, with a lower biomass in June than in May and July, however the difference was not quite significant (repeated measures ANOVA $P = 0.078$). There was a significant difference in biomass at 2 and 5 m over the sampling season (Figure 9, Repeated measures ANOVA $P = 0.044$). Despite their small biovolume, Choanoflagellida also dominated flagellate biomass (Tables 9, 10 and 11). The biomass of Cryptomonadida and Gymnodiniales was higher at 2 m than at 5 m in May, June and July.

Ciliate abundance, biomass and community composition

At 2 m ciliate abundance ranged from 51.9 to 75.2 $cells \cdot mL^{-1}$, with no temporal difference in abundance from May to July (Figure 10, repeated

measures ANOVA P = 0.138). Ciliate abundance was significantly lower at 5 m, ranging from 45.0 to 49.2 cells·mL^{-1} (Repeated measures ANOVA P = 0.048). Class Spirotrichea dominated ciliate abundance at both depths on all three grazing experiment dates; Classes Oligohymenophorea and Litostomatea were also prominent (Figure 10). Within Spirotrichea, *Halteria* spp. and *Strobilidium* spp. were the dominant genera in May. In June and July, however, *Strobilidium* spp. comprised most of the abundance (Tables 12, 13 and 14). Scuticociliates were the prominent group in Oligohymenophorea at both depths in May, June and July. Abundance of Vorticellidae was highest at 2 m in May. *Lagenophrya* spp. was the most abundant genus in Litostomatea, with *Mesodinium* spp. most abundant in June (Tables 12, 13 and 14).

Spirotrichea also dominated the ciliate community in terms of biomass, with total biomass ranging from 32.9 to 55.4 μg C·L^{-1} at 2 m and from 24.7 to 34.8 μg C·L^{-1} at 5 m (Figure 11). There was a significant temporal difference in biomass, however there was no difference with depth (repeated measures ANOVA P = 0.033, P = 0.119, respectively). Oligohymenophorea consistently composed a portion of the biomass at both depths during May, June and July, especially at 2 m in May. In July, Class Heterotrichea was important in terms of biomass at both depths (Figure 11), due to a slight increase in abundance of *Stentor* spp. which possess a large biovolume (Tables 12, 13). *Strombidium* spp. and Vorticellidae both accounted for most of the biomass in Spirotrichea and Oligohymenophorea respectively (Tables 15, 16 and 17).

Energy acquisition and major sources of food of the protozoan community

Putative methods of energy acquisition and major sources of food for the flagellate and ciliate communities are outlined in Tables 18 and 19 (Foissner et al. 1999, Lee et al. 2000, Yasindi 2001). Heterotrophic flagellates and ciliates

dominated the protozoan community by percent abundance and percent biomass at both depths in May, June and July (Tables 20 and 21). Percent abundance of mixotrophic and autotrophic protozoa was similar, yet mixotrophic protozoa were more important when assessed in terms of percent biomass (Tables 20 and 21).

Bacterivores dominated the protozoan community by abundance and biomass at both depths in May, June and July (Tables 22 and 23). The abundance and biomass of algivores and predatory protozoa (putative food source of protozoa), were relatively equal in the flagellate and total protozoan community. However, within the ciliate community, algivores contributed more to abundance and biomass than predatory ciliates. Predatory ciliates were more important in terms of abundance and biomass for the ciliate community compared with the flagellate community (Tables 22 and 23).

Picoplankton production and fate based on lakewater filtrates

The rate of picoplankton population change in 1-μm filtrate was negative in the May grazer removal experiment (Figure 12). Positive, but low, rates of change occurred in June and July (Figure 12, Table 24). Carbon content per cell increased in the 1-μm filtrates after one day during the June and July grazing experiments; however carbon content per cell did not change in the 1-μm filtrate in May or in whole lake water on all three grazing experiment dates (Figure 13). Only during the July experiment did the carbon content per cell in the 1-μm filtrate appear to be less than in unfiltered lake water. However, carbon content per cell in 1-μm filtrate increased to a comparable amount observed in the whole lake water approximately 30 h after the start of the experiment, whereas in June carbon content per cell was similar in the whole lake and 1-μm filtrate for the first 24 hours and then increased in the 1-μm filtrate. My goal was to estimate the

rate of cell division when the experiment began, rather than the subsequent rate of biomass increase due to filtration. Considering that cell size appears to change with filtration and time, I used the rate of increase in cell numbers to determine production rates, as opposed to biomass.

A picoplankton production value could not be calculated for May due to the negative rate of population change (Figure 12, Tables 24 and 25). Picoplankton production in June was similar to the production in July (Table 25).

Negative rates of picoplankton population change occurred in the May size fraction experiment (Figure 14). Although positive rates of change are expected in at least the < 1-μm incubation (no eukaryote predators) the most negative rate of change occurred in this fraction. Less negative rates of picoplankton population change took place in the other 3 size fractions; < 5 μm, < 40 μm and whole lake water (Figure 14). In June, rates of population change were much less in the < 40-μm fraction relative to the < 1- and < 5-μm fractions. A further decrease occurred in the whole lake water relative to the < 40-μm fraction. This indicates grazers in the 5 to 40-μm and > 40-μm size classes. These differences correspond to grazing rates of approximately 0.142 and 0.188 d^{-1} for the 5 to 40-μm and > 40-μm classes (Table 26). Total grazing rate on the picoplankton was 0.384 d^{-1}.

In July, rates of population change were lower in the other three size fractions relative to the 1-μm filtrate (Figure 14). These results suggest that the dominant grazers on the picoplankton switched from > 5 μm in June to < 5 μm in July, when grazing rates by the < 5-μm size fraction were 0.191 d^{-1} (Table 26). Differences in the rate of picoplankton population change in < 40-μm replicates in July could be due to different protozoan communities within the replicate incubations. Higher abundance of bacterivorous protozoa would be expected in the replicate with the negative rate of change in picoplankton. However,

examination of the protozoan community revealed that abundance of flagellates and ciliates (putative bacterivores) was higher in the replicate with the positive rate of change in picoplankton; thus it is inconclusive as to whether the discrepancy in picoplankton population change is due to differing grazer populations within the replicate incubations. Grazing rates determined from the average of these replicates indicate similar grazing pressure on the picoplankton by plankton between 5 and 40 μm and those > 40 μm (Table 26).

Dilution Experiments

Rates of population change of prey (i.e. picoplankton and protozoa) can be determined with increasing dilution of whole lake water. It is expected that rates of population change of the prey will increase relative to whole lake water incubations due to fewer encounters with predators and lower predation rate while growth rate is unaffected. The relationship between dilution and rates of population change can be used to estimate growth and grazing.

Picoplankton rate of population change, production and predation rate

There was no significant relationship between picoplankton growth rate and dilution on May 30 and July 11, 2002, however in June the rate of picoplankton population change was estimated as 0.281 d^{-1} (Table 24, Figure 15). The estimated predation rate, 0.489 d^{-1}, on picoplankton exceeded the rate of picoplankton population change (Table 24, Figure 15). Volumetric production of picoplankton using this estimate of growth rate is 180.0 μg $C \cdot L^{-1} \cdot d^{-1}$ instead of 110.0 μg $C \cdot L^{-1} \cdot d^{-1}$ obtained using the growth rate estimated in the 1-μm filtrate (Table 25).

Rate of protozoan population change as a function of dilution

Dilution of whole lake water with 0.7-μm filtrate did not increase the population growth rate of protists, but instead resulted in low and usually non-

significant declines in population growth rate. In June, there was no increase in the growth rate of the ciliate community in 50 or 35 % diluted lake water relative to the rate of population change in undiluted lake water (Figure 16a). Specific ciliate groups with different putative food sources also showed no change in population growth compared to respective growth rates in whole lake water (Figure 16b). The lack of increase in population growth with dilution likely indicates food limitation rather than grazer control of the ciliate community.

Flagellate (autotrophic and heterotrophic) and centric diatom counts also exhibited the same pattern as seen in the ciliate community (Figure 17a). A non-significant downward trend was observed in Cryptomonidida and heterotrophic flagellates (Figure 17b).

Dilution experiments in July (Figure 18) exhibited slightly positive, yet non-significant changes in population growth rate with dilution in the flagellate and diatom counts. The same trend was seen within the specific flagellate groups. However, in a dilution experiment performed on < 40-μm filtrate, significant decreases occurred with dilution in the total flagellate and diatom counts and with heterotrophic flagellates.

Production and fate of protists based on lake water filtrates

In July, size-fractionation experiments were also performed in order to obtain population growth rates of the protozoa. The rate of flagellate population change was 0.196 d^{-1} in the < 40-μm filtrate (Table 27). This rate is a conservative estimate of growth rate considering that flagellate grazers, such as ciliates, are present within the < 40-μm fraction. Apparent negative predation from grazers > 40 μm indicates that predation on the flagellate community is indeed mainly from plankton < 40 μm (Table 27).

Rate of population change in the ciliate community in the < 40-μm filtrate was 0.207 d^{-1}, with a predation rate from > 40-μm predators of 0.146 d^{-1} (Table 28). Litostomatea (mainly *Mesodinium* spp.) and Phyllopharyngea (*Dysteria* spp.) had apparently negative predation from plankton > 40 μm, indicating higher grazing by predators < 40 μm (Table 28). The highest rate of population growth occurred in Phyllopharyngea in whole lake water, followed by Oligohymenophorea (scuticociliates and Vorticellidae) in < 40-μm filtrate. Bactivorous ciliates (*Pleuronema* spp., scuticociliates, Vorticellidae, *Dysteria* spp.) generally appeared to have the highest rate of population change (Table 29). Algivorous/predatory and predatory guilds had negative growth rates indicating predation by < 40-μm plankton; these guilds are mainly composed from ciliates within the Classes of Litostomatea and Phyllopharyngea.

Discussion

Abundance and Biomass of picoplankton and protozoa in Napoleon Gulf

Abundance in relationship to lake trophic level (Chl *a*)

It is well established that bacteria and ciliate abundance increases with increasing chlorophyll *a*. Bird and Kalff (1984) found a positive empirical relationship between bacterial abundance and chlorophyll *a* concentration based on data from marine and freshwater systems (Figure 19). Regression analysis of bacterial abundance and chlorophyll *a* concentration in Ethiopian (Zinabu and Taylor 1997) and East African lakes (Yasindi 2001) of differing salinities also produced positive relationships (Figure 19). Slopes were steeper in regressions using data from saline lakes, compared to the regression for freshwater lakes (Figure 19).

Bacterial abundance and chlorophyll *a*, at 2m and from within the euphotic zone sampled from Napoleon Gulf on May 30, June 20 and July 11, align closely to the regression line for Ethiopian freshwater lakes (Figure 19). Lake Malawi and values external from this study for Lake Victoria also conform closely to the Ethiopian freshwater regression, while Lake Tanganyika values were closer to the regression developed by Bird and Kalff (1984) (Figure 19).

Significant positive relationships have been found between ciliate abundance and chlorophyll *a* (Figure 20) from tropical, subtropical and temperate lakes (Beaver and Crisman 1989, Hwang and Heath 1997b, Yasindi 2001, Yasindi *et al*. 2002). Slopes of the tropical and subtropical lake regressions were steeper than the regression slope for temperate lakes, indicating that ciliate abundance per unit chlorophyll increases with increasing trophy more quickly in tropical/subtropical lakes than in temperate lakes (Figure 20, Beaver and Crisman 1989). Ciliate abundance sampled at 2 and 5 m from Napoleon Gulf on my three

sampling dates conforms closely to the regression for subtropical lakes (Figure 20). Alignment closer to the subtropical as opposed to the east African regression of Yasindi (2001) indicates that I found greater abundance of ciliates relative to chlorophyll in Napoleon Gulf than he found in other African lakes or in Lake Victoria, including Napoleon Gulf (Yasindi and Taylor 2003). The higher abundance found during this study may be due to differences in methodology. Yasindi and Taylor (2003) used the Quantitative Protargol Staining (QPS) technique developed by Montagnes and Lynn (1993) to enumerate and identify the ciliate community, whereas I used Lugol's Iodine to preserve protozoan samples and enumerated them using inverted microscopy. In the previous study, Yasindi and Taylor (2003) collected samples from an offshore site and two inshore sites at depths that were not included in the current study, which could also account for the different range in abundance between the two studies. The east African regression (Yasindi 2001) also includes saline lakes which could account for some of the discrepancy.

A relationship between heterotrophic flagellates and chlorophyll *a* has not been published; however, a positive relationship (Figure 21) was found between abundance of heterotrophic nanoflagellates (HNF) and picoplankton abundance in a regression analysis of 108 different freshwater systems collected worldwide (Berninger et al. 1991). In these systems, abundance of both heterotrophic flagellates and picoplankton increased with increasing productivity (Berninger et al. 1991); considering the strong relationship found between bacteria and chlorophyll *a*, picoplankton abundance could be viewed as a measure of trophy. This suggests that there is a positive relationship between HNF abundance and chlorophyll *a*, as found with bacteria and ciliates. Total HNF (including what we tentatively call Choanoflagellida, see results) in Napoleon Gulf from 2 and 5 m were close to an order of magnitude above the regression line (Figure 21). The

majority of HNF abundance in Napoleon Gulf was Choanoflagellida. When Choanoflagellida are excluded, the abundance of 'other HNF' drops over 2 orders of magnitude, falling below the regression line for other freshwater systems (Figure 21).

Comparison of picoplankton and protozoan abundance to other Great Lakes

Conforming to the positive relationship between picoplankton and ciliates with chlorophyll *a*, abundances of picoplankton and ciliates were higher in eutrophic Lake Victoria compared to previously reported values found in the oligotrophic African Great Lakes Malawi and Tanganyika (Tables 30 and 31, Figure 19). Picoplankton abundance was comparable to abundance found from other studies in Lake Victoria (Table 30, Figure 19). Although the range in ciliate abundance previously reported for Lake Victoria includes the range found during the current study, average ciliate abundance is higher in the present study (Table 31). Abundance of HNF has not been examined previously in Lake Victoria.

In general, abundance of picoplankton, HNF and ciliates are higher in Lake Victoria compared to abundances found in the Laurentian Great Lakes. Picoplankton abundance was higher than in oligotrophic Lakes Superior and Michigan, with the low end of the range in picoplankton abundance from the current study overlapping with the upper range of picoplankton abundance for oligo-mesotrophic Lakes Erie and Ontario (Table 32). Abundance was comparable to a shallow eutrophic site from Lake Erie (Table 32). Picoplankton abundance from Laurentian Great Lakes and African Great lakes of similar trophy are comparable indicating trophy has a large role in picoplankton abundance as opposed to temperate versus tropical systems (Table 32).

Ciliate abundance was higher in Napoleon Gulf than has been reported for oligo-mesotrophic offshore sites in the Laurentian Great Lakes (Table 31). However the range in ciliate abundance in a shallow eutrophic site from Lake Erie was above the range (45 -75 cells·mL^{-1}) found in the current study (Table 31).

Flagellate abundance in Napoleon Gulf was considerably higher than abundances found the Laurentian Great Lakes (Table 31). However, with the exclusion of Choanoflagellida, flagellate abundance drops to within the ranges for the Laurentian Great Lakes (Table 31).

Picoplankton and protozoan abundance in comparison to other tropical and subtropical lakes

Picoplankton abundance was comparable to picoplankton abundance in other East African freshwater lakes despite differing trophy. However, Lake Koriftu had both higher chlorophyll *a* and picoplankton abundance (Table 33). Moderately saline East African lakes with comparable chlorophyll *a* to Napoleon Gulf also had picoplankton abundances within the range found in this study, with the exception of Lake Hora, which had higher concentrations of picoplankton (Table 33). Lakes higher in picoplankton abundance also had elevated chlorophyll *a* relative to Lake Victoria. Lake Methara had lower chlorophyll *a* and picoplankton abundance (Table 33). Picoplankton abundance in East African saline lakes were highly elevated relative to picoplankton abundance for the current study (Table 33). The majority of these saline lakes also had elevated chlorophyll *a* values. Despite the difference in chlorophyll *a*, picoplankton abundance was comparable to Palau Jellyfish lake, a tropical saline oligotrophic sulphur lake (Venkateswaran et al. 1993).

The range in total ciliate abundance for Lake Victoria (45.0 to 51.9 cells·mL^{-1}) from May-July at 2 and 5 m overlapped with the low end of the range (55.5 - 145.1 cells·mL^{-1}) reported for ciliate abundance in other eutrophic systems

(Chl *a* 10-56 μg·L^{-1} Beaver and Crisman 1989). Ciliate abundance in the current study was quite high in comparison to other East African lakes of similar trophy and picoplankton abundance (range of averages: 3.4 – 8.8 cells mL^{-1} Yasindi 2001).

HNF abundance was an order of magnitude higher than eutrophic Lake Simbi (1.4 – 7.5 $x10^3$ mL^{-1}), a saline Kenyan lake with picoplankton abundance ranging from 1.2 – 2.3 $x10^7$ mL^{-1} (Finlay et al. 1987). HNF abundance in shallow Lake Nakuru, Kenya was comparable to the HNF range found in the current study (Figure 21). The similarity in HNF abundance between the two lakes despite high picoplankton abundance in Lake Nakuru, may be due to salinity differences. Finlay et al. (1987) considered the HNF abundance low considering the high abundance of picoplankton; this theory is supported when compared to freshwater systems of similar picoplankton abundance. However, the regression for HNF abundance and picoplankton abundance does not include any saline systems (Figure 21).

Picoplankton Size

Mean size of picoplankton from Napoleon Gulf (0.320 – 0.414 μm^3) is similar to that reported for Fieldings Bay (0.186 – 0.375 μm^3, North unpublished Department of Biology University of Waterloo, Waterloo, ON), another inshore site in Lake Victoria. Biovolumes reported for Lake Tanganyika (0.25 μm^3, Hecky and Kling 1981) and inshore sites from Lake Malawi (0.133 – 0.320 μm^3, North unpublished Department of Biology University of Waterloo, Waterloo, ON) are also comparable, despite the large differences compared to Lake Victoria in chlorophyll *a* and bacterial abundance. Picoplankton biovolume reported for the Laurention Great Lakes of similar trophy, including biovolume from a eutrophic coastal site in Lake Erie, was lower than for the African Great Lakes (Table 32).

Picoplankton biovolume in Lake Awassa (0.09 – 0.160 μm^3), a freshwater eutrophic East African Lake, remained relatively constant seasonally, indicating that the observed change in bacterial biomass was more dependant on the change in bacterial abundance than on cell biovolume (Zinabu and Taylor 1989). Similar to Lake Awassa, there was minor temporal difference in picoplankton biovolume between May and July in Napoleon Gulf. Change in abundance over the three months and with depth suggests this could also be a factor responsible for the observed change in biomass in this system. Seasonality was observed in picoplankton biovolume in Lake Michigan, with an increase occurring from spring to summer followed by a decrease in the fall to below spring levels (Scavia et al. 1986).

The slopes of the regressions of picoplankton abundance against chlorophyll *a* (Figure 19) are less than one, indicating that the abundance of picoplankton does not increase proportionally to chlorophyll *a* (Bird and Kalff 1984). Bird and Kalff (1984) examined a hypothesis put forth by Pedros-Alio and Brock (1982) suggesting that bacterial cell size increases with increasing trophy; which would mean that as lake trophy increases, bacterial biomass would increase faster than bacterial number. Bird and Kalff (1984) did not find a positive relationship between cell size and bacterial abundance based on biovolume estimates from scanning electron microscopy (slight negative trend) or epifluorescence (no relationship). No relationship was found between biovolume and chlorophyll *a* from literature values reported for African and Laurentian Great Lakes (Figure 22). Analyses based solely on abundance may be misleading considering the difference in picoplankton size between tropical and temperate lakes, and the lack of a relationship between picoplankton size and chlorophyll *a*. Biomass of picoplankton should be taken into account when comparing picoplankton communities.

Composition of the flagellate community

The flagellate community in Napoleon Gulf was dominated numerically (> 98.8%) and by biomass (> 51.8%) by very small flagellates we believe to be Choanoflagellida. The abundance of Choanoflagellida was extremely high (69.8 - 127.2 cells x $10^3 \cdot mL^{-1}$) with the abundance of the remaining flagellate community reaching a maximum of 2.5 cells x $10^3 \cdot mL^{-1}$ at 5 m in June. Abundance of the choanoflagellate *Codosiga* sp. in Sandusky Bay, a eutrophic site in Lake Erie, ranged from 20 – 240 cells$\cdot mL^{-1}$ (Hwang and Heath 1997a). Choanoflagellida were a component of the HNF communities in Lakes Ontario, Erie, Huron and Michigan (Pick and Caron 1987, Hwang and Heath 1997b, Carrick and Fahnenstial 1990). In Lake Erie, Choanoflagellida dominated the biomass of heterotrophic nanoplankton (HNAN) along with chrysomonads and a small unidentified zooflagellate. In contrast to Napoleon Gulf, where Choanoflagellida composed the majority of the biomass of the total flagellate community and likely a large percent of total heterotrophic nanoplankton biomass, percent contribution to total biomass of HNAN in Lake Erie was fairly equal among groups. Most of the time, Choanoflagellida contributed < 5% to HNAN (Figure 4, Hwang and Heath 1997b). In Lakes Huron and Michigan, colourless cryptomonads and chrysomonds equally dominated the HNF community, with other zooflagellates (mainly choanoflagellates) being subdominant (Carrick and Fahnenstial 1990). In the heterotrophic nanoplankton community (< 20 μm) of Lake Ontario, HNF were more important than ciliates by biomass (Pick and Caron 1987). Ciliate abundance in Napoleon Gulf was consistently dominated by small (~< 20 μm) species of *Strobilidium* spp., *Halteria* spp. and scuticociliates. The range in biomass for these ciliates was 3.8 to 7.3 μg C$\cdot L^{-1}$ in comparison to the range for total HNF of 28.6 to 59.9 μg C$\cdot L^{-1}$, indicating that the biomass of HNF is

greater than that of ciliates in the heterotrophic nanoplankton community in Napoleon Gulf. Although Choanoflagellida (1.6 – 3.9 μm) were the prevalent taxa in Napoleon Gulf, predominance by small HNFs (chrysomonads) also occurred in Lakes Huron, Michigan and Erie. The small chrysomonads resulted in a small community composition in Lakes Huron and Michigan. The smallest HNF (*Chromulina* sp., a chrysomonad 2-3 x 3-4 μm) numerically dominated the heterotrophic nanoplankton of Lake Erie (Hwang and Heath 1997b, Carrick and Fahnenstial 1990). As in Napoleon Gulf, cryptomonads were consistently important in the phototrophic nanoflagellate community of Lakes Erie, Ontario, Huron and Michigan (Pick and Caron 1987, Hwang and Heath 1997b, Carrick and Fahnenstial 1990).

Ciliate community composition

Strobilidium spp., *Halteria* spp. and scuticociliates dominated the ciliate community by percent abundance at 2 and 5 m on all three grazing experiment dates. This is consistent with other East African Lakes, where scuticociliates and oligotrichs (eg. *Strobilidium*, *Strombidium*, *Halteria*) were the most abundant (Yasindi 2001, Yasindi and Taylor 2003). A review by Beaver and Crisman (1989) reported that planktonic ciliate communities tend to be numerically dominated by oligotrichs, scuticociliates, and haptorids, with relative dominance switching from oligotrichs in oligotrophic systems to scuticociliates as trophy increases; with relative abundance of Haptorids typically remaining constant. In contrast to this review, *Strobilidium* and *Halteria* were more abundant than the scuticociliates in Napoleon Gulf. However, in Lake Nakuru, Kenya, a eutrophic saline lake, the scuticociliate *Cyclidium* was 74% of total ciliate abundance and oligotrichs were absent (Yasindi et al. 2002). In sub tropical Florida lakes ciliates between 20-30 μm (mainly scuticociliates) were more important numerically in eutrophic

systems compared to larger ciliates, mainly oligotrichs (40-50 μm) which dominated oligotrophic lakes. Although the abundant genera dominating the ciliate community in Napoleon Gulf were generally smaller sized ciliates (approximate range 10 - 25 μm), the majority were *Strobilidium* and *Halteria*, as opposed to scuticociliates. In November 1999, *Strobilidium* and *Halteria* were also abundant in Napoleon Gulf, along with *Strombidium* (Yasindi and Taylor 2003). Although *Strombidium* was not as numerically dominant as other genera during this study, it was the dominant genus by biomass at both depths in May, June and July. *Stentor*, another large bodied ciliate, *Strobilidium*, although smaller, and Vorticellidae were also prominent in terms of biomass. Protozoan biomass in Napoleon Gulf in November 1999 was also dominated by *Strombidium* and *Vorticella*. However, two genera, *Linostomella* and *Frontonia*, not found during this study were also important (Yasindi and Taylor 2003). In oligotrophic lakes Malawi and Tanganyika, *Strombidium* sp. dominated the protozoan community in terms of biomass; with *Lagynophyra* and *Halteria* being important contributors to protozoan biomass in Lake Malawi (Hecky and Kling 1981, Yasindi and Taylor 2003). In Lake Nakuru, large ciliates contributed the majority of the biomass despite low abundances (Yasindi et al. 2002). In Lake Erie ciliate biomass was also dominated by oligotrichs and scuticociliates with similar proportions of total ciliates found at both eutrophic and oligotrophic offshore sites. However, *Strobilidium* sp. were rare at the offshore site (Hwang and Heath 1997b).

Twenty four ciliate genera (including 4 which were not identified) were present in Napoleon Gulf from May through July. However, this is probably an underestimate considering that rare taxa were grouped into 'unknown' categories; as well, several groups, such as Scuticociliate A, likely contain more than one genus but these were indistinguishable with Lugol's Iodine counts. Shifts in the species composition of Lake Victoria occurred between 1998/1999

and 2002. Yasindi and Taylor (2003) reported 17 ciliate genera in Lake Victoria, 5 of which were not found in the current study. This could be due to the absence of these genera during my sampling period, or I may not have identified them with my methods. Nine genera (*Askenasia, Didinium, Dileptus, Mesodinium, Dysteria, Phascolodon, Coleps, Urotricha and Tinntinidium*) were present in Lake Victoria in May - July 2002, yet were absent in Napoleon Gulf and Bugaia during November 1998 and in Winam Gulf in October 1999 (Yasindi and Taylor 2003). The absence of genera between years has also been reported to occur in the East African lakes Elementia and Nakuru (Yasindi 2001).

The diversity of ciliates also increases with increasing trophy (Beaver and Crisman 1989). The number of genera reported in Napoleon Gulf is higher than the number reported for Lakes Malawi and Tanganyika; however, the genera found are similar. Six of the 8 genera observed in Lake Malawi were also found during this study. *Linostomella* was one genus which was not. However, it was previously reported in Lake Victoria by Yasindi and Taylor (2003). Ten out of 14 genera listed for Lake Tanganyika were also found in Napoleon Gulf (Hecky et al. 1978). The number of taxa found at a shallow site (4.5 m) in Kavirondo Gulf, Lake Victoria was low (Bamforth et al. 1987). Peritrichs numerically dominated the taxa and were associated with filamentous cyanobacteria. The raptorial ciliates *Bursaria* and *Paradileptus* were present, yet not found in Napoleon Gulf during the current study. The low number of taxa could be due to the shallowness of the site, or due to the rupturing of cells during the collection of samples with a 10 μm aperature net. Higher diversity and a different composition of the ciliate community was found in Lake Nakuru (Yasindi et al. 2002). Only seven genera were found in Lake Victoria of the 29 reported in Lake Nakuru, however some of the genera not observed in this study were found in previous studies on the ciliate community of Lake Victoria (Yasindi et al. 2002,

Yasindi and Taylor 2003). Differences within the diversity and composition of these ciliate communities is probably attributable to extreme chemical, physical, and biological differences between the two lakes, such as salinity, depth and composition of the zooplankton community. Yasindi et al. (2002) concluded that the high equivalent spherical diameter (ESD) of 43 μm may indicate that this is not be a true pelagic environment or that metazoan zooplankton are not abundant, reducing competition and predation from Crustacea on the large ciliates.

Temporal Variation in the abundance and biomass of picoplankton and protozoa

Picoplankton abundance exhibited temporal variation, with higher abundance and biomass in May than June and July. Temporal variation was also observed in the abundance and biomass of picoplankton in Lake Awassa (Zinabu and Taylor 1989). There was seasonal variation in the flagellate abundance and ciliate biomass in Napoleon Gulf. Ciliate biomass also varied seasonally in both Lakes Victoria and Malawi (Yasindi and Taylor 2003). In Lake Malawi, ciliate biomass was higher over a three year period during the windy mixing season (June) compared to October to December when the water column was more stratified (Yasindi and Taylor 2003). In June, 1999, the higher ciliate biomass coincided with a phytoplankton and chlorophyll a maximum which occurred at approximately 30 m. However, in another African lake, Lake Nakuru, the observed seasonal change was not significant against the high spatial variation in ciliate biomass (Yasindi et al. 2002).

There was no significant difference in flagellate biomass and ciliate abundance in Napoleon Gulf on May 30, June 20 and July 11, 2002. In Lake Nakuru, Yasindi et al. (2002) also found no significant temporal difference in ciliate abundance.

In this study, data collection only encompassed the mixing season; to obtain a better understanding of seasonal trends in the abundance and biomass of the picoplankton and protozoa, further research is required at the onset of stratification and during full stratification.

Vertical Variation in the abundance and biomass of picoplankton and protozoa

Variation in picoplankton abundance and biomass between 1 and 10 m depth was observed in May, yet appears relatively constant through the water column in June and July. In Lake Awassa no variability was detected with depth for picoplankton abundance or biomass (Zinabu and Taylor 1989). From May through July ciliate abundance was significantly higher at 2 m compared to 5 m. Yasindi and Taylor (2003) also found higher ciliate abundances at the surface in Napoleon Gulf (1 m) and Bugaia (10 m), with abundance declining with depth in November 1998.

Although there was a significant seasonal difference in ciliate biomass, there was no difference in biomass between 2 and 5 m. In Lake Tanganyika, depth profiles from March through October exhibited vertical variation in ciliate biomass at the offshore site, Bujumbura (Hecky et al. 1978). Yasindi and Taylor (2003) found biomass to vary temporally and with depth in both Lakes Malawi and Victoria. The lack of variation in ciliate biomass with depth in this study could be a factor of only two shallow depths being compared or differences in the season when sampling occurred, with the water column mixing in May through July (this study) and stratification occurring in November (Yasindi and Taylor 2003). Seasonal influences on the food sources of ciliates could account for changes in ciliate abundance and biomass on both a temporal and vertical scale. Seasonal succession was observed in the ciliate community of Lake Tanganyika with the appearance of tintinnids and *Vorticella* sp. coinciding with the

succession of algal genera (Hecky and Kling 1981). This was also observed in Lake Nakuru, with a peak in the abundance of *Cyclidium* sp. co-occurring with the period of maximal bacterial abundance.

Role in Food Web

Picoplankton biomass dominated the microbial community (heterotrophic picoplankton and protozoa) in Napoleon Gulf from May to July at both 2 and 5 m depth (Table 34). Hecky and Kling (1981) found estimated bacterial biomass to exceed protozoan biomass in the euphotic zone of Lake Tanganyika. Flagellate biomass exceeded ciliate biomass at 5 m on all three dates and at 2 m in May, yet approximately equaled it in June and July at 2 m. Protozoan biomass was 9 to 18% of the total microbial biomass from May to July, 2002 (Table 34). Within the flagellate community, HNF biomass was greater than auto- and mixotrophic flagellate biomass. As in this study, HNF were more abundant than autotrophic nanoflagellates (ANF) in Lakes Huron and Michigan (Carrick and Fahnestiel 1989); however, biomass of ANF (24.7 $\mu g\ C \cdot L^{-1}$) exceeded the biomass of HNF (9.6$\mu g\ C \cdot L^{-1}$). Phytoplankton biomass, except for Cryptomonidida, was not measured in this study. However, in Lake Ontario autotrophic nano- and picoplankton biomass was greater than heterotroph biomass from April to November (Pick and Caron 1987). Ramlal et al. (2001) reported protozoan biomass as 0.03 % of phytoplankton biomass in Napoleon Gulf.

Growth, production and grazing rates of the microbial food web in Napoleon Gulf

In order to supplement experimental results and to analyze the potential dynamics occurring in the microbial food web of Napoleon Gulf, calculations of clearance rates and carbon consumption were performed for protozoa and zooplankton. Individual clearance rates on picoplankton-sized particles and

algal-sized particles were extracted from the literature (Tables 35, 36 and 37). Community clearance rates were determined by multiplying population abundance by individual clearance rates (Tables 38, 39, 40, 41 and 42). Minimum production (g $C \cdot m^{-2} \cdot d^{-1}$) for protozoa was determined using observed growth rates (Table 43). Maximum production for flagellates was determined using a growth rate of 1 d^{-1} (i.e. equal to biomass, Table 43). Maximum production of ciliates (Tables 44 and 45) was calculated using observed biovolume and the growth rate equation by Müller and Geller (1993). The amount of carbon consumption required by picoplankton, protozoa and zooplankton was calculated from estimated production by assuming 50% carbon conversion efficiency. This is slightly below net growth efficiency reported for bacteria (Fenchel 1987) and within the range reported for protozoa (Fenchel 1987, Laybourn-Parry 1992). Carbon consumption of picoplankton and phytoplankton production required by protozoa and zooplankton was based on total production for each feeding guild even though more than one food source may be consumed by that guild (Tables 45 and 46).

Picoplankton growth rate and production

Picoplankton growth rates were comparable to the range found in Lake Awassa (Zinabu and Taylor 1990) but lower than the range reported for Lake Michigan (Scavia and Laird 1987). Despite low growth rates in Napoleon Gulf, higher picoplankton abundance and larger picoplankton cell size resulted in greater volumetric picoplankton production (μg C L^{-1} d^{-1}) in Napoleon Gulf than in Lake Michigan. In Lake Tanganyika picoplankton production, estimated by apportioning oxygen consumption (Hecky et al. 1981) and incorporation of leucine (Sarvala et al. 1999) was also lower than in Napoleon Gulf. However, picoplankton growth rate calculated from estimated biomass and production,

was 0.9 d^{-1}, which is higher than the rates of population change estimated in this study (Hecky et al. 1981). Picoplankton production in Napoleon Gulf was at the high end of the range reported for volumetric production in a review of fresh and saltwater systems, with areal production falling in the middle of the range (Cole et al. 1988).

Picoplankton production was a large fraction of phytoplankton production. Phytoplankton production derived using Silsbe's model (Silsbe 2004) ranged from 5.2 to 5.5 g C m^{-2} d^{-1} between May and August (Figure 23). These derived values match well with previously reported measured values (Mugidde 1992) from the same sampling station (Table 47). Areal picoplankton production, based on rates of picoplankton population change from 1-μm filtrate for June and July, was 24 and 26 percent of empirically derived phytoplankton production from Silsbe's model (Silsbe 2004). Picoplankton production in June was 38% of phytoplankton production based on rates of picoplankton population change in the predator dilution experiment (Table 47). When compared to literature values of primary production in Napoleon Gulf, picoplankton production was approximately 20 percent of phytoplankton production for the sampling season (Table 47). Similar percentages were found in Lake Awassa (Zinabu and Taylor 1990) and within a review of fresh and saltwater systems (Cole et al. 1988). In Lake Tanganyika Sarvala et al. (1999) found picoplankton production to be 21% of phytoplankton production, however, Hecky et al. (1981) reported a higher value with picoplankton production 55% of phytoplankton production. Picoplankton production could be a substantial fraction of phytoplankton production in other bays within Lake Victoria with comparable picoplankton abundance, biomass and phytoplankton production to Napoleon Gulf (Figure 19, Table 30, Table 48).

The negative rates of picoplankton population change I observed in May are problematical; however, some suggestions can be put forward. Viruses could be exerting top-down pressure on the picoplankton population. Viral induced mortality on picoplankton has equaled and even exceeded that of grazing mortality in other systems (Weinbauer and Hofle 1998, Fuhrman 2000). Virus-sized particles were observed in DAPI stained samples from Napoleon Gulf collected on 0.02 μm filters, however viral abundance, biomass and their affect on picoplankton (i.e. induced mortality) was not determined. Less negative growth rates were observed in incubations containing grazers, which could indicate grazing mortality on the virioplankton by flagellates. Bacterial community composition was not determined in this study; however shifts in bacterial community composition have been observed in other eutrophic lakes (Muylaert et al. 2002) and within experimental incubations (Gattuso et al. 2002). Considering that viruses are host specific (Wommack and Colwell 2000), seasonal shifts in the bacterial community composition could explain why negative rates of population change were observed only in May.

Disturbance of bacteria-phytoplankton interaction by removal of phytoplankton during filtration could have affected the rate of picoplankton population change, however positive growth rates were obtained in June and July in the 1-μm filtrate. Toxins released by cyanobacteria within the incubations could also be an explanation for the negative rate of picoplankton population change observed in May.

Consumption of picoplankton production

Decreases in picoplankton abundance in the size fraction experiment indicate that the dominant grazers of picoplankton switched from > 5 μm in June

to < 5 μm in July (Table 26). The > 40-μm grazers exhibited higher grazing rates than the 5 to 40-μm grazers in both June and July (Table 26).

Community clearance rates of protozoa and zooplankton for May 30, June 20 and July 11, 2002 suggest that ciliates are the dominant grazers of picoplankton in the > 40-μm grazing community (Table 41). Estimated clearance rates also indicate that bacterivorous ciliates are the dominant grazers in the 5 to 40-μm fraction, with clearance rates of flagellates > 5 μm an order of magnitude below those for ciliates < 40 μm in May, June and July (Table 41).

In contrast to the size fraction experiment, the clearance rate calculations indicate that flagellates < 5 μm are the dominant bacterial grazers, followed by grazers between 5 to 40 μm on all three dates (Table 41). The grazing rate from the 5 to 40-μm grazers in the size fractionation (predator removal) experiment may have been underestimated because of the exclusion during filtration of some bacterivorous ciliates, such as Vorticellidae, that are attached to filamentous cyanobacteria. Exclusion of protozoa may have also occurred in the < 5-μm filtrate. Colonial choanoflagellida exceeding 5 μm may have been excluded from the < 5-μm incubations, resulting in an underestimation of observed grazing in the 5-μm filtrate, yet overestimating the observed grazing due to organisms > 5 μm. The calculated clearance and consumption rates of the picoplankton by flagellates < 5 μm, based on the total abundance of Choanoflagellida, appear to be overestimated in comparison to the observed grazing rates. Exclusion of colonial choanoflagellida from the 5-μm filtrate could account for the discrepancy between the observed and calculated results.

Minimal consumption of picoplankton production, based on growth rates determined from the size fraction experiment, indicates that flagellates < 5 μm consumed most of the picoplankton production (Table 46). The minimal consumption estimates of grazers on the picoplankton are in agreement with

grazing rates of different size-classes of predators on the picoplankton (Table 26, Figure 14). However, if growth rates were underestimated and the maximum rates are closer to correct, then bacterivorous ciliates may play an important role in the grazing of picoplankton with maximal consumption rates indicating that bacterivorous ciliates were the major grazers of picoplankton in July (Table 46).

It appears that protozoa are the dominant grazers of picoplankton in Napoleon Gulf. However, within the protozoan community, the source of predation pressure can switch between flagellates and ciliates.

Grazing on phytoplankton

Based on maximum clearance rates, herbivorous ciliates were the main consumers of edible phytoplankton on May 30, June 20 and July 11, 2002 (Table 42). However, minimal clearance estimates suggest that in May both flagellates and ciliates were the major grazers of edible algae. Within the ciliate community, most of the grazing on phytoplankton was by ciliates < 40 μm. While zooplankton had minimal community clearance rates, flagellates also had high community clearance rates on the phytoplankton; indicating that protozoa are the main grazers of phytoplankton in Napoleon Gulf.

However, minimal consumption estimates of phytoplankton production indicate that zooplankton are responsible for consuming majority of the phytoplankton production, as opposed to ciliates. A growth rate for algivorous ciliates was not obtained in the size fraction experiment due to low abundance, resulting in an underestimation of their production, and resulting consumption of phytoplankton production (Tables 29 and 45). A growth rate of 0.555 d^{-1} determined using an equation by Montagnes et al. (1988) was substituted as a minimal growth rate for obligate algivorous ciliates. Obligate algivores in this study consisted of one genus, *Strobilidium* C (Table 19). This growth rate is a

reasonable estimate falling within the range of growth rates determined for other feeding guilds in this study (Table 43). It is comparable to maximum growth rates for nano- and microciliates in Lake Ontario (Taylor and Johannsson 1991) and below growth rates reported for Class Spirotrichea in East African lakes, including Lake Victoria (Yasindi 2001). However, even with the substitution, production of algivorous ciliates on July 11, 2002 only increased to 0.019 g $C \cdot m^{-2} \cdot d^{-1}$ with a carbon consumption of 0.039 g $C \cdot m^{-2} \cdot d^{-1}$. Required consumption of phytoplankton by ciliates is raised to 0.146 g $C \cdot m^{-2} \cdot d^{-1}$; however it is still lower than the level required by zooplankton. Ciliate consumption of phytoplankton exceeds that of zooplankton when maximal growth rates are used to determine carbon consumption rates (Table 46).

Branstrator et al. (1996) found that crustacean zooplankton > 100 μm did not alter algal biomass, measured by chlorophyll *a*, in grazing experiments. However, inedible phytoplankton, such as colonial cyanobacteria, could account for a large fraction of total chlorophyll *a*; thus zooplankton could still be important grazers of edible algae. Fish could also be significant grazers of phytoplankton. Phytoplankton was 6% of the stomach contents of Nile tilapia (*Oreochromis niloticus*) in Northern Lake Victoria and was a consistent portion of the diet in all size classes (Balirwa 1998). However, consistent with the previous study, stable isotope analysis indicates that most of their diet consists of detritus and chironomids (Campbell et al. 2003). While clearance rates suggest that both ciliates and zooplankton are the major grazers of edible phytoplankton in Napoleon Gulf, further research is required to determine grazers of the phytoplankton and its pathway in the food web.

Regulation of ciliate production

Predation rate on the total ciliate community indicates there is grazing on the ciliate community from grazers > 40 μm (Table 28). It appears that grazing from this fraction is weak, however, it is also possible that the gazing by this fraction is masked by interactions within the ciliate community. Yasindi (2001) also concluded that grazing on the ciliate community was from grazers > 40 μm in Winam Gulf, Lake Victoria. However the predation rate (1.684 d^{-1}) was much higher than the one in this study for Napoleon Gulf. Although lower than the previously reported predation rate for Lake Victoria, the predation rate determined in this study is within the range (0.00 – 4.23 d^{-1}) of predation rates from grazers > 40 μm reported for 8 East African lakes (Yasindi 2001).

In the dilution experiment the rate of change in the ciliate population did not increase as expected with release from predation pressure, indicating food limitation of the ciliate community on June 20, 2002 (Figure 16). However, rates of Cryptomonidida population change also did not increase with dilution on June 20, 2002 (Figure 17). Autotrophic flagellates, such as Cryptomonidida, should exhibit high rates of change with dilution considering light availability was at least equal in the diluted incubations and nutrient limitation would be unlikely in this eutrophic system. The lack of increase in Cryptomonidida population growth with dilution suggests that factors other than food limitation were limiting growth of protozoa in the predator dilution incubations.

Total carbon required to support the production of predatory zooplankton is 0.378 g $C \cdot m^{-2} \cdot d^{-1}$, which exceeds total ciliate production (Table 43, Figure 24). However, zooplankton in the predatory feeding guild (Table 40) also consume phytoplankton, flagellates and bacteria; which contribute an unknown fraction to this total. Grazing rates in July indicate that the flagellate community is consumed by grazers < 40 μm, i.e. predatory protozoa (Table 27). Most of the

picoplankton production was consumed by flagellates (Table 26). Therefore, in July it appears that zooplankton production is based on carbon obtained from phytoplankton and ciliates.

Carbon flow and food web structure

The efficiency of carbon transfer through food webs is dependant on the number of trophic levels. This study determined that protozoa are the main grazers of the picoplankton production in Napoleon Gulf. However, the size fraction experiments showed that grazing switched from > 5-μm grazers (flagellates, ciliates and zooplankton) in June to < 5-μm grazers (flagellates) in July (Figure 25). Clearance rate estimates suggest that ciliates are the main consumers of picoplankton within the > 5-μm grazing community. In July, flagellates were grazed by predators < 40 μm, indicating predation from within the protozoan community, which in turn was controlled by grazers > 40 μm, presumably zooplankton. Thus, in July, picoplankton carbon would be transferred to zooplankton via flagellates and ciliates (Figure 25). However, in June, picoplankton carbon could be transferred more efficiently to zooplankton via bacterivorous ciliates. I was not able to make strong conclusions regarding the dominant grazers on edible phytoplankton, however, it appears that ciliates and zooplankton have the potential to consume a large portion of the edible phytoplankton. Although carbon transfer from phytoplankton to zooplankton via ciliates would be a less efficient transfer than direct grazing on algae by zooplankton, ciliates could be important to zooplankton by increasing the nutritional value of a nutrient-poor phytoplankton diet.

Summary

Abundance and Biomass of picoplankton and protozoa in Napoleon Gulf

- Picoplankton and ciliate abundance was higher in Napoleon Gulf compared to abundances found in Laurentian and other African Great Lakes, except for sites of comparable trophy.

- Abundance of heterotrophic nanoflagellates was considerably higher than found in the Laurentian Great Lakes, due to extremely high abundances of small flagellates that we tentatively call Choanoflagellida.

- Within the microbial community, picoplankton dominated the biomass (> 80%) at both 2 and 5 m depth on May 30, June 20, and July 11, 2002. Heterotrophic flagellates composed 3 to 6 percent of the total, while heterotrophic ciliates were approximately 2 % of the total, although they equaled heterotrophic flagellate biomass in July.

Growth, production and grazing rates of the microbial food web in Napoleon Gulf

The four following summaries correspond numerically to the hypotheses outlined in the introduction.

1. Picoplankton production was a large fraction of primary production in Napoleon Gulf. Despite low picoplankton growth rates compared to growth rates found in the Laurentian Great Lakes, high picoplankton abundance and large cell size contributed to higher picoplankton production in Napoleon Gulf.

2. Protozoa are the main grazers on the picoplankton community, consuming most of the picoplankton production. Within the protozoan community, the dominant grazers vary temporally. In June, predator removal experiments indicated that the dominant grazers on picoplankton were > 5 μm, and by comparing abundance and literature values for clearance rates I conclude that ciliates are the prominent grazers of picoplankton within the > 5-μm grazing community. However, in July grazing of the picoplankton community was by grazers < 5 μm, presumably heterotrophic nanoflagellates.

3. Community clearance rate estimates calculated with individual clearance rates from the literature indicate that protozoa are likely the dominant grazers on edible phytoplankton, with ciliates consuming most of the edible phytoplankton production. Estimates of carbon consumption, based on estimated production and a 50% carbon conversion efficiency also indicate a significant contribution of ciliates to grazing, but their contribution relative to crustaceans depends on which literature values are used. Although my estimates indicate that ciliates consume a large fraction of phytoplankton production, further research is required to clarify the amount of phytoplankton production consumed by protozoa versus zooplankton.

4. Size fraction experiments indicate that ciliate production is controlled by grazers > 40 μm, i.e. zooplankton. Predator dilution experiments indicated that growth of protozoa was not limited by predation and indicated food limitation. However in the predator dilution experiments, autotrophic flagellates should exhibit high rates of population change with dilution considering ample light availability and nutrients; yet the rates of population

change of autotrophic flagellates (Cryptomonidida) did not increase with dilution as expected. The lack of increase in the Cryptomonidida population with dilution suggests that factors other than food limitation were limiting growth of protozoa in the predator dilution incubations. While a previous study in Lake Victoria also found that ciliate production was regulated by grazers > 40 μm, the low growth rates of the ciliate community in the current study from the size fraction experiment and inconclusive results from the predator dilution experiment, suggest true growth rates of the ciliate population are not being observed in these incubations. Further research on the rate of ciliate population change and control of the resulting production is needed.

Table 1. Basin parameters for Lake Victoria and Napoleon Gulf (Silsbe 2003; Silsbe, Department of Biology, University of Waterloo, ON, Canada, personal communication).

	Lake Victoria	**Napoleon Gulf**
Volume (km^3)	2598	0.22
Surface Area (km^2)	66,368	26.5
Maximum Depth (m)	75	20.5
Mean Depth (m)	39	7.9

Table 2. Geometric shapes and corresponding formulae used to determine biovolume for each flagellate group from linear dimensions of cells. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida. V = volume (μm^3); D = depth assumption (set at 1); L = measurement of cell (μm; 1 = length, 2 = width, 3 = third measurement).

Classification	**Group**	**Shape**	**Formula**
Choanoflagellida	Choanoflagellates	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
Cryptomonadida	Rhodomonas/Cryptomonas	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Gymnodiniales	Gymnodinium	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Prymnesiida	< 5 and > 5 μm	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Other HNF	< 5 and > 5 μm	Prolate spheroid	$V = \pi*D*L1*L2^2/6$

Table 3. Geometric shapes and corresponding formulae used to determine biovolume for each ciliate group from linear dimensions of cells. V = volume (μm^3); D = depth assumption (set at 1); L = measurement of cell (μm; 1 = length, 2 = width, 3 = third measurement).

Class	Genus	Shape	Formula
Heterotrichea	*Stentor* A, B	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
Litostomatea	*Askenasia*	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
	Didinium	Cylinder, sphere	$V = \pi*D*((L3*L2^2/4)+(L1-L3)^3/6)$
	Dileptus	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
	Lagenophrya A, B, C	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
	Mesodinium A	Cylinder, cone	$V = \pi*D*L2^2*(L1-0.667*L3)/4$
	Mesodinium B	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Monodinium	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Unknown	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Oligohymenophorea	*Pleuronema*	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Scuticociliate A, B, C	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Vorticellidae A, B, C, D	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Vorticellidae E	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
Phyllopharyngea	*Dysteria*	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Periacineta	Truncated cone	$V = \pi*D*(L1^2+L2^2+L1*L2)*L3/12$
	Phascolodon	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Sphaerophrya	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Suctorian	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Prostomatea	*Coleps*	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Unknown	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
	Urotricha	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Spirotrichea	*Halteria* A, B, C, D	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Strobilidium A, B, C	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Strombidium A	Cone	$V = \pi*D*L1* L2^2/12$
	Strombidium B	Cylinder, cone	$V = \pi*D*L2^2*(L1-0.667*L3)/4$
	Strombidium C	Cylinder, ½ prolate	$V = \pi*D*L2^2*(3*L1-L3)/12$
	Tinntinidium A	Cylinder, ½ prolate	$V = \pi*D*L2^2*(3*L1-L3)/12$
	Tinntinidium B, C	Cone, ½ prolate	$V = \pi*D*(L1+L3)*L2^2/12$
		Prolate spheroid	$V = \pi*D*L1*L2^2/6$
Unknown	Unknown A	Cone	$V = \pi*D*L1* L2^2/12$
		Lateral Cylinder	$V = \pi*D*L1* L2^2/4$
	Unknown B	Prolate spheroid	$V = \pi*D*L1*L2^2/6$
	Unknown C	Prolate spheroid	$V = \pi*D*L1*L2^2/6$

Table 4. Size-fractioned chlorophyll *a* (± 95% C.I.) at discrete depths between May and August 2002. Calculated according to Lorenzen (1967). Confidence limits are based on 3 replicates except in 2 cases (N = 2) marked by *. Average chlorophyll *a* values less than zero were reported as zero with the upper confidence limit.

Date (Day of Year)	Depth (m)	Chlorophyll *a* > 0.7 μm ($\mu g \cdot L^{-1}$)	Chlorophyll *a* 0.7 - 2.0 μm ($\mu g \cdot L^{-1}$)
16/05/02 (136)	1-1.5	31.4 ± 11.4	8.2 ± 5.1
23/05/02 (143)	1	19.2 ± 4.3	2.3 ± 10.6
	5	21.2 ± 1.1	
	10	16.5 ± 4.9	
30/05/02 (150)	2	29.7 ± 4.5	16.6 ± 4.9
	5	21.4 ± 2.2	
	10	13.9 ± 4.3	
06/06/02 (157)	2	26.4 ± 6.6	0.3 ± 4.3
	5	29.7 ± 13.6	
	10	19.8 ± 6.6	
13/06/02 (164)	0	22.8 ± 4.5	
	2	25.0 ± 10.5	0.0 + 5.4
	5	24.7 ± 5.6	
	10	22.5 ± 6.3	
20/06/02 (171)	0	24.6 ± 2.1	
	2	26.7 ± 2.8	0.0 + 1.2
	5	21.7 ± 19.0*	
	10	17.5 ± 2.1	
27/06/02 (178)	0	35.2 ± 8.5	
	2	28.2 ± 3.0	0.0 + 5.2
	5	28.5 ± 6.5	
	10	23.5 ± 1.1	
04/07/02 (185)	0	26.5 ± 5.0	
	2	27.7 ± 8.5	0.0 + 2.5
	5	23.5 ± 3.9	
	10	19.5 ± 3.7	
11/07/02 (192)	0	26.5 ± 8.8	
	2	29.9 ± 0.0	0.0 + 9.6
	5	24.4 ± 3.9	
	10	19.7 ± 4.6	
01/08/02 (213)	0	16.6 ± 6.0	
	2	18.1 ± 5.6*	0.0 + 84.3
	5	18.4 ± 2.3	
	10	17.0 ± 4.2	

Table 5. Abundance (cells x $10^3 \cdot mL^{-1}$ ± 95% C.I.) of the flagellate community at 2 m on each grazing experiment date. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida.

Classification		May 30			June 20			July 11		
Choanoflagellida		110.40	±	96.82	69.77	±	113.18	91.14	±	142.83
Cryptomonadida		0.21	±	0.10	0.17	±	0.21	0.19	±	0.70
Gymnodiniales		0.07	±	0.31	0.03	±	0.16	0.10	±	0.29
Prymnesiida	< 5 μm	0.05	±	0.10	0.04	±	0.10	0.17	±	0.39
	> 5 μm	0.01	±	0.05	0.00	±	0.03	0.00	±	0.06
	Total	0.06	±	0.16	0.04	±	0.06	0.17	±	0.33
Other HNF	< 5 μm	0.29	±	0.26	0.18	±	0.44	0.24	±	0.72
	> 5 μm	0.32	±	1.12	0.19	±	0.60	0.38	±	1.51
	Total	0.61	±	1.46	0.37	±	0.16	0.62	±	0.79

Table 6. Abundance (cells x $10^3 \cdot mL^{-1}$ ± 95% C.I.) of the flagellate community at 5 m on each grazing experiment date. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida.

Classification		May 30			June 20			July 11		
Choanoflagellida		127.23	±	49.54	78.58	±	0.49	107.56	±	141.85
Cryptomonadida		0.11	±	0.56	0.04	±	0.12	0.07	±	0.35
Gymnodiniales		0.03	±	0.12	0.01	±	0.04	0.04	±	0.19
Prymnesiida	< 5 μm	0.07	±	0.24	0.01	±	0.01	0.06	±	0.17
	> 5 μm	0.04	±	0.21	0.01	±	0.04	0.02	±	0.09
	Total	0.11	±	0.45	0.02	±	0.03	0.08	±	0.26
Other HNF	< 5 μm	0.08	±	0.29	0.13	±	0.45	0.13	±	0.49
	> 5 μm	0.33	±	1.07	0.26	±	0.24	0.34	±	1.13
	Total	0.41	±	0.78	0.39	±	0.21	0.46	±	1.62

Table 7. Composition of the flagellate community by percent abundance for each grazing experiment date at 2 and 5 m depths. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida.

Classification		May 30		June 20		July 11	
		2 m	5 m	2 m	5 m	2 m	5 m
Choanoflagellida		99.1	99.5	99.1	99.4	98.8	99.4
Cryptomonadida		0.2	0.1	0.2	0.1	0.2	0.1
Gymnodiniales		0.1	0.0	0.0	0.0	0.1	0.0
Prymnesiida	< 5 μm	0.0	0.1	0.1	0.0	0.2	0.1
	> 5 μm	0.0	0.0	0.0	0.0	0.0	0.0
	Total	0.1	0.1	0.1	0.0	0.2	0.1
Other HNF	< 5 μm	0.3	0.1	0.3	0.2	0.3	0.1
	> 5 μm	0.3	0.3	0.3	0.3	0.4	0.3
	Total	0.6	0.3	0.5	0.5	0.7	0.4

Table 8. Cell biovolume (μm^3 ± 95% C.I.) of the flagellate community on each grazing experiment date. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida. R = Replicate.

Classification		R	May 30			June 20			July 11		
Choanoflagellida		A	1.5	±	0.2 •	1.5	±	0.2 •	1.8	±	0.2 •
		B	1.6	±	0.3 •	1.4	±	0.2 •	1.5	±	0.2 •
Cryptomonadida		A	224.6	±	74.2 •	271.6	±	107.9 •	276.7	±	130.0 •
		B	379.8	±	105.1 •	218.5	±	109.2 •	279.5	±	84.1 •
Gymnodiniales		A	580.4	±	155.1 •	884.5	±	206.0 •	508.7	±	140.3 •
		B	532.0	±	139.1 •	827.3	±	196.5 •	437.2	±	147.1 •
Prymnesiida	< 5 μm	A	21.0	±	3.9 •	19.6	±	3.2 •	21.2	±	4.4 •
		B	24.1	±	4.2 •	24.4	±	6.7 •	24.9	±	4.0 •
Prymnesiida	> 5 μm	A	35.5	±	5.2 *	35.5	±	5.2 *	35.5	±	5.2 *
		B									
Other HNF	< 5 μm	A	18.8	±	3.7 •	15.3	±	4.8 •	19.9	±	4.1 •
		B	18.6	±	4.0 •	20.5	±	6.7 •	19.9	±	4.7 •
Other HNF	> 5 μm	A	100.7	±	37.6 •	49.9	±	17.1 •	81.2	±	31.8 •
		B	124.6	±	53.7 •	61.6	±	22.5 •	75.9	±	30.6 •

*Biovolume determined by averaging biovolume values from the 3 grazing experiment dates
•Biovolume values determined by averaging values from individual replicates on respective grazing dates

Table 9. Biomass (μg C·L^{-1} ± 95% C.I.) of the flagellate community at 2 m on each grazing experiment date. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida.

Classification		May 30			June 20			July 11		
Choanoflagellida		32.69	±	35.21	19.27	±	44.56	28.04	±	16.92
Cryptomonadida		12.34	±	45.82	7.84	±	20.52	10.20	±	37.62
Gymnodiniales		6.80	±	29.14	5.43	±	28.85	8.49	±	17.69
Prymnesiida	< 5 μm	0.21	±	0.63	0.16	±	0.18	0.75	±	2.43
	> 5 μm	0.08	±	0.35	0.02	±	0.23	0.03	±	0.39
	Total	0.30	±	0.98	0.17	±	0.05	0.78	±	2.04
Other HNF	< 5 μm	1.03	±	0.98	0.64	±	2.67	0.91	±	2.74
	> 5 μm	6.70	±	16.26	1.94	±	3.69	5.68	±	24.99
	Total	7.73	±	17.25	2.58	±	1.02	6.59	±	22.25

Table 10. Biomass (μg C·L^{-1} ± 95% C.I.) of the flagellate community at 5 m on each grazing experiment date. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida.

Classification		May 30			June 20			July 11		
Choanoflagellida		37.65	±	22.22	21.55	±	15.37	33.67	±	76.43
Cryptomonadida		6.73	±	51.82	1.89	±	2.83	3.47	±	18.40
Gymnodiniales		2.94	±	10.66	1.87	±	6.86	3.72	±	20.40
Prymnesiida	< 5 μm	0.31	±	1.29	0.03	±	0.08	0.28	±	0.45
	> 5 μm	0.24	±	1.43	0.05	±	0.28	0.14	±	0.64
	Total	0.55	±	2.72	0.08	±	0.20	0.41	±	1.08
Other HNF	< 5 μm	0.29	±	1.03	0.44	±	2.34	0.48	±	1.85
	> 5 μm	7.20	±	32.34	2.74	±	1.11	4.98	±	14.68
	Total	7.49	±	31.30	3.19	±	3.45	5.46	±	16.54

Table 11. Composition of the flagellate community by percent biomass for each grazing experiment date at 2 and 5 m depths. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida.

Classification		May 30		June 20		July 11	
		2 m	5 m	2 m	5 m	2 m	5 m
Choanoflagellida		54.6	68.0	54.6	75.4	51.8	72.1
Cryptomonadida		20.6	12.1	22.2	6.6	18.9	7.4
Gymnodiniales		11.4	5.3	15.4	6.6	15.7	8.0
Prymnesiida	< 5 μm	0.4	0.6	0.4	0.1	1.4	0.6
	> 5 μm	0.1	0.4	0.1	0.2	0.1	0.3
	Total	0.5	1.0	0.5	0.3	1.4	0.9
Other HNF	< 5 μm	1.7	0.5	1.8	1.6	1.7	1.0
	> 5 μm	11.2	13.0	5.5	9.6	10.5	10.7
	Total	12.9	13.5	7.3	11.2	12.2	11.7

Table 12. Ciliate abundance (cells·mL^{-1} ± C.I.) at 2 m on each grazing experiment date.

Class	Genus	May 30	June 20	July 11
Heterotrichea	*Stentor A*	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.56
	Stentor B	0.09 ± 0.00	0.44 ± 3.35	0.26 ± 2.24
Litostomatea	*Askenasia*	0.00 ± 0.00	0.09 ± 0.00	0.04 ± 0.56
	Didinium	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.56
	Dileptus	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 1.12
	Lagenophrya A	1.01 ± 3.91	0.48 ± 0.56	0.88 ± 4.47
	Lagenophrya B	0.22 ± 0.56	0.66 ± 3.91	1.19 ± 3.91
	Lagenophrya C	0.09 ± 1.12	0.00 ± 0.00	0.04 ± 0.56
	Mesodinium A	0.31 ± 2.80	3.21 ± 8.39	1.72 ± 6.15
	Mesodinium B	0.09 ± 0.00	0.62 ± 5.59	0.13 ± 0.56
	Monodinium	0.62 ± 1.12	0.40 ± 1.68	0.79 ± 2.80
	Unknown	0.53 ± 0.00	1.06 ± 2.24	1.72 ± 1.12
Oligohymenophorea	*Pleuronema*	0.31 ± 0.56	0.44 ± 2.24	0.40 ± 1.68
	Scuticociliate A	2.16 ± 2.80	2.42 ± 7.27	2.42 ± 5.03
	Scuticociliate B	2.16 ± 3.91	1.58 ± 1.12	3.48 ± 0.56
	Scuticociliate C	1.89 ± 3.91	0.09 ± 0.00	0.40 ± 2.80
	Vorticellidae A	2.33 ± 8.39	0.84 ± 0.56	0.92 ± 1.68
	Vorticellidae B	2.51 ± 9.50	0.70 ± 4.47	1.72 ± 0.56
	Vorticellidae C	0.44 ± 5.59	0.00 ± 0.00	0.48 ± 1.68
	Vorticellidae D	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Vorticellidae E	0.09 ± 0.00	0.04 ± 0.56	0.00 ± 0.00
Phyllopharyngea	*Dysteria*	3.48 ± 16.21	0.62 ± 1.12	5.37 ± 4.47
	Periacineta	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Phascolodon	0.22 ± 2.80	0.75 ± 3.91	0.62 ± 2.24
	Sphaerophrya	0.09 ± 0.00	0.09 ± 0.00	0.04 ± 0.56
	Suctorian	0.00 ± 0.00	0.04 ± 0.56	0.00 ± 0.00
Prostomatea	*Coleps*	0.70 ± 2.24	1.19 ± 0.56	1.28 ± 0.00
	Unknown	0.26 ± 0.00	0.70 ± 3.35	0.44 ± 3.91
	Urotricha	1.63 ± 9.50	1.28 ± 1.68	1.14 ± 1.12
Spirotrichea	*Halteria A*	2.55 ± 14.54	0.88 ± 6.71	1.89 ± 7.27
	Halteria B	7.83 ± 16.77	3.30 ± 5.03	7.79 ± 15.10
	Halteria C	0.88 ± 2.24	0.57 ± 0.56	1.85 ± 2.24
	Halteria D	0.04 ± 0.56	0.00 ± 0.00	0.00 ± 0.00
	Strobilidium A	7.96 ± 1.68	11.48 ± 3.91	18.66 ± 12.30
	Strobilidium B	0.57 ± 0.56	2.82 ± 7.83	1.89 ± 2.80
	Strobilidium C	0.53 ± 0.00	1.41 ± 2.24	2.11 ± 6.71
	Strombidium A	2.20 ± 20.13	1.72 ± 7.27	3.21 ± 13.98
	Strombidium B	0.48 ± 1.68	0.92 ± 6.15	0.53 ± 2.24
	Strombidium C	0.57 ± 5.03	0.35 ± 2.24	0.13 ± 0.56
	Tinntinidium A	1.19 ± 6.15	0.92 ± 1.68	2.60 ± 0.56
	Tinntinidium B	0.31 ± 1.68	0.66 ± 1.68	1.23 ± 0.00
	Tinntinidium C	0.00 ± 0.00	0.09 ± 1.12	0.00 ± 0.00
Unknown	Unknown A	2.73 ± 10.06	3.61 ± 11.18	3.61 ± 10.06
	Unknown B	2.77 ± 2.80	5.32 ± 2.80	3.74 ± 7.27
	Unknown C	0.09 ± 1.12	0.22 ± 0.56	0.18 ± 2.24

Table 13. Ciliate abundance (cells·mL^{-1} ± C.I.) at 5 m on each grazing experiment date.

Class	Genus	May 30	June 20	July 11
Heterotrichea	*Stentor A*	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.37
	Stentor B	0.07 ± 0.25	0.04 ± 0.56	0.18 ± 0.00
Litostomatea	*Askenasia*	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 1.07
	Didinium	0.00 ± 0.00	0.01 ± 0.19	0.01 ± 0.19
	Dileptus	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.00
	Lagenophrya A	1.40 ± 7.10	0.25 ± 1.06	0.75 ± 3.19
	Lagenophrya B	0.31 ± 0.35	0.34 ± 0.00	0.84 ± 2.13
	Lagenophrya C	0.03 ± 0.37	0.01 ± 0.19	0.03 ± 0.00
	Mesodinium A	1.20 ± 8.16	4.86 ± 14.91	2.35 ± 12.78
	Mesodinium B	0.00 ± 0.00	1.09 ± 1.06	0.34 ± 0.00
	Monodinium	0.45 ± 1.42	0.25 ± 1.06	1.17 ± 6.39
	Unknown	1.23 ± 9.23	0.59 ± 1.07	1.26 ± 3.19
Oligohymenophorea	*Pleuronema*	0.31 ± 0.35	0.42 ± 1.06	0.67 ± 2.13
	Scuticociliate A	1.87 ± 4.61	2.68 ± 4.26	1.76 ± 1.07
	Scuticociliate B	3.86 ± 4.26	0.92 ± 3.20	2.93 ± 5.32
	Scuticociliate C	2.07 ± 19.88	0.00 ± 0.00	0.08 ± 1.07
	Vorticellidae A	0.81 ± 3.90	0.50 ± 4.26	0.84 ± 8.52
	Vorticellidae B	1.40 ± 7.10	1.09 ± 1.06	1.51 ± 0.00
	Vorticellidae C	0.06 ± 0.43	0.03 ± 0.37	0.04 ± 0.19
	Vorticellidae D	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.19
	Vorticellidae E	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Phyllopharyngea	*Dysteria*	2.26 ± 13.84	0.34 ± 2.13	3.18 ± 2.13
	Periacineta	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.19
	Phascolodon	0.50 ± 4.26	0.67 ± 2.13	0.17 ± 2.13
	Sphaerophrya	0.08 ± 1.07	0.00 ± 0.00	0.00 ± 0.00
	Suctorian	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Prostomatea	*Coleps*	1.31 ± 2.48	0.84 ± 0.00	1.93 ± 7.45
	Unknown	0.00 ± 0.00	0.75 ± 1.06	0.59 ± 1.07
	Urotricha	0.45 ± 1.42	1.01 ± 2.13	0.42 ± 1.06
Spirotrichea	*Halteria A*	2.43 ± 11.71	0.84 ± 6.39	2.10 ± 5.32
	Halteria B	5.42 ± 19.88	2.93 ± 7.45	3.27 ± 13.84
	Halteria C	0.70 ± 1.77	0.84 ± 4.26	1.09 ± 3.19
	Halteria D	0.00 ± 0.00	0.01 ± 0.19	0.00 ± 0.00
	Strobilidium A	8.30 ± 33.01	8.05 ± 29.82	7.46 ± 15.97
	Strobilidium B	1.68 ± 0.00	1.93 ± 13.84	1.84 ± 4.26
	Strobilidium C	0.89 ± 2.84	2.26 ± 5.32	1.59 ± 3.19
	Strombidium A	1.19 ± 2.05	0.26 ± 0.37	0.62 ± 0.75
	Strombidium B	0.62 ± 3.35	0.59 ± 1.49	0.21 ± 0.00
	Strombidium C	0.26 ± 1.49	0.07 ± 0.56	0.09 ± 0.37
	Tinntinidium A	1.20 ± 2.17	0.63 ± 0.19	1.33 ± 1.68
	Tinntinidium B	0.65 ± 2.98	0.34 ± 0.19	0.67 ± 0.00
	Tinntinidium C	0.00 ± 0.00	0.01 ± 0.19	0.04 ± 0.56
Unknown	Unknown A	4.11 ± 1.07	4.69 ± 6.39	3.27 ± 3.19
	Unknown B	1.79 ± 5.68	4.44 ± 7.45	3.52 ± 8.52
	Unknown C	0.34 ± 2.48	0.41 ± 1.12	0.16 ± 0.19

Table 14. Ciliate community composition by percent abundance on each grazing experiment date.

Class	Range		Genus	May 30		June 20		July 11	
	2 m	5 m		2 m	5 m	2 m	5 m	2 m	5 m
Heterotrichea	0.2 - 0.8	0.1 - 0.6	*Stentor A*	0.0	0.0	0.0	0.0	0.2	0.2
			Stentor B	0.2	0.1	0.8	0.1	0.4	0.4
Litostomatea	6 - 13	9 - 17	*Askenasia*	0.0	0.0	0.2	0.0	0.1	0.2
			Didinium	0.0	0.0	0.0	0.0	0.1	0.0
			Dileptus	0.0	0.0	0.0	0.0	0.1	0.1
			Lagenophrya A	1.9	2.8	0.9	0.6	1.2	1.6
			Lagenophrya B	0.4	0.6	1.3	0.7	1.6	1.7
			Lagenophrya C	0.2	0.1	0.0	0.0	0.1	0.1
			Mesodinium A	0.6	2.4	6.2	10.8	2.3	4.8
			Mesodinium B	0.2	0.0	1.2	2.4	0.2	0.7
			Monodinium	1.2	0.9	0.8	0.6	2.3	2.4
			Unknown	1.0	2.5	2.0	1.3	1.1	2.6
Oligohymenophorea	12 - 23	13– 21	*Pleuronema*	0.6	0.6	0.8	0.9	0.5	1.4
			Scuticociliate A	4.2	3.8	4.7	6.0	4.6	3.6
			Scuticociliate B	4.2	7.8	3.0	2.0	0.5	6.0
			Scuticociliate C	3.6	4.2	0.2	0.0	3.2	0.2
			Vorticellidae A	4.5	1.6	1.6	1.1	1.2	1.7
			Vorticellidae B	4.8	2.8	1.4	2.4	2.3	3.1
			Vorticellidae C	0.8	0.1	0.0	0.1	0.6	0.1
			Vorticellidae D	0.0	0.0	0.0	0.0	0.0	0.0
			Vorticellidae E	0.2	0.0	0.1	0.0	0.0	0.0
Phyllopharyngea	3 - 8	2 - 7	*Dysteria*	6.7	4.6	1.2	0.7	7.1	6.6
			Periacineta	0.0	0.0	0.0	0.0	0.0	0.0
			Phascolodon	0.4	1.0	1.4	1.5	0.8	0.3
			Sphaerophrya	0.2	0.2	0.2	0.0	0.1	0.0
			Suctorian	0.0	0.0	0.1	0.0	0.0	0.0
Prostomatea	4 - 6	4 - 6	*Coleps*	1.4	2.7	2.3	1.9	0.6	4.0
			Unknown	0.5	0.0	1.4	1.7	1.7	1.2
			Urotricha	3.1	0.9	2.5	2.2	1.5	0.9
Spirotrichea	48 - 56	42 - 47	*Halteria A*	4.9	4.9	1.7	1.9	2.5	4.3
			Halteria B	15.1	11.0	6.3	6.5	10.4	6.7
			Halteria C	1.7	1.4	1.1	1.9	2.5	2.2
			Halteria D	0.1	0.0	0.0	0.0	0.0	0.0
			Strobilidium A	15.3	16.9	22.1	17.9	24.8	15.3
			Strobilidium B	1.1	3.4	5.4	4.3	2.5	3.8
			Strobilidium C	1.0	1.8	2.7	5.0	2.8	3.3
			Strombidium A	4.2	2.4	3.3	0.6	4.3	1.3
			Strombidium B	0.9	1.3	1.8	1.3	0.7	0.4
			Strombidium C	1.1	0.5	0.7	0.2	0.2	0.2
			Tinntinidium A	2.3	2.4	1.8	1.4	3.5	2.7
			Tinntinidium B	0.6	1.3	1.3	0.7	1.6	1.4
			Tinntinidium C	0.0	0.0	0.2	0.0	0.0	0.1
Unknown	10 - 18	13 - 21	Unknown A	5.3	8.3	6.9	10.4	4.8	6.7
			Unknown B	5.3	3.6	10.2	9.9	5.0	7.2
			Unknown C	0.2	0.7	0.4	0.9	0.2	0.3

Table 15. Ciliate biomass (μg C·L^{-1} ± C.I.) at 2 m on each grazing experiment date.

Class	Genus	May 30	June 20	July 11
Heterotrichea	*Stentor A*	0.00 ± 0.00	0.00 ± 0.00	10.99 ± 46.53
	Stentor B	0.81 ± 0.00	3.74 ± 28.53	2.44 ± 20.69
Litostomatea	*Askenasia*	0.00 ± 0.00	0.06 ± 0.00	0.03 ± 0.36
	Didinium	0.00 ± 0.00	0.00 ± 0.00	0.32 ± 4.06
	Dileptus	0.00 ± 0.00	0.00 ± 0.00	1.77 ± 22.50
	Lagenophrya A	0.22 ± 0.85	0.09 ± 0.11	0.15 ± 0.75
	Lagenophrya B	0.13 ± 0.32	0.31 ± 1.83	0.79 ± 2.61
	Lagenophrya C	0.54 ± 6.80	0.00 ± 0.00	0.27 ± 3.40
	Mesodinium A	0.02 ± 0.17	0.20 ± 0.34	0.10 ± 0.41
	Mesodinium B	0.03 ± 0.00	0.24 ± 2.19	0.05 ± 0.22
	Monodinium	0.13 ± 0.23	0.08 ± 0.34	0.15 ± 0.21
	Unknown	0.05 ± 0.00	0.11 ± 0.22	0.16 ± 0.33
Oligohymenophorea	*Pleuronema*	0.14 ± 0.25	0.22 ± 1.13	0.18 ± 0.76
	Scuticociliate A	0.54 ± 0.24	0.60 ± 1.69	0.54 ± 1.04
	Scuticociliate B	0.15 ± 0.15	0.09 ± 0.05	0.21 ± 0.36
	Scuticociliate C	0.19 ± 0.47	0.01 ± 0.00	0.04 ± 0.06
	Vorticellidae A	0.96 ± 2.54	0.28 ± 0.19	0.35 ± 0.63
	Vorticellidae B	3.45 ± 23.05	0.78 ± 4.96	2.50 ± 6.20
	Vorticellidae C	3.62 ± 45.96	0.00 ± 0.00	4.59 ± 15.90
	Vorticellidae D	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Vorticellidae E	0.02 ± 0.00	0.01 ± 0.12	0.00 ± 0.00
Phyllopharyngea	*Dysteria*	0.90 ± 4.37	0.18 ± 0.32	1.07 ± 0.68
	Periacineta	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Phascolodon	0.23 ± 2.87	0.91 ± 4.74	0.59 ± 2.13
	Sphaerophrya	0.12 ± 0.00	0.12 ± 0.00	0.06 ± 0.76
	Suctorian	0.00 ± 0.00	0.09 ± 1.20	0.00 ± 0.00
Prostomatea	*Coleps*	0.57 ± 1.82	0.83 ± 1.15	0.99 ± 2.70
	Unknown	0.01 ± 0.00	0.02 ± 0.11	0.02 ± 0.00
	Urotricha	0.11 ± 0.52	0.12 ± 0.26	0.09 ± 0.05
Spirotrichea	*Halteria A*	0.43 ± 3.01	0.12 ± 0.93	0.25 ± 1.00
	Halteria B	2.87 ± 0.23	1.15 ± 4.08	2.45 ± 5.02
	Halteria C	0.78 ± 1.99	0.57 ± 0.55	1.33 ± 2.97
	Halteria D	1.35 ± 17.15	0.00 ± 0.00	0.00 ± 0.00
	Strobilidium A	1.16 ± 0.39	1.73 ± 1.41	2.27 ± 3.14
	Strobilidium B	0.08 ± 0.07	0.35 ± 0.52	0.22 ± 0.39
	Strobilidium C	1.39 ± 0.00	1.90 ± 8.09	2.95 ± 4.11
	Strombidium A	4.62 ± 42.27	4.25 ± 14.50	6.25 ± 32.48
	Strombidium B	3.18 ± 11.01	5.02 ± 33.40	2.86 ± 12.10
	Strombidium C	5.02 ± 44.13	3.14 ± 19.94	1.18 ± 4.99
	Tinntinidium A	0.89 ± 4.61	0.78 ± 1.42	2.29 ± 1.94
	Tinntinidium B	0.20 ± 1.07	0.43 ± 1.09	0.78 ± 0.66
	Tinntinidium C	0.00 ± 0.00	0.19 ± 2.40	0.00 ± 0.00
Unknown	Unknown A	1.40 ± 6.29	1.56 ± 1.11	2.08 ± 7.05
	Unknown B	0.16 ± 0.10	0.34 ± 0.06	0.25 ± 0.66
	Unknown C	0.90 ± 11.45	2.25 ± 5.72	1.80 ± 22.89

Table 16. Ciliate biomass (μg C·L^{-1} ± C.I.) at 5 m on each grazing experiment date.

Class	Genus	May 30	June 20	July 11
Heterotrichea	*Stentor A*	0.00 ± 0.00	0.00 ± 0.00	9.77 ± 31.02
	Stentor B	0.63 ± 2.30	0.37 ± 4.75	1.63 ± 0.00
Litostomatea	*Askenasia*	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.69
	Didinium	0.00 ± 0.00	0.11 ± 1.35	0.11 ± 1.35
	Dileptus	0.00 ± 0.00	0.00 ± 0.00	1.18 ± 0.00
	Lagenophrya A	0.30 ± 1.53	0.05 ± 0.20	0.13 ± 0.53
	Lagenophrya B	0.18 ± 0.21	0.16 ± 0.00	0.56 ± 1.42
	Lagenophrya C	0.18 ± 2.27	0.09 ± 1.13	0.18 ± 0.00
	Mesodinium A	0.07 ± 0.50	0.30 ± 0.65	0.14 ± 0.80
	Mesodinium B	0.00 ± 0.00	0.43 ± 0.42	0.13 ± 0.00
	Monodinium	0.09 ± 0.29	0.05 ± 0.22	0.22 ± 1.22
	Unknown	0.12 ± 0.90	0.06 ± 0.11	0.12 ± 0.35
Oligohymenophorea	*Pleuronema*	0.14 ± 0.16	0.21 ± 0.54	0.31 ± 0.97
	Scuticociliate A	0.48 ± 1.57	0.66 ± 1.17	0.39 ± 0.54
	Scuticociliate B	0.27 ± 0.52	0.05 ± 0.25	0.18 ± 0.28
	Scuticociliate C	0.21 ± 2.08	0.00 ± 0.00	0.01 ± 0.11
	Vorticellidae A	0.35 ± 2.00	0.17 ± 1.44	0.32 ± 3.21
	Vorticellidae B	1.97 ± 15.14	1.21 ± 1.18	2.21 ± 6.17
	Vorticellidae C	0.52 ± 3.57	0.26 ± 3.31	0.42 ± 1.77
	Vorticellidae D	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Vorticellidae E	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Phyllopharyngea	*Dysteria*	0.59 ± 3.69	0.10 ± 0.60	0.64 ± 0.30
	Periacineta	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Phascolodon	0.52 ± 4.38	0.81 ± 2.58	0.16 ± 2.03
	Sphaerophrya	0.11 ± 1.44	0.00 ± 0.00	0.00 ± 0.00
	Suctorian	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Prostomatea	*Coleps*	1.07 ± 2.02	0.58 ± 0.54	1.49 ± 5.29
	Unknown	0.00 ± 0.00	0.02 ± 0.03	0.02 ± 0.04
	Urotricha	0.03 ± 0.06	0.09 ± 0.11	0.03 ± 0.10
Spirotrichea	*Halteria A*	0.37 ± 1.19	0.12 ± 0.88	0.28 ± 0.68
	Halteria B	1.95 ± 3.28	1.04 ± 4.65	1.03 ± 4.47
	Halteria C	0.62 ± 1.58	0.83 ± 4.22	0.79 ± 3.09
	Halteria D	0.00 ± 0.00	0.45 ± 5.72	0.00 ± 0.00
	Strobilidium A	1.22 ± 5.46	1.22 ± 5.06	0.91 ± 2.60
	Strobilidium B	0.22 ± 0.00	0.26 ± 2.10	0.22 ± 0.45
	Strobilidium C	2.36 ± 7.49	2.96 ± 10.53	2.36 ± 8.86
	Strombidium A	2.49 ± 4.31	0.66 ± 0.34	1.18 ± 2.56
	Strombidium B	4.04 ± 22.01	3.19 ± 8.10	1.11 ± 0.00
	Strombidium C	2.32 ± 13.07	0.65 ± 4.98	0.78 ± 3.32
	Tinntinidium A	0.90 ± 1.63	0.53 ± 0.16	1.18 ± 2.22
	Tinntinidium B	0.41 ± 1.89	0.22 ± 0.12	0.43 ± 0.36
	Tinntinidium C	0.00 ± 0.00	0.03 ± 0.40	0.39 ± 4.98
Unknown	Unknown A	2.07 ± 2.37	2.25 ± 11.19	1.87 ± 3.02
	Unknown B	0.10 ± 0.29	0.28 ± 0.28	0.23 ± 0.39
	Unknown C	3.50 ± 25.44	4.20 ± 11.45	1.65 ± 1.91

Table 17. Ciliate community composition by percent biomass for each grazing experiment date.

Class	Range		Genus	May 30		June 20		July 11	
	2 m	5 m		2 m	5 m	2 m	5 m	2 m	5 m
Heterotrichea	2 – 24	2 - 33	*Stentor A*	0.0	0.0	0.0	0.0	19.8	28.1
			Stentor B	2.2	2.1	11.4	1.5	4.4	4.7
Litostomatea	3 - 7	3 - 8	*Askenasia*	0.0	0.0	0.2	0.0	0.1	0.2
			Didinium	0.0	0.0	0.0	0.4	0.6	0.3
			Dileptus	0.0	0.0	0.0	0.0	3.2	3.4
			Lagenophrya A	0.6	1.0	0.3	0.2	0.3	0.4
			Lagenophrya B	0.3	0.6	0.9	0.6	1.4	1.6
			Lagenophrya C	1.4	0.6	0.0	0.4	0.5	0.5
			Mesodinium A	0.1	0.2	0.6	1.2	0.2	0.4
			Mesodinium B	0.1	0.0	0.7	1.7	0.1	0.4
			Monodinium	0.3	0.3	0.2	0.2	0.3	0.6
			Unknown	0.1	0.4	0.3	0.2	0.3	0.3
Oligohymenophorea	6 - 24	10 - 13	*Pleuronema*	0.4	0.5	0.7	0.9	0.3	0.9
			Scuticociliate A	1.5	1.6	1.8	2.7	1.0	1.1
			Scuticociliate B	0.4	0.9	0.3	0.2	0.4	0.5
			Scuticociliate C	0.5	0.7	0.0	0.0	0.1	0.0
			Vorticellidae A	2.6	1.2	0.9	0.7	0.6	0.9
			Vorticellidae B	9.2	6.5	2.4	4.9	4.5	6.4
			Vorticellidae C	9.7	1.7	0.0	1.1	8.3	1.2
			Vorticellidae D	0.0	0.0	0.0	0.0	0.0	0.0
			Vorticellidae E	0.0	0.0	0.0	0.0	0.0	0.0
Phyllopharyngea	3 - 4	2 – 4	*Dysteria*	2.4	1.9	0.5	0.4	1.9	1.8
			Periacineta	0.0	0.0	0.0	0.0	0.0	0.0
			Phascolodon	0.6	1.7	2.8	3.3	1.1	0.5
			Sphaerophrya	0.3	0.4	0.4	0.0	0.1	0.0
			Suctorian	0.0	0.0	0.3	0.0	0.0	0.0
Prostomatea	2 - 3	3 - 5	*Coleps*	1.5	3.5	2.5	2.4	1.8	4.3
			Unknown	0.0	0.0	0.1	0.1	0.0	0.1
			Urotricha	0.3	0.1	0.4	0.4	0.2	0.1
Spirotrichea	41 - 60	31 - 56	*Halteria A*	1.2	1.2	0.4	0.5	0.5	0.8
			Halteria B	7.7	6.4	3.5	4.2	4.4	3.0
			Halteria C	2.1	2.0	1.7	3.4	2.4	2.3
			Halteria D	3.6	0.0	0.0	1.8	0.0	0.0
			Strobilidium A	3.1	4.0	5.3	5.0	4.1	2.6
			Strobilidium B	0.2	0.7	1.1	1.1	0.4	0.6
			Strobilidium C	3.7	7.8	5.8	12.0	5.3	6.8
			Strombidium A	12.4	8.2	12.9	2.7	11.3	3.4
			Strombidium B	8.5	13.3	15.3	12.9	5.2	3.2
			Strombidium C	13.4	7.6	9.6	2.6	2.1	2.3
			Tinntinidium A	2.4	3.0	2.4	2.2	4.1	3.4
			Tinntinidium B	0.5	1.3	1.3	0.9	1.4	1.2
			Tinntinidium C	0.0	0.0	0.6	0.1	0.0	1.1
Unknown	7- 13	11 - 27	Unknown A	3.8	6.8	4.7	9.1	3.7	5.4
			Unknown B	0.4	0.3	1.0	1.1	0.4	0.7
			Unknown C	2.4	11.5	6.9	17.0	3.3	4.7

Table 18. Putative methods of energy acquisition and major sources of food for the flagellate community. Other HNF = Includes all heterotrophic nanoflagellates excluding Choanoflagellida; N.A. = not applicable.

Classification	Group	Energy Acquisition	Major Food Sources
Choanoflagellida	Choanoflagellates	Heterotroph	Bacteria
Cryptomonadida	Rhodomonas/Cryptomonas	Autotroph	N.A.
Gymnodiniales	Gymnodinium	Mixotroph	Algae, Protozoa
Prymnesiida	< 5 and > 5 μm Prymnesiida	Mixotroph	Bacteria
Other HNF	< 5 and > 5 μm Heterotrophs	Heterotroph	Bacteria

Table 19. Putative methods of energy acquisition and sources of food for the ciliate community.

Class	Genus	Energy Acquisition	Major Food Sources
Heterotrichea	*Stentor A*	Heterotroph	Algae, Bacteria, Protozoa
	Stentor B	Heterotroph	Algae, Bacteria, Protozoa
Litostomatea	*Askenasia*	Heterotroph	Algae, Protozoa
	Didinium	Heterotroph	Protozoa
	Dileptus	Mixotroph	Protozoa
	Lagenophrya A	Heterotroph	Algae, Protozoa
	Lagenophrya B	Heterotroph	Algae, Protozoa
	Lagenophrya C	Heterotroph	Algae, Protozoa
	Mesodinium A	Heterotroph	Protozoa
	Mesodinium B	Heterotroph	Protozoa
	Monodinium	Heterotroph	Algae, Protozoa
	Unknown	Heterotroph	Protozoa
Oligohymenophorea	*Pleuronema*	Heterotroph	Bacteria
	Scuticociliate A	Heterotroph	Bacteria
	Scuticociliate B	Heterotroph	Bacteria
	Scuticociliate C	Heterotroph	Bacteria
	Vorticellidae A	Heterotroph	Bacteria
	Vorticellidae B	Heterotroph	Bacteria
	Vorticellidae C	Heterotroph	Bacteria
	Vorticellidae D	Heterotroph	Bacteria
	Vorticellidae E	Heterotroph	Bacteria
Phyllopharyngea	*Dysteria*	Heterotroph	Bacteria
	Periacineta	Heterotroph	Protozoa
	Phascolodon	Heterotroph	Algae, Bacteria
	Sphaerophrya	Heterotroph	Protozoa
	Suctorian	Heterotroph	Protozoa
Prostomatea	*Coleps*	Mixotroph	Algae, Bacteria, Protozoa
	Unknown	Heterotroph	Protozoa
	Urotricha	Heterotroph	Algae, Bacteria, Protozoa
Spirotrichea	*Halteria A*	Heterotroph	Algae, Bacteria, Protozoa
	Halteria B	Heterotroph	Algae, Bacteria, Protozoa
	Halteria C	Heterotroph	Algae, Bacteria, Protozoa
	Halteria D	Heterotroph	Algae, Bacteria, Protozoa
	Strobilidium A	Heterotroph	Algae, Bacteria
	Strobilidium B	Heterotroph	Algae, Bacteria
	Strobilidium C	Heterotroph	Algae
	Strombidium A	Mixotroph	Algae, Bacteria, Protozoa
	Strombidium B	Mixotroph	Algae, Bacteria, Protozoa
	Strombidium C	Mixotroph	Algae, Bacteria, Protozoa
	Tinntinidium A	Heterotroph	Algae, Bacteria, Protozoa
	Tinntinidium B	Heterotroph	Algae, Bacteria, Protozoa
	Tinntinidium C	Heterotroph	Algae, Bacteria, Protozoa
Unknown	Unknown A, B, C		

Table 20. Putative methods of energy acquisition for the protozoan community by percent abundance and biomass at 2 m depth (refer to Tables 18 and 19).

	Percent Abundance			Percent Biomass		
	May 30	**June 20**	**July 11**	**May 30**	**June 20**	**July 11**
Flagellates						
Heterotrophic	99.7	99.7	99.5	67.5	61.9	64.0
Mixotrophic	0.1	0.1	0.3	11.9	15.9	17.1
Autotrophic	0.2	0.2	0.2	20.6	22.2	18.9
Ciliates						
Heterotrophic	91.5	90.2	92.3	61.6	53. 9	74.6
Mixotrophic	8.5	9.8	7.7	38.4	46.1	25.4
Autotrophic	0.0	0.0	0.0	0.0	0.0	0.0
Total Protozoa						
Heterotrophic	99.7	99.7	99.5	65.4	58.3	69.1
Mixotrophic	0.1	0.1	0.3	21.6	29.4	21.2
Autotrophic	0.2	0.2	0.2	13.0	12.3	9.7

Table 21. Putative methods of energy acquisition for the protozoan community by percent abundance and biomass at 5 m depth (refer to Tables 18 and 19).

	Percent Abundance			Percent Biomass		
	May 30	**June 20**	**July 11**	**May 30**	**June 20**	**July 11**
Flagellates						
Heterotrophic	99.8	99.9	99.8	81.5	86.5	83.7
Mixotrophic	0.1	0.0	0.1	6.3	6.8	8.8
Autotrophic	0.1	0.1	0.1	12.1	6.6	7.4
Ciliates						
Heterotrophic	92.1	95.0	93.0	59.9	71.7	81.5
Mixotrophic	7.9	5.0	7.0	40.1	28.3	18.5
Autotrophic	0.0	0.0	0.0	0.0	0.0	0.0
Total Protozoa						
Heterotrophic	99.8	99.9	99.8	74.9	80.8	82.8
Mixotrophic	0.1	0.0	0.1	16.8	15.1	12.7
Autotrophic	0.1	0.1	0.1	8.4	4.1	4.5

Table 22. Putative major food sources for the heterotrophic and mixotrophic protozoan community by percent abundance and biomass at 2 m depth. Allocation by abundance/biomass was equally divided between the food sources when more than one major food source existed for a particular group or genus (refer to Tables 18 and 19). Percent allocated to food sources for mixotrophic protozoa does not take into account autotrophic capabilities.

	Percent Abundance			Percent Biomass		
	May 30	**June 20**	**July 11**	**May 30**	**June 20**	**July 11**
Flagellates						
Algae	0.0	0.0	0.1	7.2	9.9	9.7
Bacteria	99.9	100.0	99.9	85.7	80.2	80.7
Protozoa	0.0	0.0	0.1	7.2	9.9	9.7
Ciliates						
Algae	26.0	32.3	31.8	27.4	36.4	30.8
Bacteria	55. 9	42.8	49.0	50.6	36.4	42.2
Protozoa	18.1	24.8	19.2	22.0	27.3	26.9
Total Protozoa						
Algae	0.0	0.0	0.1	15.7	23.4	21.1
Bacteria	99.9	99.9	99.9	70.8	57.8	60.0
Protozoa	0.0	0.00	0.1	13.4	18.8	19.0

Table 23. Putative major food sources for the protozoan community by percent abundance and biomass at 5 m depth. Allocation by abundance/biomass was equally divided between the food sources when more than one major food source existed for a particular group or genus (refer to Tables 18 and 19). Percent allocated to food sources for mixotrophic protozoa does not take into account autotrophic capabilities.

	Percent Abundance			Percent Biomass		
	May 30	**June 20**	**July 11**	**May 30**	**June 20**	**July 11**
Flagellates						
Algae	0.0	0.0	0.0	3.0	3.5	4.3
Bacteria	100.0	100.0	100.0	93.9	93.0	91.4
Protozoa	0.0	0.0	0.0	3.0	3.5	4.3
Ciliates						
Algae	27.9	30.5	28.3	35.0	40.1	33.1
Bacteria	52.7	39.8	47.5	42.3	37.5	38.0
Protozoa	19.5	29.7	24.2	22.7	22.3	28.9
Total Protozoa						
Algae	0.0	0.0	0.0	13.8	18.2	16.3
Bacteria	100.0	100.0	99.9	76.5	70.7	69.1
Protozoa	0.0	0.0	0.0	9.7	11.1	14.6

Table 24. Rate of picoplankton population change (d^{-1}) in Napoleon Gulf on May 30, June 20, and July 11, 2002 determined in the size fraction (1-μm filtrates) and predator dilution experiment. N.D. = not determined, see text.

Date	Size Fraction Rate of Population Change	Predator Dilution Rate of Population Change
May 30	N.D.	N.D.
June 20	0.175	0.281
July 11	0.186	N.D.

Table 25. Picoplankton production in Napoleon Gulf during the three grazing experiment dates. Volumetric production was determined using biomass and growth rate from the size fraction experiment (1-μm filtrates) and predator dilution experiment from 2 m depth. Areal production was estimated by assuming growth rate is the same at all depths. N.A. = not applicable, see text.

Date	Volumetric (μg C L^{-1} d^{-1})			Areal (g C m^{-2} d^{-1})		
	Size Fraction	Predator Dilution	Average Production	Size Fraction	Predator Dilution	Average Production
May 30	N.A.	N.A.	-	N.A.	N.A.	-
June 20	110.0	180.0	150.0	1.3	2.1	1.7
July 11	90.0	N.A.	-	1.4	N.A.	-

Table 26. Grazing rates (d^{-1}) on the picoplankton from grazers in different size fractions for June and July, 2002. N.A. = not applicable.

Date	1 – 5 μm	5 – 40 μm	> 40 μm
May 30	N.A.	N.A.	N.A.
June 20	0.054	0.142	0.188
July 11	0.191	0.011	0.020

Table 27. Rates of population change (d^{-1}) and predation rate (d^{-1}) on the flagellate community on July 11, 2002. Other HNF includes all heterotrophic nanoflagellates excluding Choanoflagellida. Predatory indicates predation on protozoa.

		Rate of Population Change (d^{-1})		Predation Rate (d^{-1})
Classification	**Putative Feeding Guilds**	**Whole Lake Water**	**< 40-μm Lake Water**	
< 5 μm Other HNF		0.494	0.316	-0.178
< 5 μm Prymensiida		0.564	0.008	-0.557
	< 5 μm Bacterivores	0.515	0.214	-0.301
> 5 μm Other HNF		0.619	0.382	-0.237
> 5 μm Prymensiida		0.794	0.403	-0.392
	> 5 μm Bacterivores	0.638	0.385	-0.253
Cryptomonadida	Photosynthesis	-0.600	-0.550	0.049
Gymnodiniales	Algivore/Predatory	-0.436	-0.359	0.077
Total		0.395	0.196	-0.198

Table 28. Rates of population change (d^{-1}) of the ciliate community by class in whole lake water and 40-μm lake water filtrate and predation rate (d^{-1}) on the ciliate community from > 40 μm predators on July 11, 2002.

	Rate of Population Change (d^{-1})		Predation Rate (d^{-1})
Class	**Whole Lake Water**	**< 40-μm Lake Water**	
Heterotrichea	-1.196	-0.602	0.594
Litostomatea	0.085	-0.066	-0.150
Oligohymenophorea	0.029	0.411	0.383
Phyllopharyngea	1.242	1.075	-0.167
Prostomatea	-0.146	0.215	0.361
Spirotrichea	-1.103	-0.836	0.267
Unknown	0.128	0.562	0.434
Total	0.061	0.207	0.146

Table 29. Rates of population change (d^{-1}) of the ciliate community by putative feeding guilds in whole lake water and 40 μm lake water filtrate and predation rate (d^{-1}) on the ciliate community from > 40 μm predators on July 11, 2002. Predatory indicates predation on protozoa. N.D. = not determined.

	Rate of Population Change (d^{-1})		**Predation Rate (d^{-1})**
Putative Feeding Guilds	**Whole Lake Water**	**< 40-μm Lake Water**	
Algivore	-1.092	N.D.	N.D.
Algivore/Bacterivore	-1.014	-0.473	0.541
Algivore/Bacterivore/Predatory	-0.903	-0.777	0.125
Algivore/Predatory	-0.614	-0.771	-0.156
Bacterivore	0.635	0.811	0.176
Predatory	0.300	0.260	-0.040
Unknowns	0.128	0.562	0.434
Total	0.061	0.207	0.146

Table 30. Chlorophyll *a*, picoplankton abundance and picoplankton biomass in African Great Lakes. St. z = station depth (m); Sample z = sample depth (m), I = integrated sample; Chl *a* = chlorophyll *a* (μg·L^{-1}); B.A. = bacterial abundance (cells x 10^6·mL^{-1}); B.B. = bacterial biomass (mg·C·L^{-1}); Date (month-year); C.M. = count method (AODC = acridine orange direct count, DAPI DC = DAPI direct count, DAPI NE= DAPI Northern Eclipse Imaging System); R = reference; NR = not reported; *Only one sample taken; ▫ Samples were taken at 0.5 m; ◊ Whole lake water was filtered through a 1 μm filter prior to preservation of samples.

Lake	St. z	Sample z	Chl *a*	B.A.	B.B.	Date	C.M.	R
Tanganyika	NR	I: 0-25	1.7	0.76▫▫	0.19	10–11-1975	AODC	1
Whole Lake			3.1▫					
Tanganyika South Basin	NR	I: 0-25	0.7▫	0.72	NR	10–11-1975	AODC	1
Tanganyika Central Basin	NR	I: 0-25	4.6▫	0.41	NR	10–11-1975	AODC	1
Tanganyika North Basin	NR	I: 0-25	1.5▫	0.89	NR	10–11-1975	AODC	1
Malawi	150	25-30	0.73	1.46◊	0.05◊	06-1999	DAPI DC	2
Malawi	150	140-155	NR	0.76◊	0.03◊	06-1999	DAPI DC	2
Malawi	150	20	0.87	1.52*	0.02	01- 2000	DAPI DC	2
Malawi	150	40	0.62	0.87*	0.01	01-2000	DAPI DC	2
Malawi	150	140-150	NR	0.21	0.01	01-2000	DAPI DC	2
Malawi	180	40	0.25	1.37◊	0.02◊	01-2000	DAPI DC	2
Malawi	180	160-170	NR	0.92◊	0.01◊	01-2000	DAPI DC	2
Malawi	180	160	NR	0.95*	0.01	01- 2000	DAPI DC	2
Malawi	150	I: 0-30	0.66	2.44	NR	10-2001	DAPI DC	3
Malawi	2	1	0.48	2.76*	0.21	10-2002	DAPI NE	3
Malawi	6.5	3	0.73	2.89	0.13	10–11-2002	DAPI NE	3
Malawi	150	15	0.63	2.97*	0.08	10-2002	DAPI NE	3
Victoria			30.8	8.3	NR			4
Victoria	8	2	47.26	12.35	0.48	11-2002	DAPI NE	3
Victoria	8	2	79.23	8.46*	0.63	12-2002	DAPI NE	3

1. Hecky and Kling 1981

2. Guildford unpublished, Department of Biology, University of Waterloo, ON, Canada

3. North unpublished, Department of Biology, University of Waterloo, ON, Canada

4. Yasindi 2001

¤ Silsbe 2003; Silsbe personal communication, Department of Biology, University of Waterloo, ON, Canada

▫▫ see Hecky et al. 1978

Table 31. Abundance and biomass of heterotrophic nanoflagellates (HNF) and ciliates in African and Laurentian Great Lakes. HNF abundance = average (range) (x 10^3 cells·mL^{-1}); HNF biomass = average (range)(μg C·L^{-1}); ciliate abundance = average (range) (cells·mL^{-1}); ciliate biomass = average (range)(μg C·L^{-1}); R = reference; NR = not reported.

	Heterotrophic Nanoflagellates		Ciliates		
Lake	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**R**
Victoria	98.2 (70.4 – 127.9)	46.7 (28.6 – 59.9)	53.7 (45.0 – 75.2)	35.9 (24.7 – 55.4)	1
Victoria	NR	NR	20.0 (0.5 – 63.0)	35.7 24.2 – 61.82	2
Malawi	NR	NR	1.5 (0.2 – 11.8)	1.3 (0.03 – 7.8)	2
Tanganyika	NR	NR	NR	43.3 (10 – 391)	3
Erie: (Sandusky Bay)	(1.8 – 8.5)*	(10 – 110)‡	(110-113)*	(2 – 27) ‡	4
Erie: (offshore)	(1.5 – 3.5)*	(5 – 25)‡	(1- 22)*	(< 1-5)‡	4
Ontario	NR	NR	12.8	68.6	5
Ontario	2.0¤ 5.5¤				6
Huron	2.28** (0.7 – > 5.0)	(2-13)	NR	45.4** (9.9 – 87.3)**	7
Michigan	2.28** (0.6 – 5.0)	(2- 24)	7 (2-14)	45.4** (9.9 – 87.3)**	7

1. This study
2. Yasindi and Taylor 2003
3. Hecky et al. 1978, Hecky and Kling 1981
4. Hwang and Heath 1997b *taken from Figure 2, ‡taken from Figure 3
5. Taylor and Heynen 1987
6. Pick and Hamilton 1994 ¤different sites
7. Carrick and Fahnenstial 1990 **average for Huron and Michigan

Table 32. Chlorophyll *a*, picoplankton abundance and biovolume in Laurentian Great Lakes. Station z = (m); Sample z = sample depth (m); Chl *a* = chlorophyll *a* ($\mu g \cdot L^{-1}$); B.A. = average bacterial abundance, (range) (cells x $10^6 \cdot mL^{-1}$); B.BV. = average bacterial biovolume (range) (μm^3); R = reference; NR = not reported; ^{M} = median value; ^{W} = weighted mean from SEM and fluorescence microscopy.

Lake	Station z	Sample z	Chl *a*	B.A.	B.BV.	R
Erie:	2	1	102.5	13.1	0.078	1
(Sandusky Bay)				(8.6 – 16.8)	(0.054 – 0.097)	
Erie:	18	4.5	2.467	5.2	0.042	1
(offshore)				(3.8 – 6.3)	(0.030 – 0.063)	
Erie	NR	surface	NR	(1.8 – 4.6)	NR	2
Ontario				(1.0 – 6.4)	NR	3
Superior	NR	20	NR	(1.2 – 4.6)	NR	4
Michigan	100	2 - 5	0.95^M	0.86^M	0.074^W	5

1. Hwang and Heath 1997
2. Wilhelm and Smith 2000
3 Pick and Caron 1987
4 Tapper and Hicks 1998
5. Scavia et al. 1986

Table 33. Chlorophyll *a* and bacterial abundance in African lakes of differing salinity and trophy. Conductivity ($\mu S \cdot cm^{-1}$) ranges of 0-1000, 1000-10000, and > 10000 were used to group the lakes into freshwater, moderately saline and saline respectively. All counts were performed using the acridine orange direct count method except for Nakuru (Yasindi et al. 2002), in which the colony count method was employed. Area (km^2); Lake z = max depth, (mean depth), station z▪ (m); Sample z = sample depth (m) (WC = water column, euphotic = euphotic zone,); Chl *a* = chlorophyll *a* ($\mu g \cdot L^{-1}$); B.A. = bacterial abundance (cells x $10^6 \cdot mL^{-1}$); Date (month-year); R = reference. NR = not reported, *Only one sample taken.

Lake	Area	Lake z	Sample z	Chl *a*	B.A.	R
Freshwater						
Ardibo	NR	NR	surface	8.0	9.4*	6
Awassa	90	17-18	WC	31.6	6.21	5
Awassa	90	23 (10.7)	surface	22	6.4	6
Awassa	90	23 (10.7)	euphotic	11.8	9.5	3
Babogaya	0.58	65 (38)	surface	33	9.7	6
Baringo	160	NR (4.4)	euphotic	43.3	9.1	3
Cresent	NR	NR	euphotic	32.2	9.5	3
Hayq	23	88 (37.4)	surface	13	12.2*	6
Kilole	0.77	6 (2.6)	surface	33	5.2	6
Koriftu	NR	NR	surface	101	22	6
Naivasha	NG	NG	1	NR	3.7	2
Naivasha	150	7-15 (5-9)	euphotic	26.2	8.2	3
Zwai	442	8 (2.5)	surface	94	11.3	6
Zwai	442	7 (2.5)	euphotic	27.3	11.3	3
Moderately Saline						
Arenguadi	0.54	19 (5.5)	surface	422	109.2	6
Bishoftu	0.93	87 (55)	surface	51	18.5	6
Budameda	NR	NR	surface	32	9.2*	6
Chamo	551	13 (NR)	surface	111	16.7	6
Chamo	551	13 (NR)	euphotic	44.2	16.7	3
Hora	1.03	38 (17.5)	surface	36	21.0	6
Langano	241	48 (17)	euphotic	13.4	7.0	3
Methara	3.2	NR	surface	7.1	4.4*	6
Oloidien	5.5	7-8.4 (5-6)	euphotic	23.0	97.2	3
Solai	8	1 (0.9)	euphotic	209.6	42.9	3
Saline						
Abijata	176	14 (7.6)	euphotic	11.6	43.8	3
Abijata	176	14 (7.6)	surface	101	43.8	6
Bogoria	NR	NR	1	NR	35	2
Bogoria	29	12 (7)	euphotic	266.1	66.7	3
Chittu	0.8	21 (NR)	surface	224	48.4*	6
Elmenteita	NR	NR	0.0-0.4	NR	360	2
Elmenteita	NR	NR	1.1-1.5	NR	350	2
Elmenteita	20-25	1.9 (0.9)	euphotic	123.1	245.0	3

continued

Table 33 continued

Lake	Area	Lake z	Sample z	Chl *a*	B.A.	R
Mechaferra	NR	NR	surface	296	116.5*	6
Nakuru	44	> 4 (2) 0.30▪	NR	NR	270	1
Nakuru	36-49	0.55 - 4.03	surface	237.4	1780.0	4
Nakuru	44	2.8 (1.3)	euphotic	123.1	255.9	3
Shalla	329	266 (87)	surface	7.1	4.4	6
Simbi	0.29	23 (13) 23▪	NR	NR	12-23	1
Simbi	0.29	23 (13)	euphotic	81.6	35.7	3
Sonachi	NR	NR	1	NR	36	2
Sonachi	NR	NR	4	NR	24	2
Sonachi	0.18	7.5 (5.2)	euphotic	88.9	40.5	3
Tilo	NR	NR	surface	53	41.1*	6

1. Finlay et al. 1987
2. Kilham 1981
3. Yasindi 2001
4. Yasindi et al. 2002
5. Zinabu and Taylor 1989
6. Zinabu and Taylor 1997

Table 34. Biomass (μg C·L^{-1}) of picoplankton and protozoa and their percent contribution to total carbon in the microbial loop in Napoleon Gulf, Lake Victoria on May 30, June 20, and July 11, 2002 at 2 and 5 m depth.

	Biomass (μg C·L^{-1})					
	2 m			5 m		
	May	**June**	**July**	**May**	**June**	**July**
Picoplankton	960.2	652.7	505.0	912.5	500.5	510.0
Flagellates						
Autotrophs	12.3	7.8	10.2	6.7	1.9	3.5
Mixotrophs	7.1	5.6	9.3	3.5	2.0	4.1
Heterotrophs	40.4	21.8	34.6	45.1	24.7	39.1
Total	59.9	35.3	54.1	55.4	28.6	46.7
Ciliates						
Mixotrophs	13.4	13.2	13.0	9.9	5.1	5.7
Heterotrophs	24.0	19.6	42.4	20.5	19.6	29.0
Total	37.3	32.9	55.4	30.4	24.7	34.8
Total Protozoa	97.2	68.1	109.5	85.8	53.3	81.5
Total Biomass	1057.4	720.9	614.5	998.2	553.8	591.5
	Percent Contribution to Total Carbon in the Microbial Loop					
Picoplankton	90.81	90.55	82.18	91.41	90.38	86.22
Flagellates						
Autotrophs	1.17	1.09	1.66	0.67	0.34	0.59
Mixotrophs	0.67	0.78	1.51	0.35	0.35	0.70
Heterotrophs	3.82	3.03	5.64	4.52	4.47	6.61
Total	5.66	4.90	8.80	5.55	5.16	7.90
Ciliates						
Mixotrophs	1.27	1.84	2.12	0.99	0.92	0.97
Heterotrophs	2.27	2.72	6.89	2.05	3.54	4.91
Total	3.53	4.56	9.02	3.05	4.46	5.88
Total Protozoa	9.19	9.45	17.82	8.59	9.62	13.78

Table 35. Minimum and maximum clearance rates ($mL \cdot cell^{-1} \cdot d^{-1}$) selected from the literature for flagellates on picoplankton sized particles. R = reference.

	Clearance Rate ($mL \cdot cell^{-1} \cdot d^{-1}$) Picoplankton Particles		Clearance Rate ($mL \cdot cell^{-1} \cdot d^{-1}$) Phytoplankton Particles		R
Classification	**Minimum**	**Maximum**	**Minimum**	**Maximum**	
< 5 μm Flagellates					
Choanoflagellida	1.7×10^{-5}	1.6×10^{-4}			1
Prymnesiida	5.3×10^{-9}	5.3×10^{-9}			2
Other HNF	1.4×10^{-6}	1.1×10^{-5}			1
> 5 μm Flagellates					
Prymnesiida	5.3×10^{-9}	5.3×10^{-9}			2
Other HNF	7.5×10^{-5}	7.5×10^{-5}			3
Gymnodiniales			1.9×10^{-2}	2.9×10^{-2}	4

1. Leakey et al. 1996
2. Martin-Cereceda et al. 2003
3. Nygaard et al. 1988
4. Strom 1991

Table 36. Minimum and maximum clearance rates (mL·cell^{-1}·d^{-1}) selected from the literature for each ciliate genus on picoplankton and algal sized particles. N.A. = not applicable; R = reference (picoplankton/phytoplankton reference).

	Clearance Rate (mL·cell^{-1}·d^{-1}) Picoplankton Particles		Clearance Rate (mL·cell^{-1}·d^{-1}) Algal Particles		
Genus	**Minimum**	**Maximum**	**Minimum**	**Maximum**	**R**
Stentor	0.026	0.046	1.272	1.272	1/2
Askenasia	N.A.	N.A.	0.001	0.001	/1
Lagenophrya A, B, C	N.A.	N.A.	0.001	0.001	/1
Monodinium	N.A.	N.A.	0.001	0.001	/1
Pleuronema	0.003	0.012	N.A.	N.A.	3/
Scuticociliates	0.003	0.012	N.A.	N.A.	3/
Vorticellidae	0.127	0.127	N.A.	N.A.	3/
Dysteria	0.004	0.004	N.A.	N.A.	3/
Phascolodon	0.004	0.004	0.028	0.028	3/1
Coleps	0.001	0.001	0.000	0.000	4/1
Urotricha	0.001	0.001	0.000	0.000	4/1
Halteria	0.003	0.006	0.028	0.028	3/1
Strobilidium A, B, C*	0.003	0.006	0.060	0.242	3/5
Strombidium A	0.094	0.180	0.041	0.113	5/5
Strombidium B, C	0.001	0.001	0.041	0.113	1/5
Tinntinidium	0.026	0.046	0.264	0.960	5/1

*Picoplankton clearance rates only apply to *Strobilidium* A and B; *Strobilidium* C is an aligivore

1. Foissner 1999
2. Fenchel 1980
3. Yasindi 2001
4 Kisand and Zingel 2000
5 Kivi and Setala 1995

Table 37. Minimum and maximum clearance rates (mL·cell^{-1}·d^{-1}) selected from the literature for zooplankton on picoplankton and algal sized particles. R = reference (picoplankton/phytoplankton reference).

	Clearance Rate Picoplankton Sized Particles		Clearance Rate Algal Sized Particles		
Taxon	**Minimum**	**Maximum**	**Minimum**	**Maximum**	**R**
Rotifera					
Asplanchna spp.	0.110	0.110	0.195	0.195	1/1
Brachionus angularis	0.726	0.726	0.043	0.043	1/1
Brachionus calyciflorus	0.039	0.039	0.684	0.684	1/1
Brachionus bidentatus	0.220	0.220	0.165	0.165	1/1
Brachionus falcatus	0.220	0.220	0.165	0.165	1/1
Brachionus forficula	0.220	0.220	0.037	0.037	1/1
Brachionus patulus	0.220	0.220	0.165	0.165	1/1
Euclanis sp.	0.009	0.009	0.021	0.055	1/4
Filinia longiseta	0.653	0.653	0.040	0.040	1/1
Filinia opoliensis	0.653	0.653	0.040	0.040	1/1
Keratella cochlearis	0.009	0.009	0.021	0.055	1/4
Keratella tropica	0.011	0.011	0.576	1.728	1/4
Synchaeta spp.	0.003	0.003	0.031	0.031	1/1
Trichocerca cylindrica	0.002	0.002	0.009	0.009	1/1
Cladocera					
*Bosmina longirostris*ξ	0.372	0.372	0.336	3.504	5/4
*Ceriodaphnia cornuta*ξ	1.680	1.680	1.626	3.295	5/5
Daphnia lumhortzi (helm.)❖	6.855	6.855	11.313	16.363	5/5
*Diaphanosoma excisum*ξ	1.680	1.680	1.626	9.744	5/4&5
*Moina micrura**	1.130	1.130	0.940	2.096	5/5
Copepoda					
Calanoida					
Calanoid copepodites	0.000	0.000	1.200	7.800	3/3
Thermodiaptomus galeboides	0.000	0.000	1.200	7.800	3/3
Cyclopoida					
Cyclopoid copepodites	0.001		0.300	0.300	1/1
Mesocyclops sp.	0.001		0.693	0.693	1/6
Thermocyclops emini	0.001		0.693	0.693	1/6
Thermocyclops incisus	0.001		0.693	0.693	1/6
Thermocyclops neglectus	0.001		0.693	0.693	1/6
Tropocyclops confinnis	0.001		0.693	0.693	1/6
Tropocyclops tenellus	0.001		0.693	0.693	1/6
Copepoda nauplii	0.003		0.111	4.000	1/1&2

*length used in clearance rate equation (Knoechel and Holtby 1986a) from Hart and Jarvis 1993
ξlength used in clearance rate equation (Knoechel and Holtby 1986a) from Knoechel and Holtby 1986b
❖ length used in clearance rate equation (Knoechel and Holtby 1986a) from Jonna and Lehman 2002
1. Kim et al. 2000

2. Paffenhofer 1971
3. Sommer et al. 2002
4. Bogdan and Gilbert 1987
5. Knoechel and Holtby 1986b
6. Adrian 1991

Table 38. Flagellate abundance (cells x 10^{3}·mL^{-1}) and community clearance (x 10^{-3}·d^{-1}) on picoplankton sized particles for May 30, June 20 and July 11, 2002. Community clearance is the product of abundance and clearance rate (Table 35). Minuimum and maximum community clearance rates were calculated using minimum and maximum clearance rates from Table 35. A = abundance; C.C. = community clearance; Min, Max = minimum and maximum respectively.

	May 30, 2002			June 20, 2002			July 11, 2002		
		C.C.			C.C.			C.C.	
	A	Min	Max	A	Min	Max	A	Min	Max
< 5 μm Flagellates									
Choanoflagellida	110.4	1907.7	18149.6	69.8	1205.7	11470.5	91.1	1575.0	14984.2
Prymnesiida	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Other HNF	0.3	0.4	3.2	0.2	0.3	2.0	0.2	0.3	2.7
Total		1908.1	18152.8		1205.9	11472.5		1575.3	14986.8
> 5 μm Flagellates									
Prymnesiida	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other HNF	0.3	24.2	24.2	0.2	14.1	14.1	0.4	28.2	28.2
Total		24.2	24.2		14.1	14.1		28.2	28.2
Total		1932.3	18177.0		1220.0	11486.6		1603.5	15015.0

Table 39. Ciliate abundance (cells·mL^{-1}) and community clearance (x 10^{-3}·d^{-1}) on picoplankton sized particles for May 30, June 20 and July 11, 2002. Community clearance is the product of abundance and clearance rate (Table 36). Minuimum and maximum community clearance rates were calculated using minimum and maximum clearance rates from Table 36. A = abundance; C.C. = community clearance; Min, Max = minimum and maximum respectively.

Genus	May 30, 2002			June 20, 2002			July 11, 2002		
		C.C.			C.C.			C.C.	
	A	Min	Max	A	Min	Max	A	Min	Max
< 40 μm									
Pleuronema	0.31	0.9	3.7	0.44	1.3	5.3	0.40	1.1	4.8
Scuticociliate A	2.16	6.2	25.9	2.42	7.0	29.0	2.42	7.0	29.0
Scuticociliate B	2.16	6.2	25.9	1.58	4.6	19.0	3.48	10.0	41.7
Scuticociliate C	1.89	5.4	22.7	0.09	0.3	1.1	0.40	1.1	4.8
Vorticellidae A	2.33	295.5	295.5	0.84	105.9	105.9	0.92	117.1	117.1
Vorticellidae B	2.51	317.8	317.8	0.70	89.2	89.2	1.72	217.5	217.5
Vorticellidae E	0.09	11.2	11.2	0.04	5.6	5.6	0.00	0.0	0.0
Dysteria	3.48	13.3	13.3	0.62	2.4	2.4	5.37	20.6	20.6
Phascolodon	0.22	0.8	0.8	0.75	2.9	2.9	0.62	2.4	2.4
Coleps	0.70	0.6	0.8	1.19	1.0	1.3	1.28	1.0	1.4
Urotricha	1.63	1.3	1.8	1.28	1.0	1.4	1.14	0.9	1.2
Halteria A	2.55	8.6	16.5	0.88	3.0	5.7	1.89	6.4	12.3
Halteria B	7.83	26.3	50.8	3.30	11.1	21.4	7.79	26.2	50.5
Halteria C	0.88	3.0	5.7	0.57	1.9	3.7	1.85	6.2	12.0
Strobilidium A	7.96	26.8	51.6	11.48	38.6	74.4	18.66	62.7	120.9
Strobilidium B	0.57	1.9	3.7	2.82	9.5	18.2	1.89	6.4	12.3
Strombidium A	2.20	205.9	396.0	1.72	160.6	308.9	3.21	300.6	578.2
Tinntinidium A	1.19	31.4	54.2	0.92	24.4	42.1	2.60	68.5	118.4
Tinntinidium B	0.31	8.1	14.0	0.66	17.4	30.1	1.23	32.5	56.2
Tinntinidium C	0.00	0.0	0.0	0.09	2.3	4.0	0.00	0.0	0.0
Total		971.3	1311.9		489.8	771.6		888.2	1401.0
> 40 μm									
Stentor A	0.00	0.0	0.0	0.00	0.0	0.0	0.13	3.5	6.0
Stentor B	0.09	2.3	4.0	0.44	11.6	20.1	0.26	7.0	12.0
Vorticellidae C	0.44	55.8	55.8	0.00	0.0	0.0	0.48	61.3	61.3
Vorticellidae D	0.00	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0
Halteria D	0.04	0.1	0.3	0.00	0.0	0.0	0.00	0.0	0.0
Strombidium B	0.48	0.7	0.7	0.92	1.4	1.4	0.53	0.8	0.8
Strombidium C	0.57	0.9	0.9	0.35	0.5	0.5	0.13	0.2	0.2
Total		59.8	61.6		13.5	22.0		72.8	80.4
Total Ciliates		1031.1	1373.5		503.3	793.6		961.0	1481.3

Table 40. Zooplankton abundance (cells·L^{-1}), biomass (g C·m^{-2}), growth rates (d^{-1}), production (g C·m^{-2}·d^{-1}) and putative feeding guilds. Production is the product of biomass and growth rate. A = abundance; B = biomass; G. R. = growth rate; P = production; P.F.G. = putative feeding guild, R = reference (biomass/growth rate); Alg = algivore; Bac = bacterivore; Pred = predatory.

Taxon	Aξ	B	G. R.	P	P.F.G.	R
Rotifera			0.792	0.004		1/2
Asplanchna spp.	0.080	0.000			Alg/Pred	
Brachionus angularis	0.214	0.001			Alg/Bac/Pred	
Brachionus calyciflorus	0.093	0.001			Alg/Bac/Pred	
Brachionus bidentatus	0.013	0.001			Alg/Bac/Pred	
Brachionus falcatus	0.038	0.001			Alg/Bac/Pred	
Brachionus forficula	0.109	0.001			Alg/Bac/Pred	
Brachionus patulus	0.038	0.001			Alg/Bac/Pred	
Euclanis sp.	0.352	0.001			Alg/Bac	
Filinia longiseta	0.019	0.001			Alg/Bac/Pred	
Filinia opoliensis	0.254	0.001			Alg/Bac/Pred	
Keratella cochlearis	0.144	0.001			Alg/Bac/Pred	
Keratella tropica	0.982	0.001			Alg/Bac/Pred	
Synchaeta spp.	0.665	0.000			Alg/Pred	
Trichocerca cylindrica	0.144	0.005			Alg/Pred	
Total	3.144	0.123				
Cladocera		0.009	0.605	0.005	Alg/Bac/Pred	3/4
Bosmina longirostris	0.245					
Ceriodaphnia cornuta	0.072					
Daphnia lumhortzi (helm.)	0.024					
Diaphanosoma excisum	0.418					
Moina micrura	0.561					
Total	1.320					
Copepoda						
Calanoids	0.000	0.077	0.300	0.023	Alg/Pred	3/4
Calanoid copepodites	3.144					
Thermodiaptomus galeboides	1.251					
Total Calanoida	4.396					
Cyclopoida	0.000	0.522	0.300	0.157	Alg/Pred	3/4
Cyclopoid copepodites	25.368					
Mesocyclops sp.	0.053					
Thermocyclops emini	3.656					
Thermocyclops incisus	0.107					
Thermocyclops neglectus	2.459					
Tropocyclops confinnis	2.987					
Tropocyclops tenellus	0.979					
Total cyclopoida	35.610					
Nauplius larvae	80.595				Alg/Pred	
Total Copepoda	120.601					
Total	125.064	0.614		0.190		

ξ Kiggundu unpublished, Fisheries Resources Research Institute, Jinja, Uganda

1. Dumont et al. 1975
2. Sarma et al. 1996
3. Biomass (Branstrator et al. 1996) was converted to g $C \cdot m^{-2}$ using a carbon conversion of 45% (Pagano and Saint-Jean 1993)
4. Production/biomass ratio for *Diaphanosoma* was selected as a growth rate for Cladocera; Instantaneous dry weight growth rate for Mesocyclops at 25°C was selected for Copepoda growth rate (Mengestou and Fernando 1991)

Table 41. Community clearance (d^{-1}) of protozoa and zooplankton divided taxonomically and by size classes on picoplankton sized particles on May 30, June 20 and July 11, 2002. Minimum and maximum community clearance rates were calculated using minimum and maximum clearance rates from Tables 35 and 36. Min, Max = minimum and maximum respectively. Zooplankton community clearance rates are $x10^{-3}$ d^{-1}, except total zooplankton community clearance (d^{-1}).

	Community Clearance (d^{-1})					
	May 30, 2002		June 20, 2002		July 11, 2002	
	Min	Max	Min	Max	Min	Max
Taxonomic Group						
Flagellates						
< 5 μm flagellates	1.908	18.15	1.21	11.47	1.58	14.99
> 5 μm flagellates	0.024	0.024	0.014	0.014	0.028	0.028
Total	1.908	18.153	1.206	11.472	1.575	14.987
Ciliates						
< 40 μm ciliates	0.971	1.312	0.490	0.772	0.888	1.401
> 40 μm ciliates	0.060	0.062	0.014	0.022	0.073	0.080
Total	1.031	1.373	0.503	0.794	0.961	1.481
Zooplankton						
Rotifera	0.406	0.406	0.406	0.406	0.406	0.406
Cladocera	1.714	1.714	1.714	1.714	1.714	1.714
Calanoida	0.000	0.000	0.000	0.000	0.000	0.000
Cyclopoida	0.036	0.036	0.036	0.036	0.036	0.036
Copepoda nauplii	0.242	0.242	0.242	0.242	0.242	0.242
Total	0.002	0.002	0.002	0.002	0.002	0.002
Size Classes of Grazers						
< 5 μm grazers	1.91	18.15	1.21	11.47	1.58	14.99
5 – 40 μm grazers	1.00	1.34	0.50	0.79	0.92	1.43
> 40 μm grazers	0.06	0.06	0.02	0.02	0.08	0.08
Total	2.97	19.55	1.73	12.28	2.57	16.50

Table 42. Community clearance (d^{-1}) of the protozoan and zooplankton communities on algal sized particles on May 30, June 20 and July 11, 2002. Minimum and maximum community clearance rates were calculated using minimum and maximum clearance rates from Tables 35 and 36.

	Community Clearance (d^{-1})					
	May 30, 2002		**June 20, 2002**		**July 11, 2002**	
	Minimum	**Maximum**	**Minimum**	**Maximum**	**Minimum**	**Maximum**
< 5 μm flagellates	0.000	0.000	0.000	0.000	0.000	0.000
> 5 μm flagellates	1.257	1.885	0.633	0.949	1.846	2.770
Flagellates	**1.257**	**1.885**	**0.633**	**0.949**	**1.846**	**2.770**
< 40 μm ciliates	1.357	4.210	1.613	5.765	2.850	9.879
> 40 μm ciliates	0.156	0.232	0.612	0.704	0.531	0.578
Ciliates	**1.514**	**4.442**	**2.224**	**6.469**	**3.381**	**10.457**
Rotifera	0.001	0.002	0.001	0.002	0.001	0.002
Cladocera	0.002	0.007	0.002	0.007	0.002	0.007
Calanoida	0.005	0.034	0.005	0.034	0.005	0.034
Cyclopoida	0.015	0.015	0.015	0.015	0.015	0.015
Copepoda nauplii	0.009	0.322	0.009	0.322	0.009	0.322
Zooplankton	**0.031**	**0.380**	**0.031**	**0.380**	**0.031**	**0.380**

Table 43. Estimated areal production (g C·m^{-2}·d^{-1}) of picoplankton, phytoplankton, protozoa and zooplankton in Napoleon Gulf on July 11, 2002. Phytoplankton production was derived from chlorophyll *a* within the euphotic zone on July 11, 2002 using an empirical model (Silsbe 2004). Zooplankton production is based on biomass and growth rates selected from literature (Table 40). Picoplankton and protozoan biomass is weighted for the water column. Picoplankton and protozoan growth rates are based on observed rates (Tables 24, 27 and 29). Growth rate is assumed to be the same at all depths. G.R. = growth rate; Other HNF = Includes all heterotrophic nanoflagellates excluding Choanoflagellida; N.D. = not determined.

		Biomass (g C·m^{-2})	**G. R. (d^{-1})**	**Production (g C·m^{-2}·d^{-1})**
Picoplankton		7.247	0.186	1.350
Phytoplankton		6.432ξ		5.490
Flagellates				
	< 5 μm Bacterivores			0.230
	< 5 μm Other HNF	0.008	0.494	0.004
	< 5 μm Prymnesiida	0.006	0.564	0.003
	Choanoflagellida	0.452	0.494	0.223
	> 5 μm Bacterivores			0.046
	> 5 μm Other HNF	0.072	0.619	0.045
	> 5 μm Prymnesiida	0.002	0.794	0.001
	Algivore/Predatory	0.069	0.077	0.005
	Nutrients	0.072	0.049	0.004
	Total	0.680		0.285
Ciliates				
	Algivore	0.035	N.D.	0.000
	Algivore/Bacterivore	0.024	0.541	0.013
	Algivore/Bacterivore/Predatory	0.323	0.125	0.040
	Algivore/Predatory	0.017	-0.156	0.000
	Bacterivore	0.080	0.811	0.065
	Predatory	0.027	0.300	0.008
	Unknowns	0.054	0.562	0.030
	Total	0.559		0.157
Zooplankton				
	Algivore/Bacterivore	0.001		0.001
	Algivore/Bacterivore/Predatory	0.012		0.008
	Algivore/Predatory	0.601		0.181
	Total	0.614		0.190

ξ Ramlal et al (2001); converted to g C·m^{-2} using depth of 14 m and carbon conversion of 0.19 pg C·μm^3 (Putt and Stoecker 1989)

Table 44. Maximum ciliate growth rates (d^{-1}) and production (g $C \cdot m^{-2} \cdot d^{-1}$) for July 11, 2002. Maximum growth rates were predicted using observed biovolume (x 10^3 μm^3) in the growth rate equation by Müller and Geller (1993). Production is a product of maximum growth rate and biomass.

Class	Genus	Biovolume (x 10^3 μm^3)	G. R. (d^{-1})	Production (g $C \cdot m^{-2} \cdot d^{-1}$)
Heterotrichea	*Stentor A*	438.07	1.00	0.141
	Stentor B	48.69	1.81	0.046
Litostomatea	*Askenasia*	3.40	3.72	0.002
	Didinium	38.18	1.94	0.004
	Dileptus	105.89	1.47	0.027
	Lagenophrya A	0.88	5.36	0.010
	Lagenophrya B	3.51	3.69	0.032
	Lagenophrya C	32.02	2.03	0.006
	Mesodinium A	0.30	7.18	0.013
	Mesodinium B	2.07	4.25	0.007
	Monodinium	0.97	5.22	0.015
	Unknown	0.50	6.23	0.011
Oligohymenophorea	*Pleuronema*	2.40	4.09	0.016
	Scuticociliate A	1.16	4.96	0.030
	Scuticociliate B	0.32	7.04	0.018
	Scuticociliate C	0.54	6.12	0.001
	Vorticellidae A	1.98	4.30	0.019
	Vorticellidae B	7.72	2.98	0.095
	Vorticellidae C	49.88	1.80	0.000
	Vorticellidae D			
	Vorticellidae E	1.09	5.05	0.000
Phyllopharyngea	*Dysteria*	1.05	5.10	0.053
	Periacineta			
	Phascolodon	5.02	3.35	0.013
	Sphaerophrya	7.13	3.04	0.001
	Suctorian	11.32	2.69	0.000
Prostomatea	*Coleps*	4.11	3.53	0.068
	Unknown	0.22	7.82	0.002
	Urotricha	0.43	6.50	0.004
Spirotrichea	*Halteria A*	0.70	5.69	0.022
	Halteria B	1.65	4.52	0.088
	Halteria C	3.75	3.62	0.047
	Halteria D	161.43	1.31	0.000
	Strobilidium A	0.64	5.84	0.102
	Strobilidium B	0.62	5.88	0.018
	Strobilidium C	7.62	2.99	0.105
	Strombidium A	9.98	2.78	0.095
	Strombidium B	28.48	2.09	0.045
	Strombidium C	46.93	1.83	0.023

continued

Table 44 continued

Class	Genus	Biovolume (x 10^3 μm^3)	G. R. (d^{-1})	Production (g C·m^{-2}·d^{-1})
	Tinntinidium A	4.63	3.42	0.070
	Tinntinidium B	3.33	3.74	0.027
	Tinntinidium C	11.30	2.69	0.011
Unknown	Unknown A	53.88	1.76	0.047
	Unknown B	2.96	3.86	0.013
	Unknown C	0.34	6.90	0.163
Total				1.512

Table 45. Minimum and maximum production on July 11, 2002, for the ciliate community by feeding guilds and the amount of daily carbon production each guild would need to consume assuming 50% production efficiency. Minimum production (g $C \cdot m^{-2} \cdot d^{-1}$) for each guild was determined using observed growth rates. Maximal production is based on growth rates obtained using observed biovolume (x 10^3 μm^3) in the growth rate equation by Müller and Geller (1993). Alg = algivore; Bac = bacterivore; Pred = predatory.

Ciliate Feeding Guilds	Production (g $C \cdot m^{-2} \cdot d^{-1}$)		Carbon Consumption (g $C \cdot m^{-2} \cdot d^{-1}$)	
	Minimum	**Maximum**	**Minimum**	**Maximum**
Alg	0.000	0.105	0.000	0.210
Alg/Bac	0.013	0.133	0.026	0.266
Alg/Bac/Pred	0.040	0.687	0.081	1.374
Alg/Pred	0.000	0.065	0.000	0.130
Bac	0.065	0.233	0.130	0.466
Pred	0.008	0.066	0.016	0.131
Unknowns	0.030	0.223	0.060	0.446
Total	0.157	1.512	0.313	3.023

Table 46. Minimal and maximal consumption of pico and phytoplankton production (g $C \cdot m^{-2} \cdot d^{-1}$) by protozoa and zooplankton on July 11, 2002. Consumption was calculated from estimated production assuming 50% C efficiency. Minimum production for protozoa was determined using observed growth rates. Maximum production for flagellates was determined using a growth rate of 1 d^{-1}. The equation by Muller and Geller (1993) was used to calculate maximum production of ciliates (Table 44). Zooplankton production was determined from biomass and growth rates extracted from the literature (Table 37).

	Consumption of picoplankton production (g $C \cdot m^{-2} \cdot d^{-1}$)		**Consumption of phytoplankton production (g $C \cdot m^{-2} \cdot d^{-1}$)**	
	Minimum	**Maximum**	**Minimum**	**Maximum**
< 5 μm Flagellates	0.461	0.931	0.000	0.000
> 5 μm Flagellates	0.092	0.147	0.011	0.137
Ciliates	0.237	2.106	0.107	1.979
Zooplankton	0.017	0.017	0.379	0.379
Total Consumption	0.806	3.201	0.497	2.496
Remaining Production	0.542	-1.853	4.993	2.994

Table 47. Comparison of picoplankton and phytoplankton production (g C·m^{-2}·d^{-1}) in Napoleon Gulf, Lake Victoria from May through July 2002. Picoplankton production and empirically derived phytoplankton production (Silsbe 2004) are specific to May 30, June 20 and July 11, 2002. Phytoplankton production (Mugidde, 1992) are monthly averages taken between 1989 and 1991. P.P. = picoplankton production (g C·m^{-2}·d^{-1}); S.F. = size fraction experiment; P.D. = predator dilution experiment; S.S.A. = sampling season average; N.A. = not applicable, see text.

					% Picoplankton Production: Phytoplankton Production			
	P.P.		Phytoplankton Production		Size Fraction Experiment		Predator Dilution Experiment	
Month	S.F.	P.D.	Empirical Model	Mugidde 1992	Empirical Model	Mugidde 1992	Empirical Model	Mugidde 1992
May	0.0	N.A.	5.52	5.75	N.A.	N.A.	N.A.	N.A.
June	1.3	2.1	5.43	8.26	23.9	15.7	38.3	25.2
July	1.4	N.A.	5.49	6.56	25.5	21.3	N.A.	N.A.
S.S.A.	1.3	-	5.44	6.83	24.8	19.8	-	-

Table 48. Phytoplankton production (g C m^{-2} day^{-1}) from different gulfs in Lake Victoria. Range for sampling period with average in parentheses.

Site	Date	Phytoplankton Production	Study
Pilkington Bay	Sept 1989 – Aug 1991	4.00 – 16.3 (10.0)	Mugidde 1993
Pilkington Bay	April 1992	1.5	Lehman and Branstrator 1993
Napoleon Gulf	Aug – Sept 2002	3.94 – 9.20 (6.30)	Silsbe 2004
Fielding Bay	Sept – Nov 2002	3.78 – 7.59 (5.82)	Silsbe 2004
Inner Murchison Bay	July – Sept 2002	4.59 – 8.05 (5.87)	Silsbe 2004

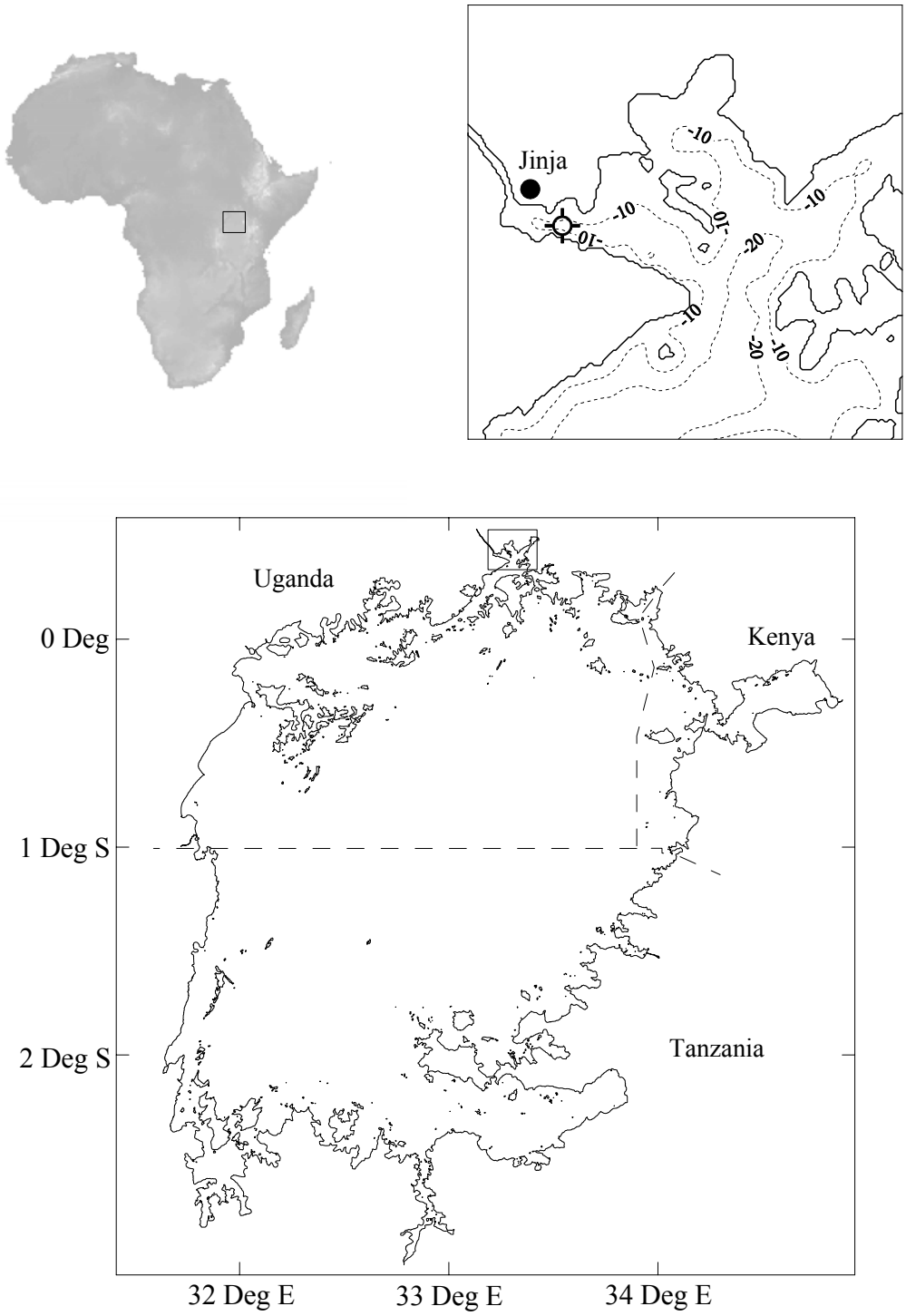

Figure 1. Maps indicating the location and bathymetry of Napoleon Gulf in Lake Victoria, East Africa (Silsbe, 2004). Sample site is indicated by ❖.

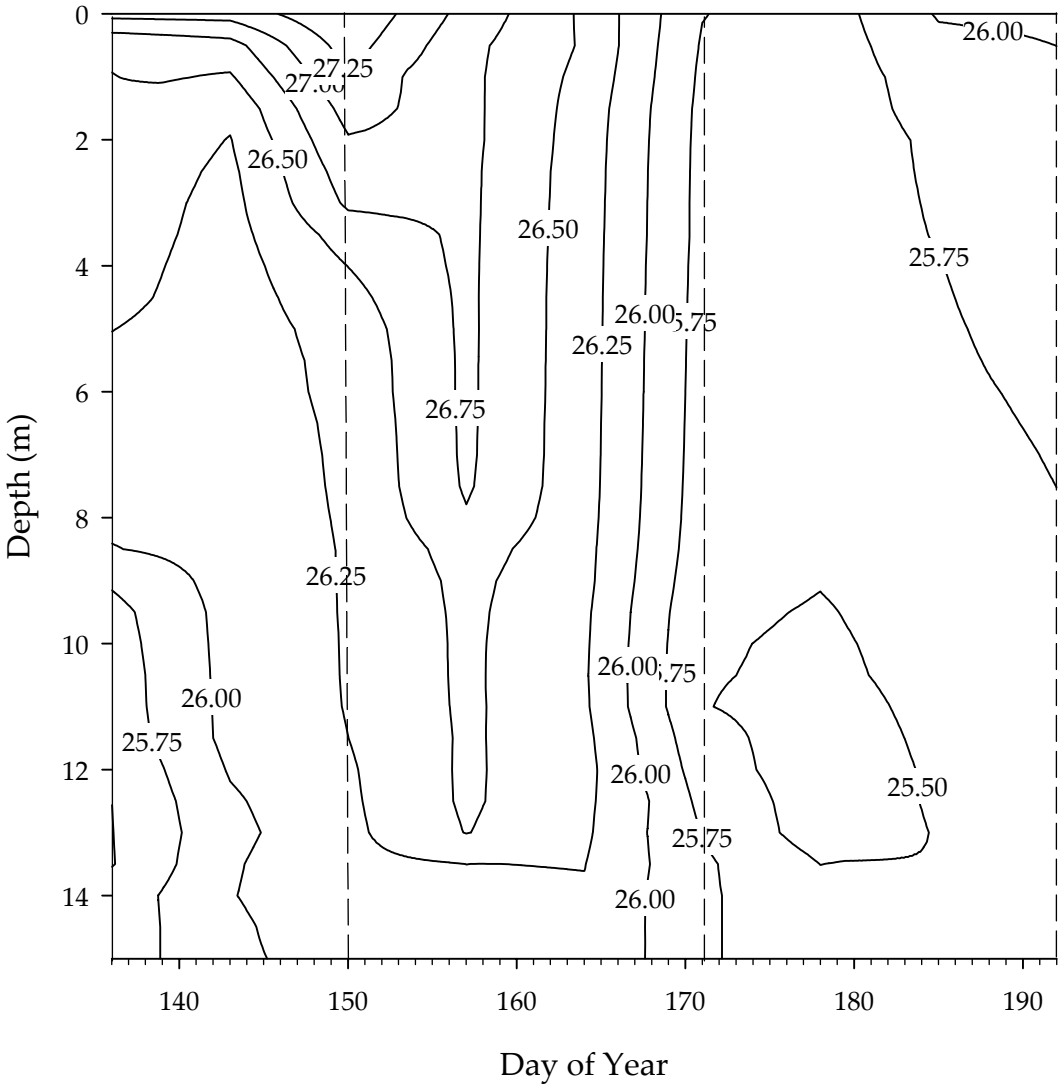

Figure 2. Water column temperature (°C) during the period of sample collection, 2002; based on weekly sampling. Dates when grazing experiments were performed are marked with dashed lines.

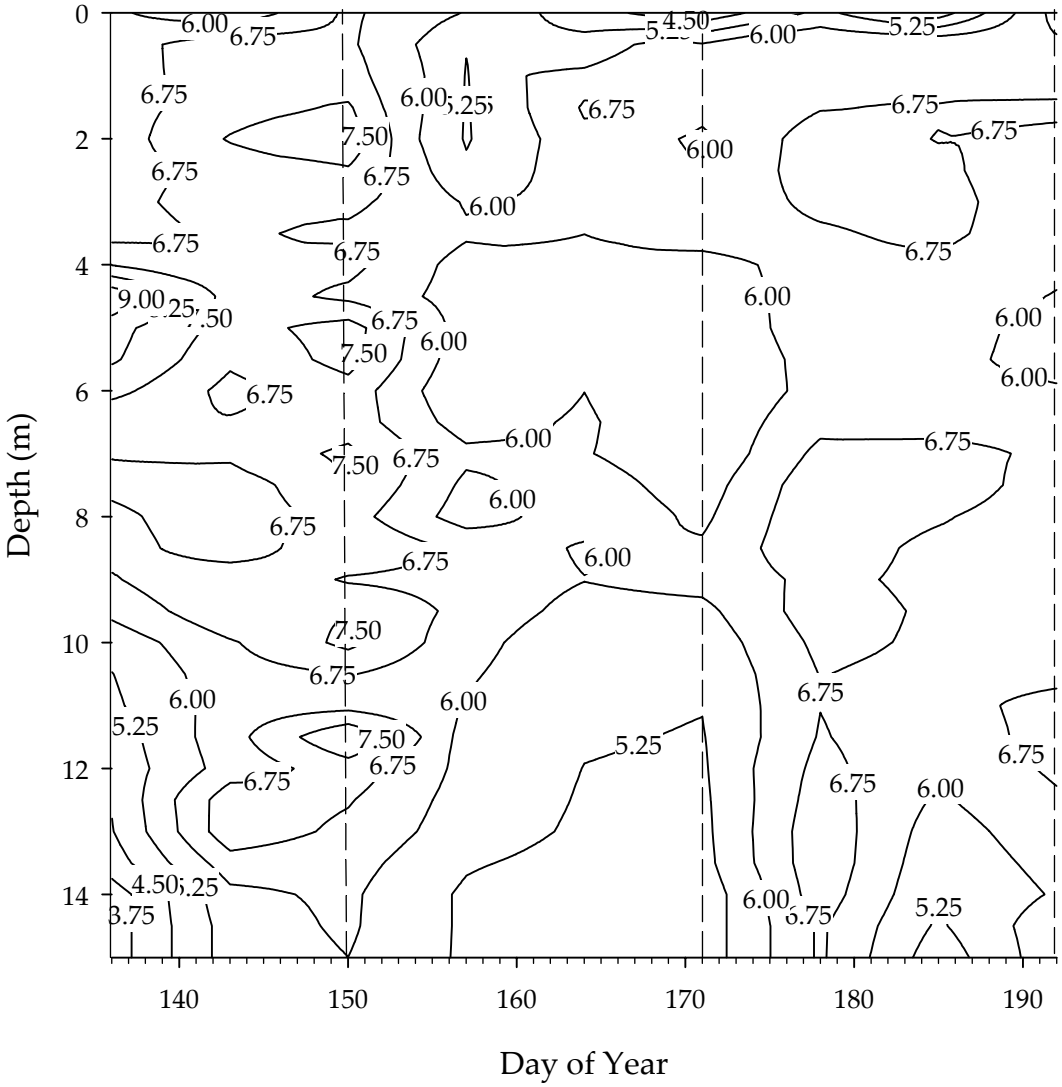

Figure 3. Water column oxygen (mg·L^{-1}) during the period of sample collection, 2002; based on weekly sampling. Dates when grazing experiments were performed are marked with dashed lines.

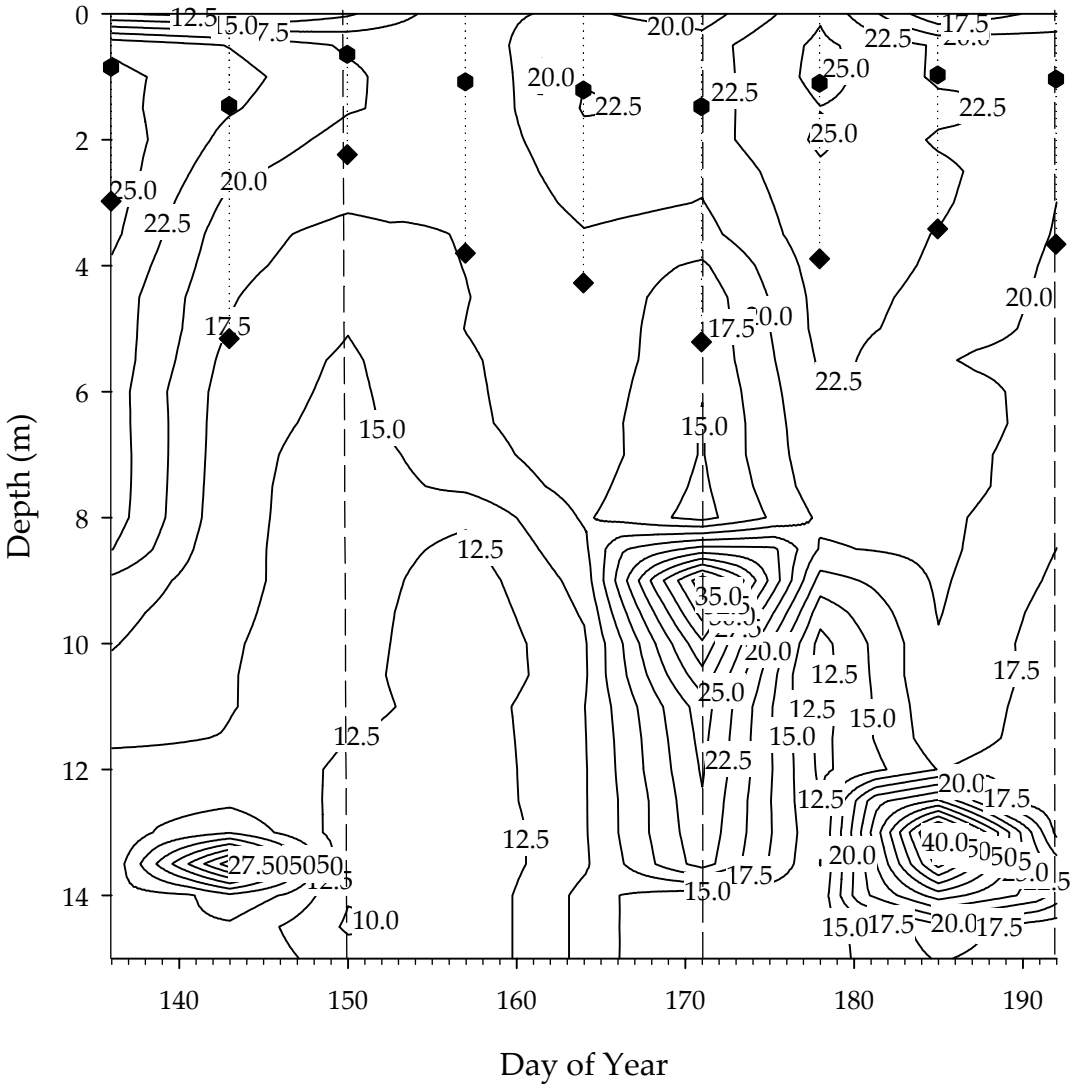

Figure 4. Chlorophyll *a* (μg·L^{-1}), as estimated by *in situ* fluorescence, during the period of sample collection, 2002; based on weekly sampling. Dates when grazing experiments were performed are marked with dashed lines. Secchi depths are indicated by hanging hexagons. Empirically derived euphotic depths are indicated by hanging diamonds.

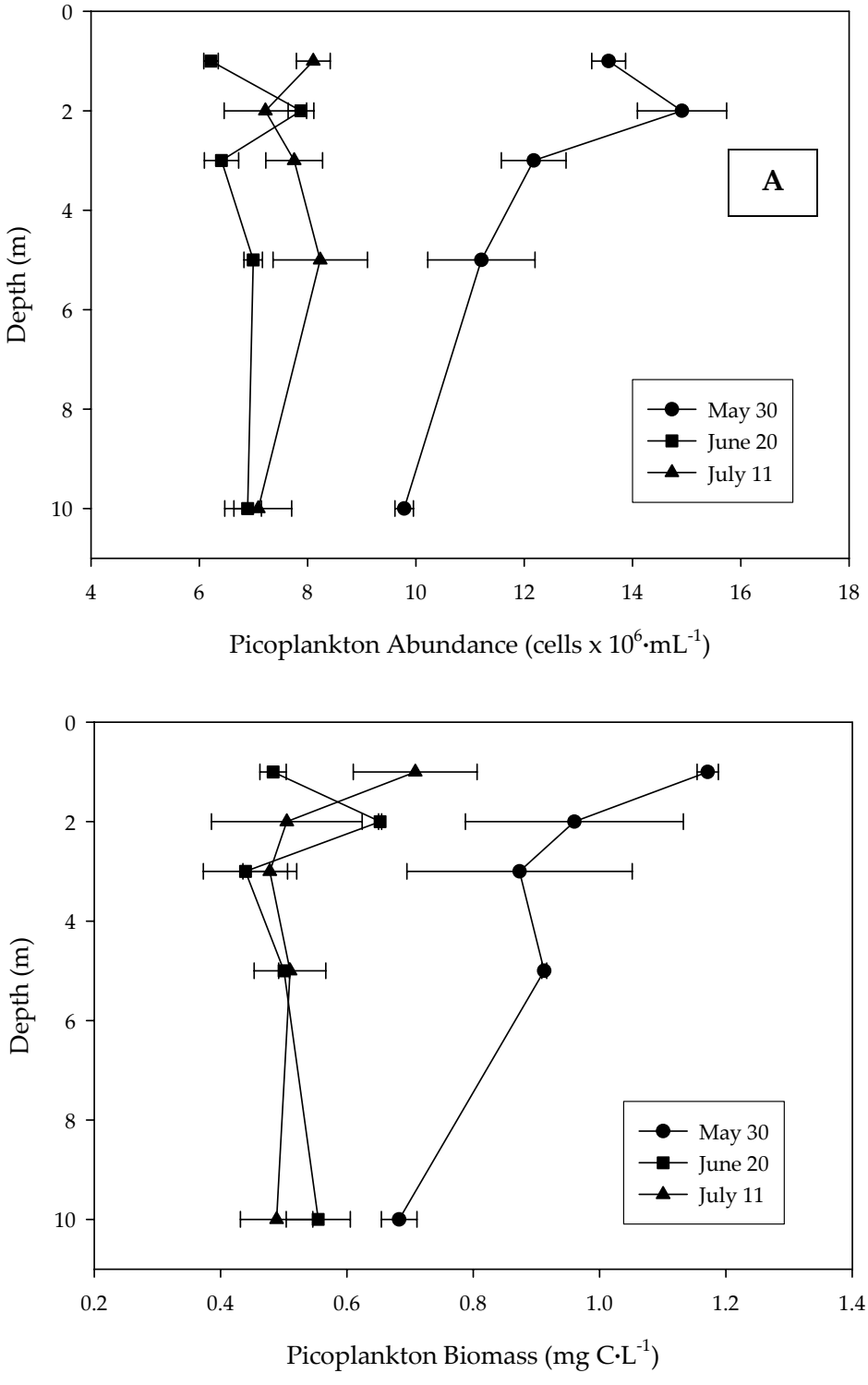

Figure 5. Picoplankton abundance (A) and biomass (B) along a depth profile on each grazing experiment date. Error bars are standard error of the mean.

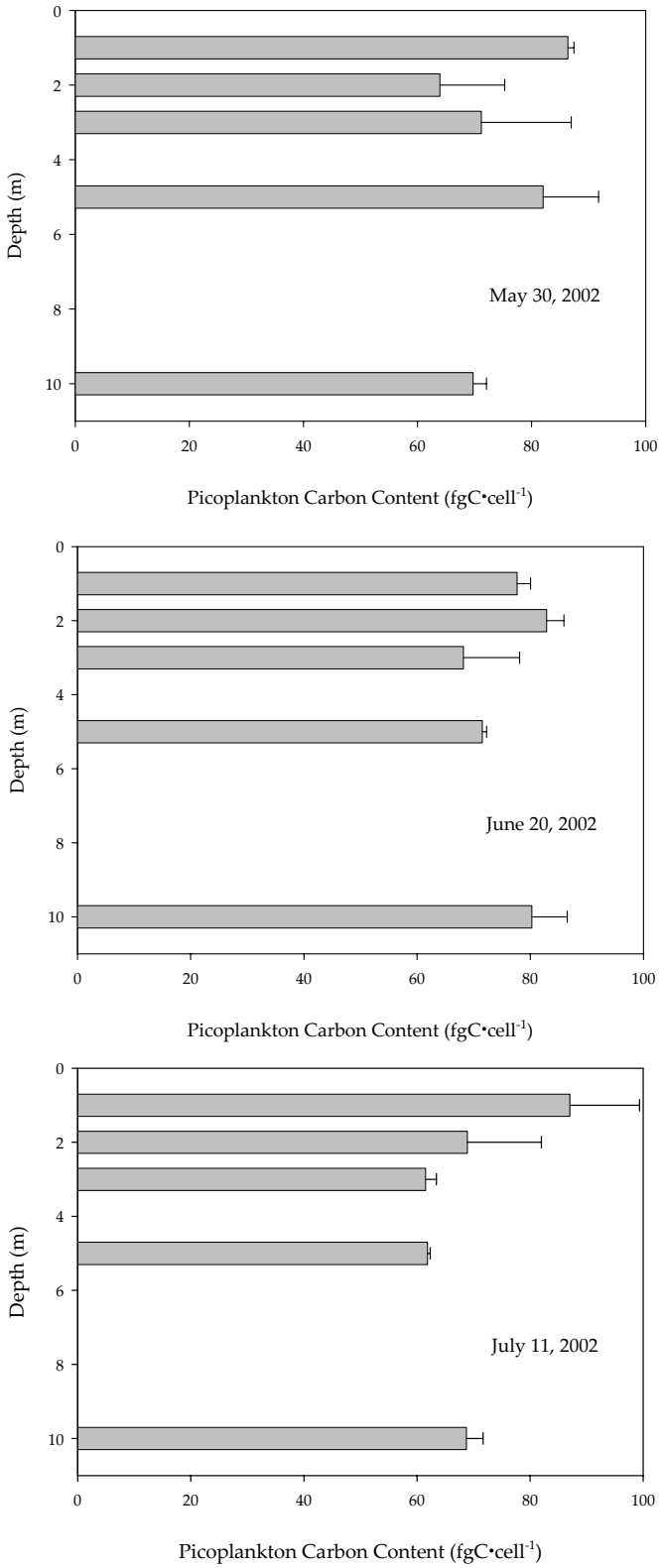

Figure 6. Carbon content of picoplankton along a depth profile on each grazing experiment date. Error bars are standard deviations.

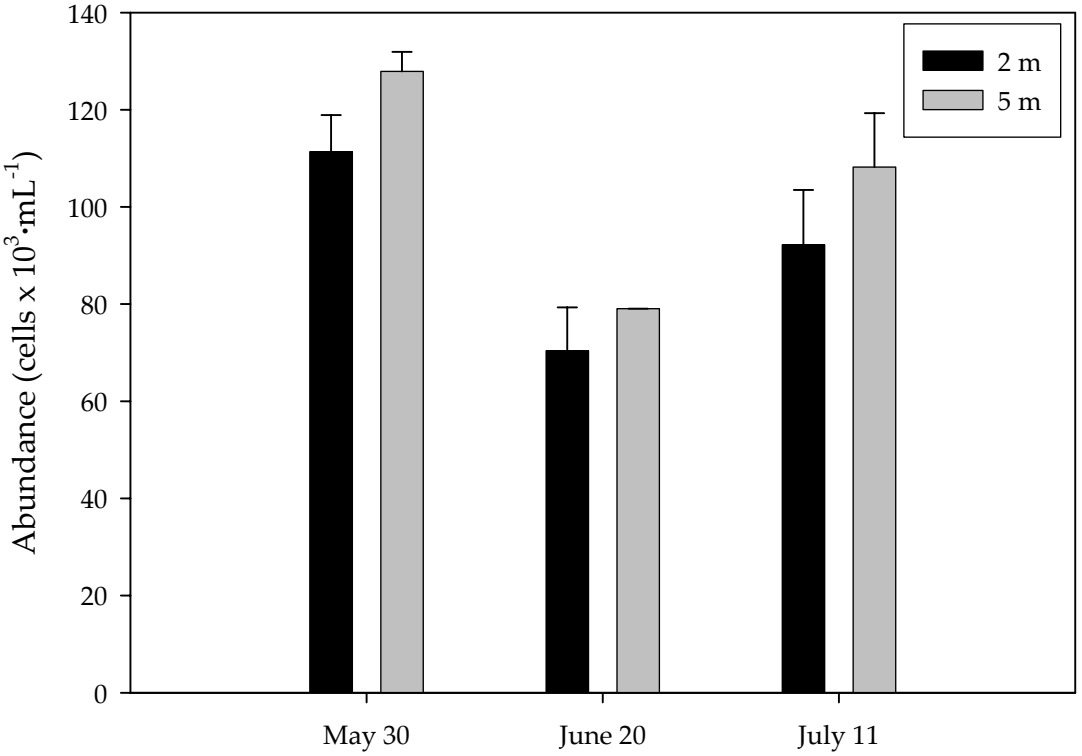

Figure 7. Abundance of flagellates at 2 and 5 m on each grazing experiment date. Error bars are standard error of the mean.

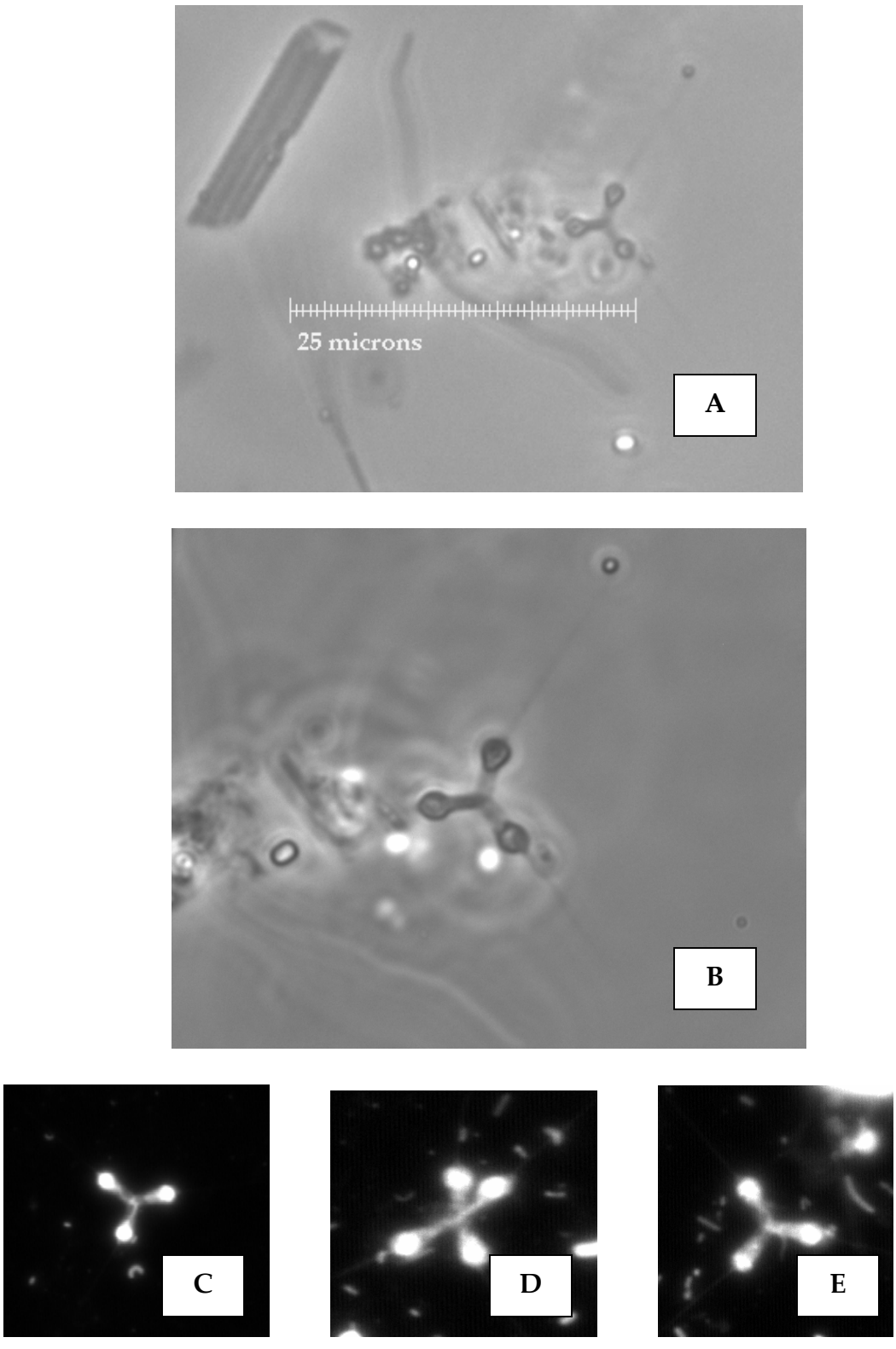

Figure 8. Small flagellates, tentatively called Choanoflagellida visualized in formalin preserved samples via inverted phase microscope, 400x (A) and 1000x (B) and DAPI stained formalin preserved samples via epifluorescence microscope, 1000x (C, D, E).

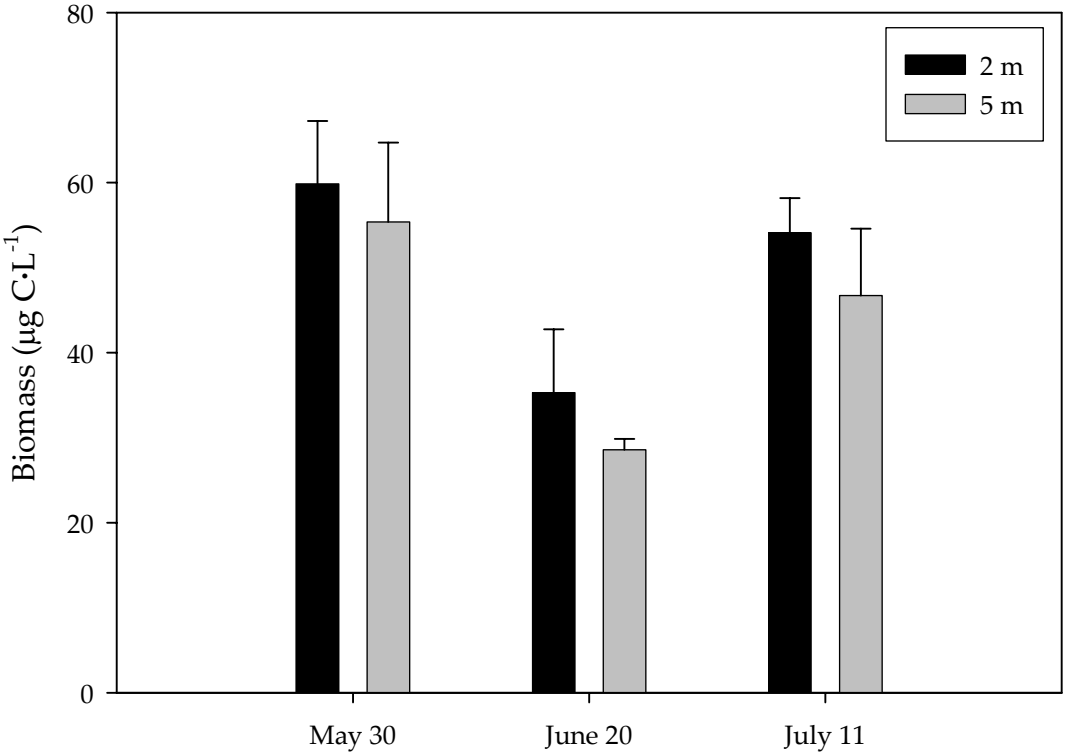

Figure 9. Biomass of flagellates at 2 and 5 m on each grazing experiment date. Error bars are standard error of the mean.

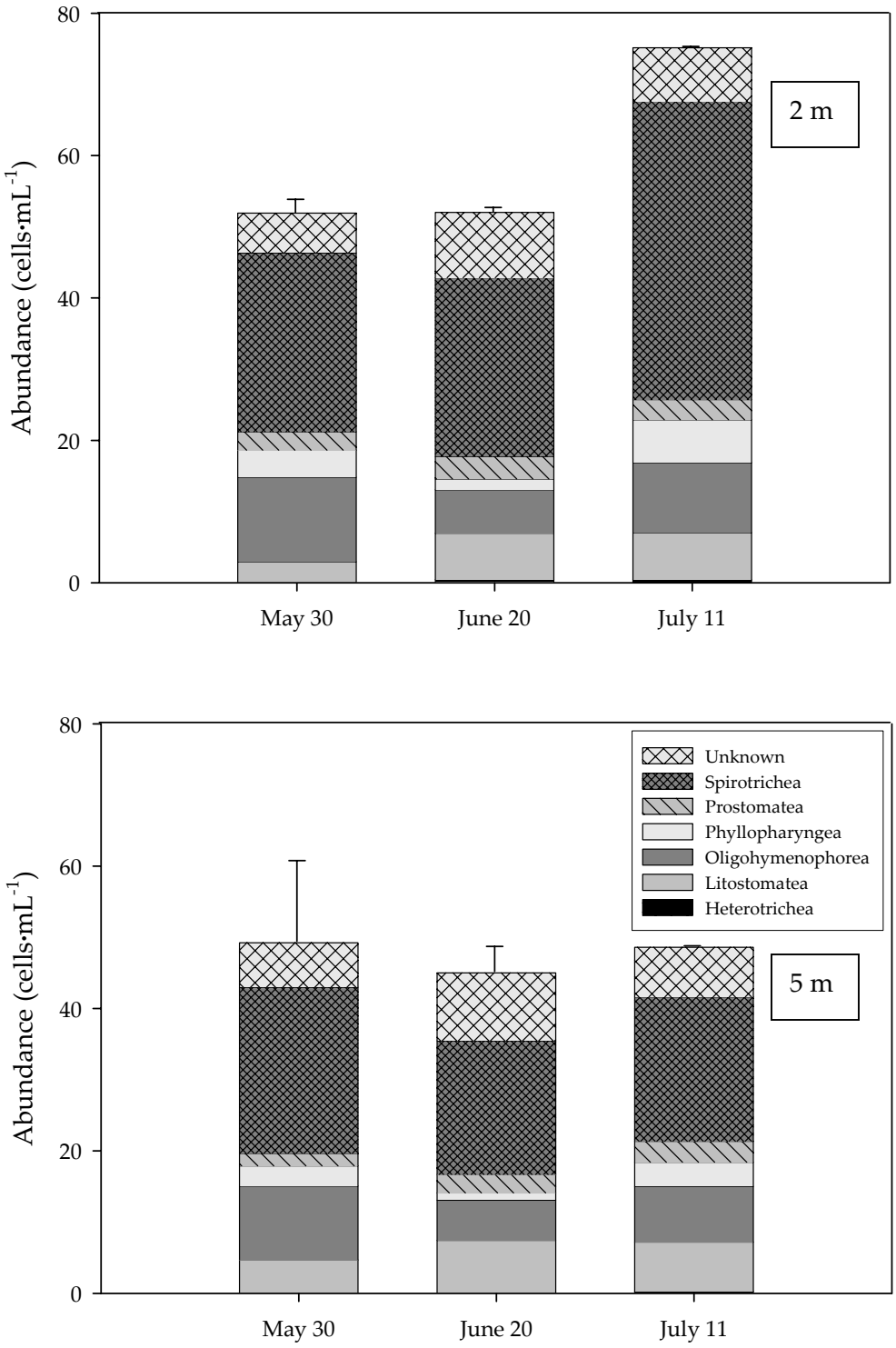

Figure 10. Ciliate abundance (cells·mL^{-1}) at 2 m and 5 m on each grazing experiment date. Error bars are standard error of the mean. At both depths abundance of Heterotrichea constituted less than 0.5 cells·mL^{-1} in May, June and July.

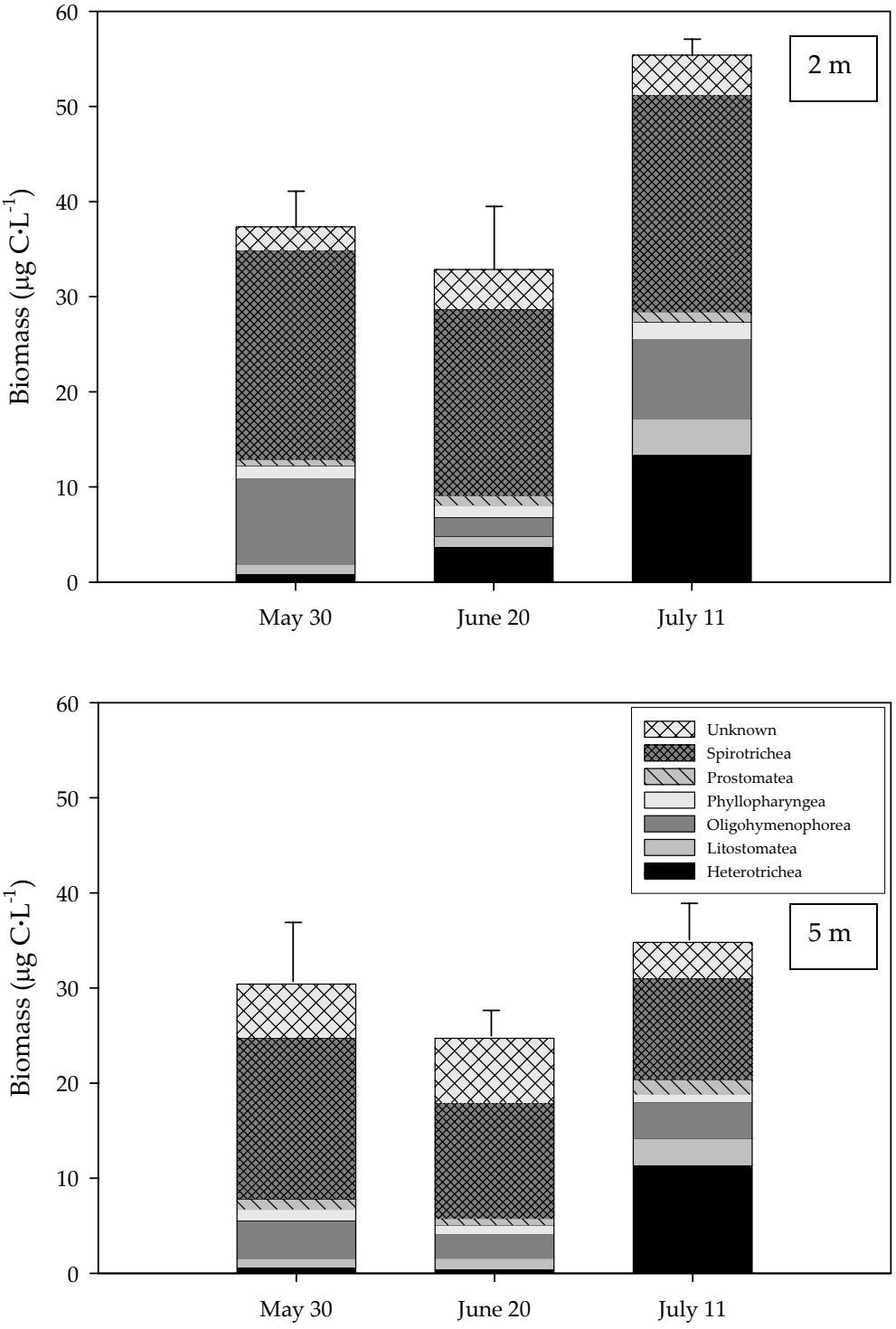

Figure 11. Ciliate biomass (µg C·L^{-1}) at 2 m and 5 m on each grazing experiment date. Error bars are standard error of the mean.

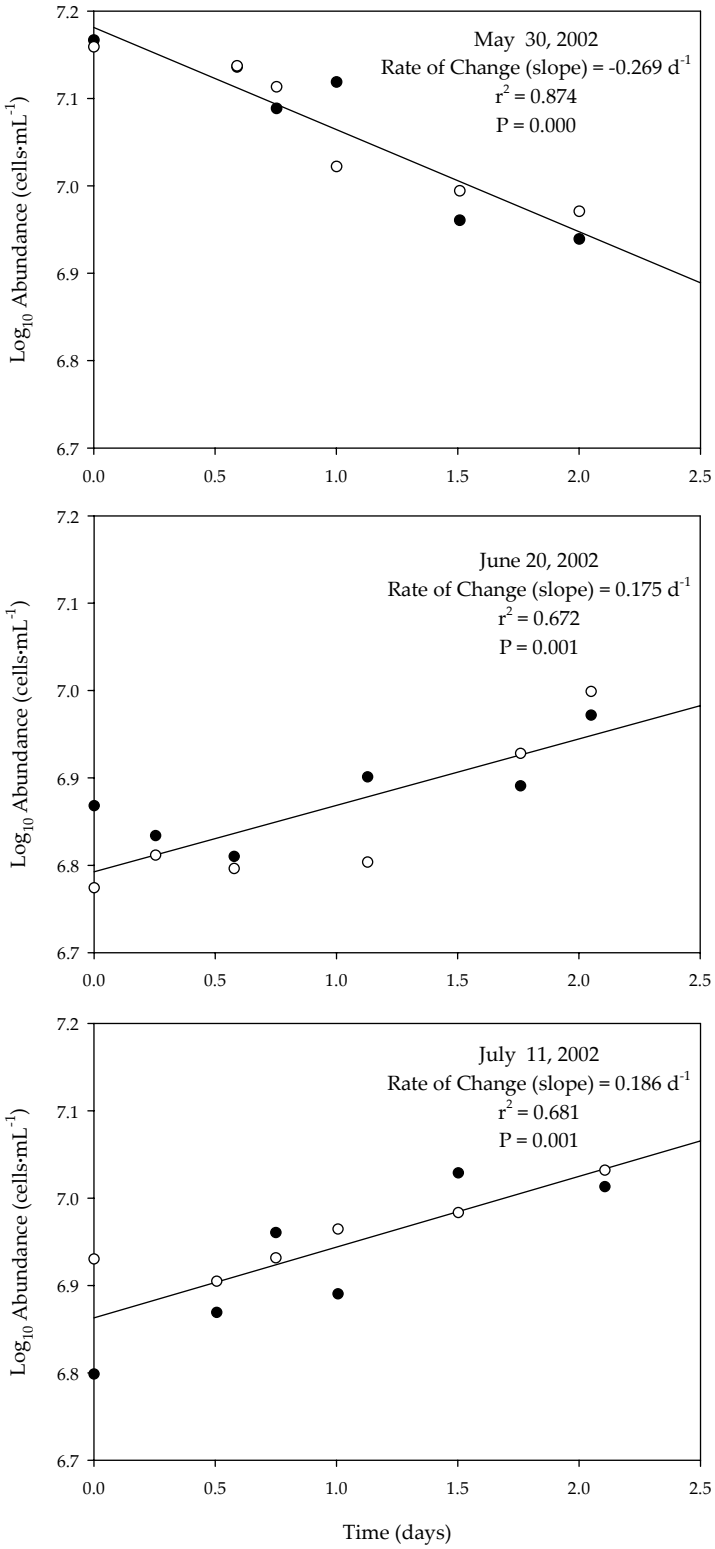

Figure 12. Picoplankton abundance versus time in 1-μm filtrates in May, June and July. Rate of change was determined from the slope of the regression line using the natural log. Open and closed circles are replicates.

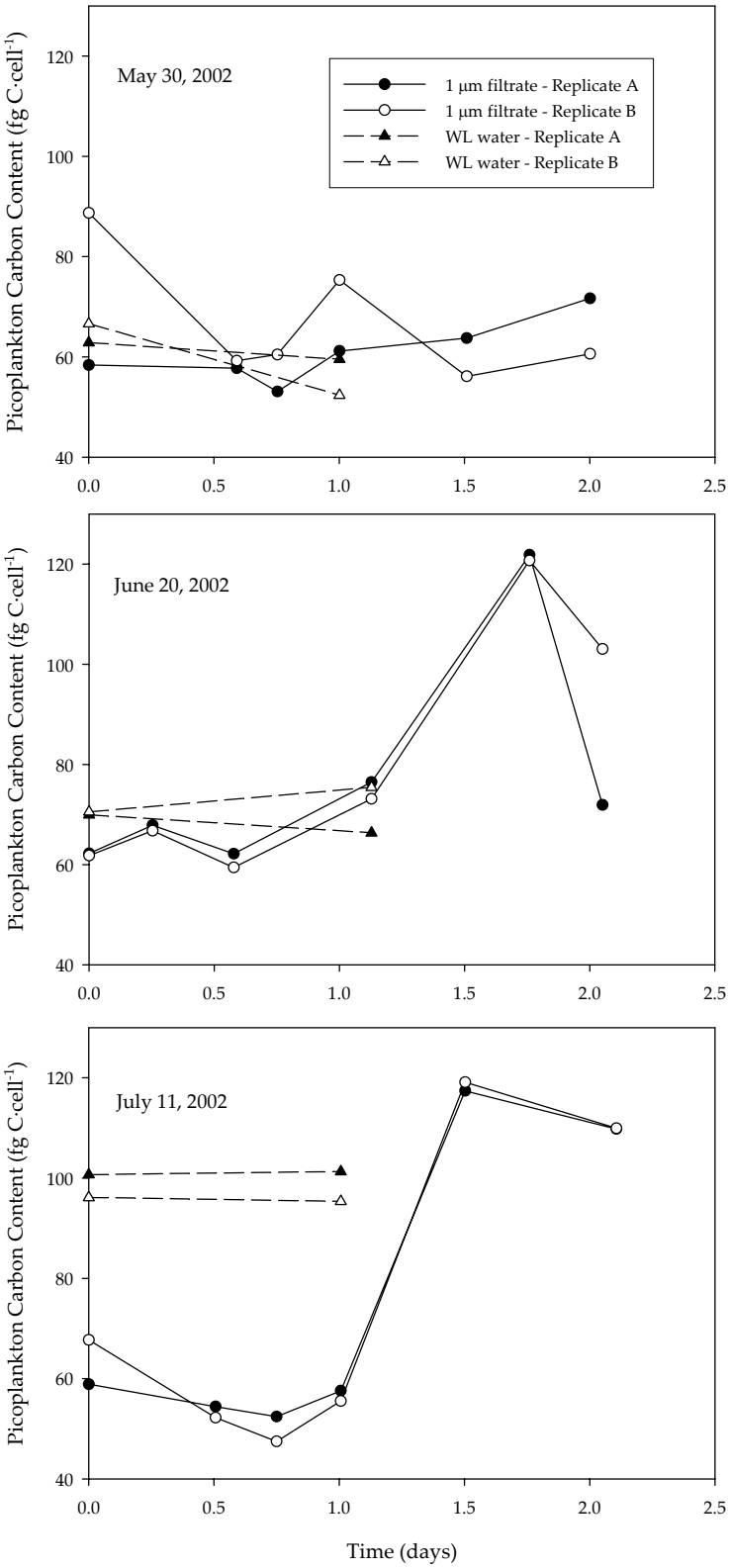

Figure 13. Change in picoplankton carbon content (fg C·cell^{-1}) in 1-µm filtrates and in whole lake water (WL water) in May, June and July, 2002. Open and closed circles are replicates.

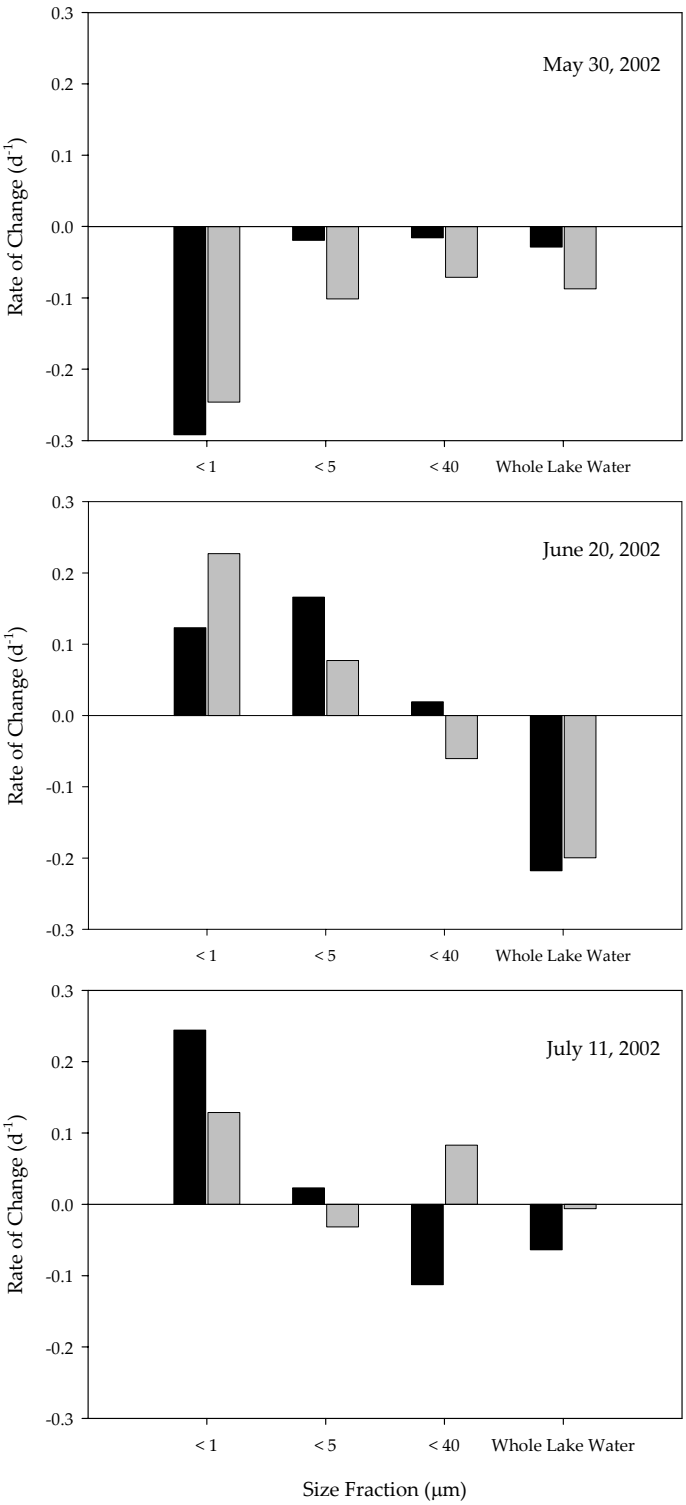

Figure 14. Rate of picoplankton population change by abundance in 1, 5 and 40-µm filtrates and whole lake water in May, June and July. Rate of change was determined from the regression slope of the natural logarithms of bacterial density in the 1-µm filtrate against time. Light and dark bars are replicates.

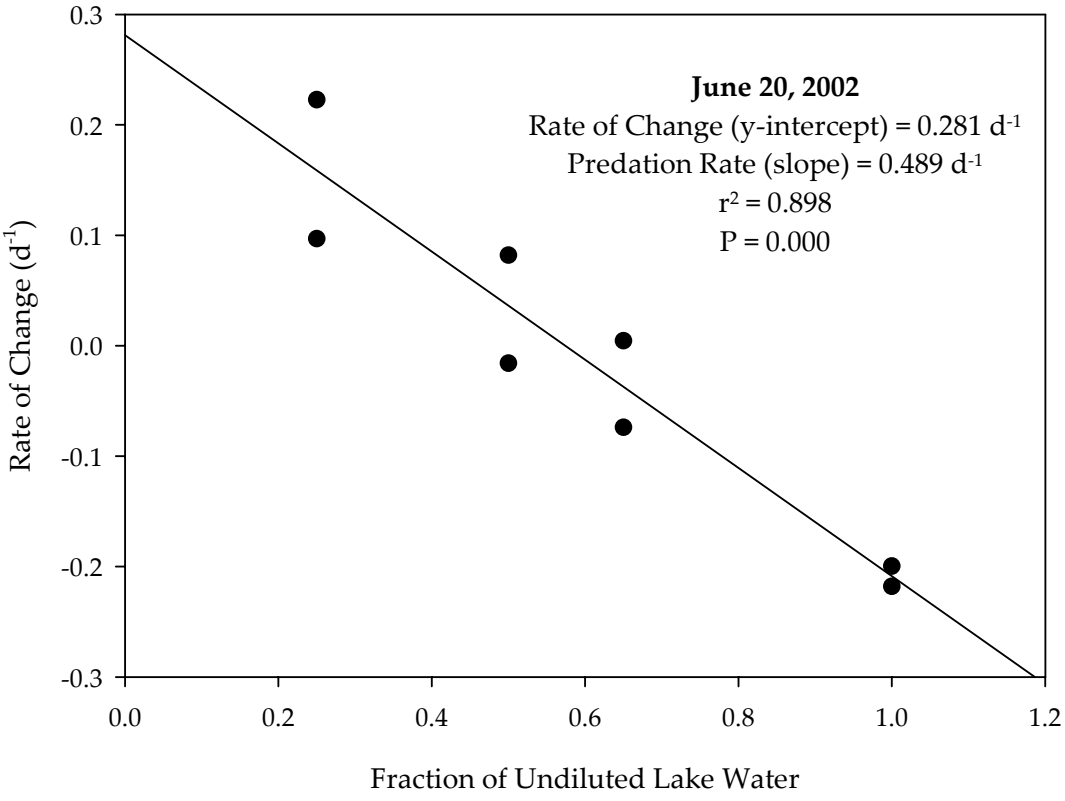

Figure 15. Rate of picoplankton population change as a function of dilution of whole lake water on June 20, 2002. Lake water was diluted with 0.7 μm lake water filtrate. Treatments were performed in duplicate.

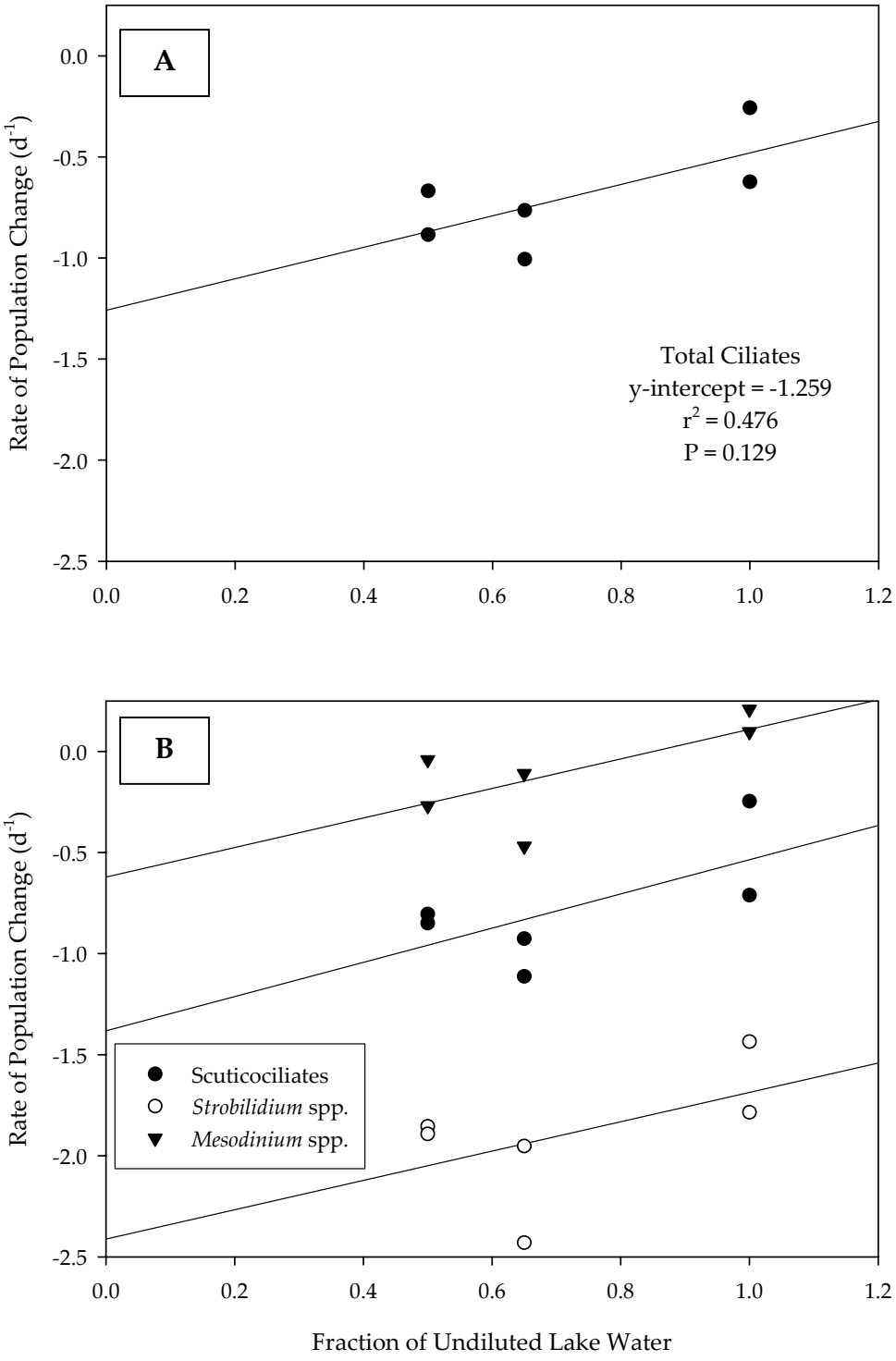

Figure 16. Rate of ciliate population change as a function of dilution of whole lake water on June 20, 2002, for total ciliates (A) and specific ciliate groups (B); scuticociliates (bacterivorous), *Strobilidium* spp. (algivorous and bacterivorous) and *Mesodinium* spp. (predacious). Lake water was diluted with 0.7 μm lake water filtrate. Lines are plotted by linear regression, but the slopes are not significantly different from zero.

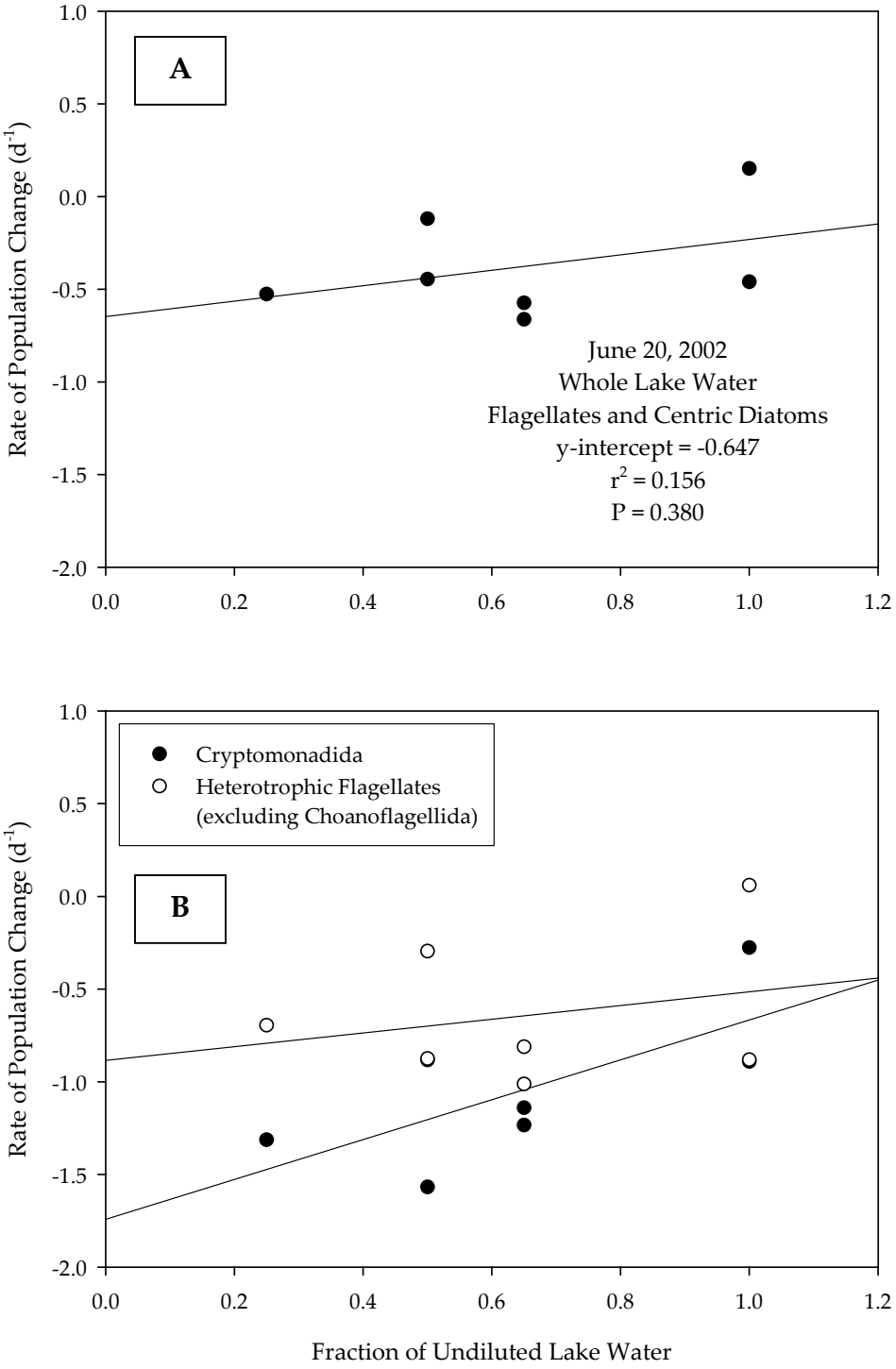

Figure 17. Rate of population change as a function of dilution of whole lake water on June 20, 2002 for flagellates (heterotrophic and autotrophic) and centric diatoms (A), as well for specific flagellate groups (B); Cryptomonadida and heterotrophic flagellates. Lake water was diluted with 0.7 μm lake water filtrate. Choanoflagellida are not included. Lines are plotted by linear regression, but the slopes are not significantly different from zero.

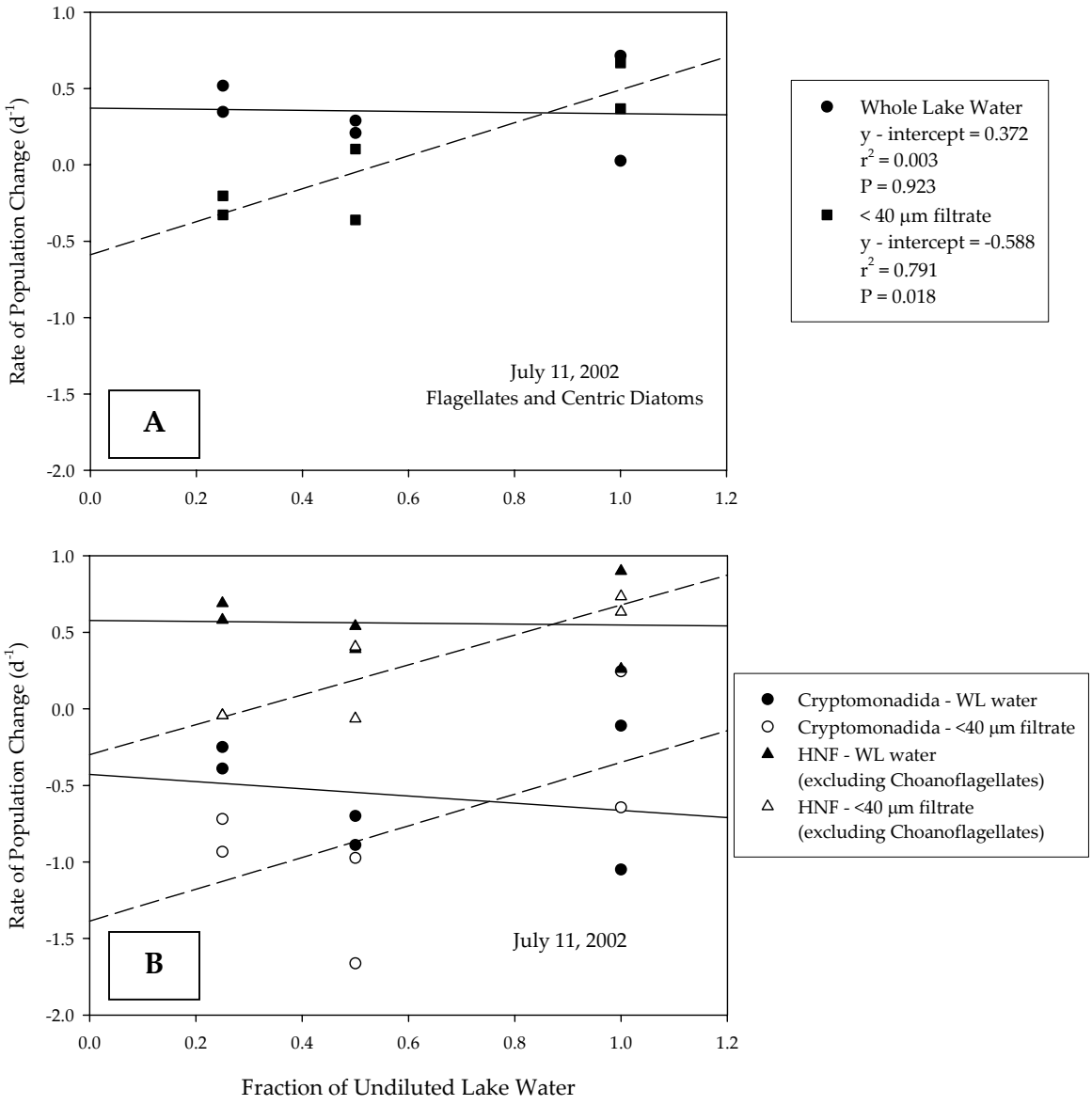

Figure 18. Rate of population change as a function of dilution of either whole lake water (solid lines) or in 40 µm filtrate (dashed lines) on July 11, 2002 for flagellates (heterotrophic and autotrophic) and centric diatoms (A), as well for specific flagellate groups (B); Cryptomonadida and heterotrophic nanoflagellates (HNF). Choanoflagellida are not included. The slopes for flagellates and centric diatoms, and HNF (excluding Choanoflagellida) in the 40 µm filtrates were significantly different from zero.

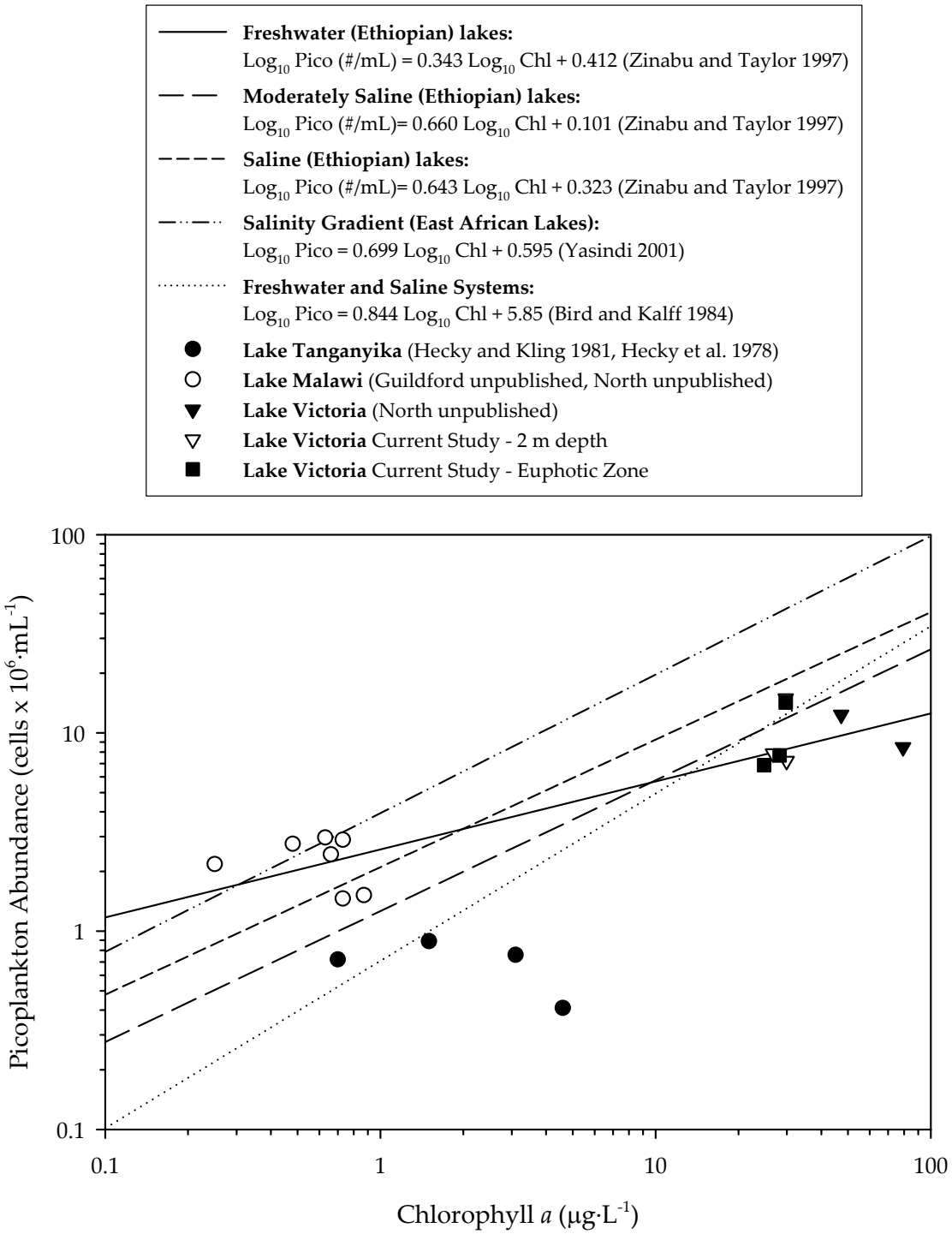

Figure 19. Picoplankton abundance versus chlorophyll *a* within the euphotic zone of the African Great Lakes. Regression lines for freshwater (Zinabu and Taylor 1997, Yasindi 2001), moderately saline and saline East African Lakes (Zinabu and Taylor 1997) and a regression line from freshwater and saline systems (Bird and Kalff 1984) are plotted on the graph. Data used to derive the regression lines are not included on the graph.

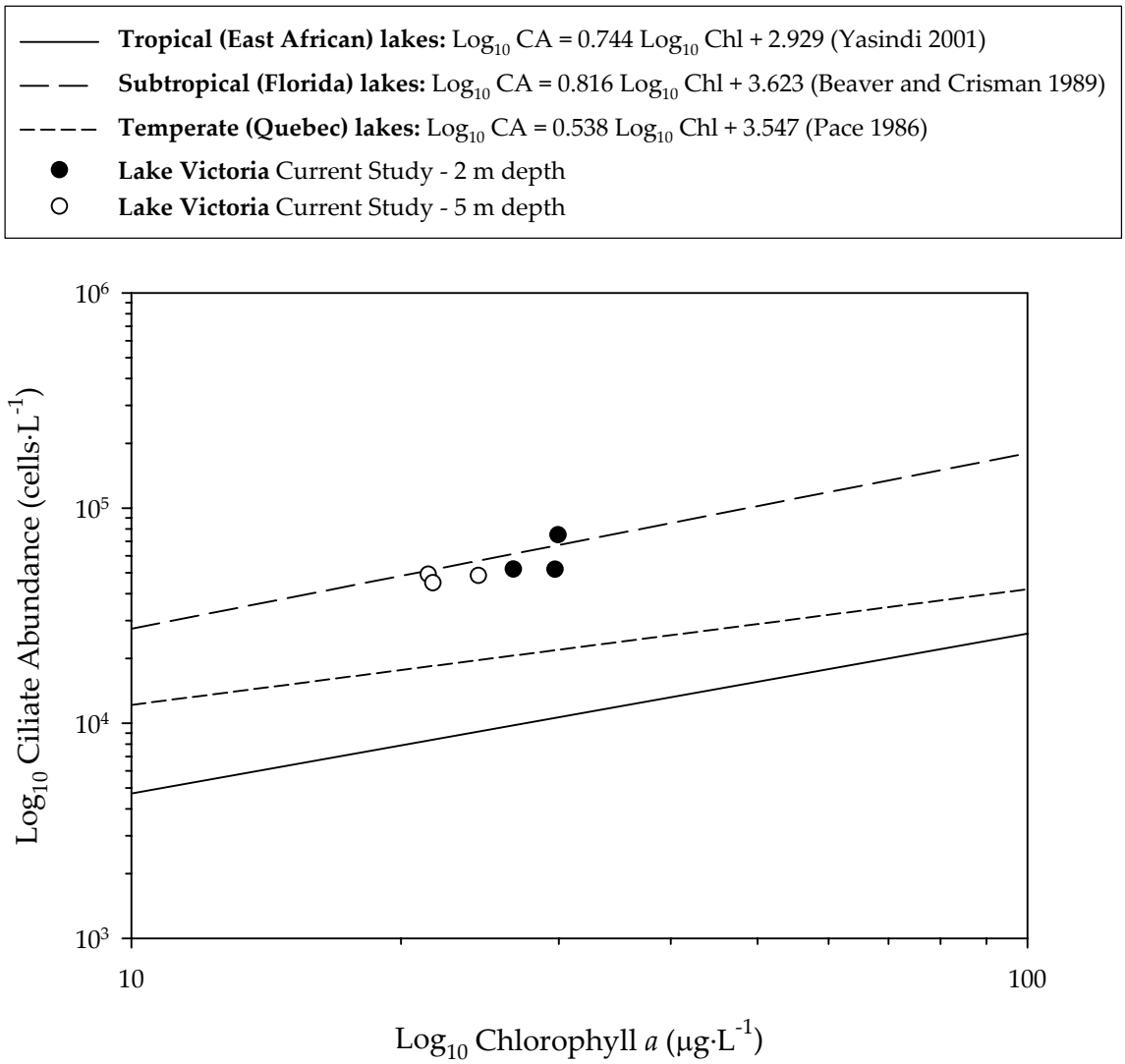

Figure 20. Ciliate abundance versus chlorophyll *a* in Napoleon Gulf, Lake Victoria. Regression lines for tropical lakes (East African lakes) by Yasindi 2001, subtropical lakes (Florida lakes) by Beaver and Crisman 1989 and temperate lakes (Quebec lakes) by Pace 1986 are plotted on the graph. Data used to derive the regression lines are not included on the graph. The tropical lake regression includes saline lakes.

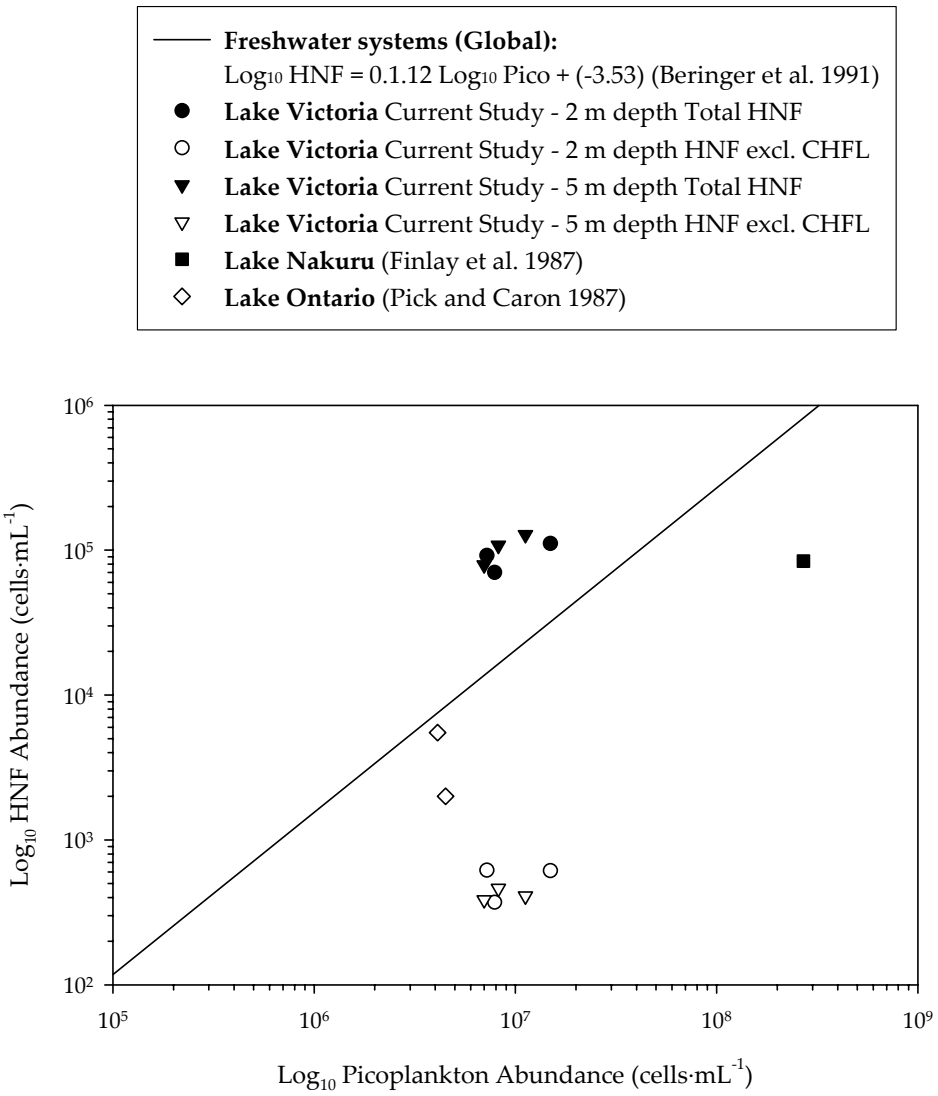

Figure 21. Heterotrophic nanoflagellate (HNF) abundance versus picoplankton abundance in Napoleon Gulf, Lake Victoria (East Africa), Lake Nakuru (Kenya) and Lake Ontario (North America). A regression line from freshwater systems worldwide is plotted on the graph (Berninger et al. 1991). Data used to derive the regression line are not included on the graph. Total HNF (including Choanoflagellida) and HNF excluding Choanoflagellida (HNF excl. CHFL) are plotted at 2m and 5m for Napoleon Gulf. Lake Ontario data points are the minimum and maximum values reported for the range in abundance of HNF and picoplankton.

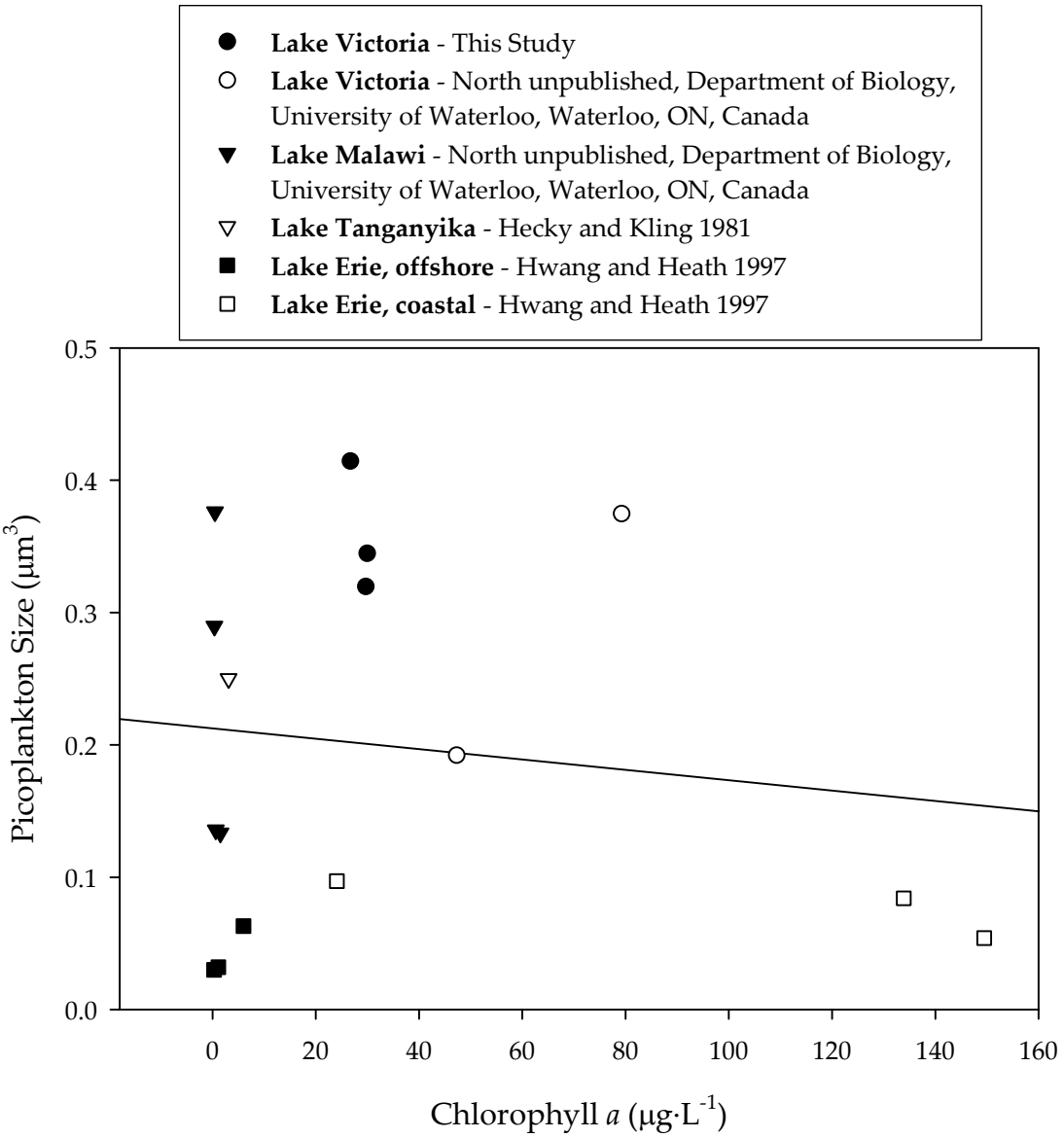

Figure 22. Picoplankton size (μm^3) versus chlorophyll *a* ($mg \cdot L^{-1}$) in the African and Laurentian Great Lakes.

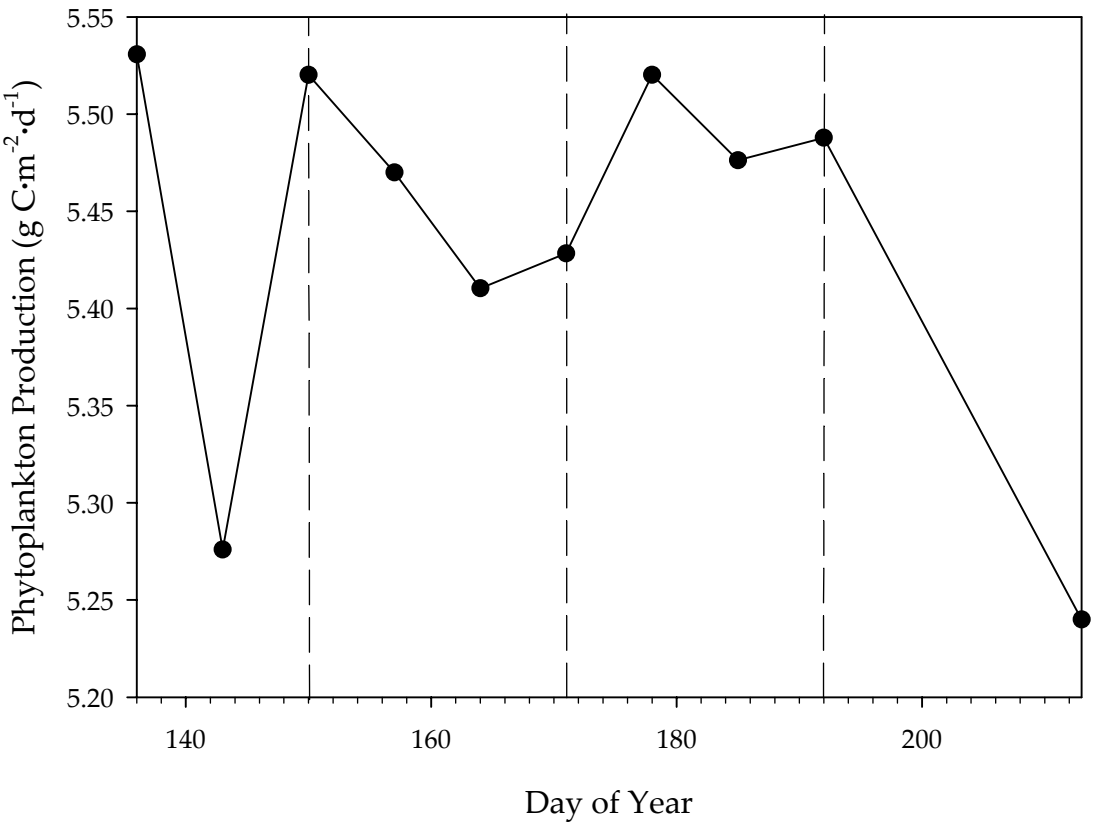

Figure 23. Phytoplankton production (g C·m^{-2}·d^{-1}) in Napoleon Gulf from May through August, 2002. Values were determined from an empirical model (Silsbe, 2004) using chlorophyll *a* (µg·L^{-1}) determined from each sample date. Dashed lines indicate when grazing experiments were performed. Note the small range in scale on the y-axis.

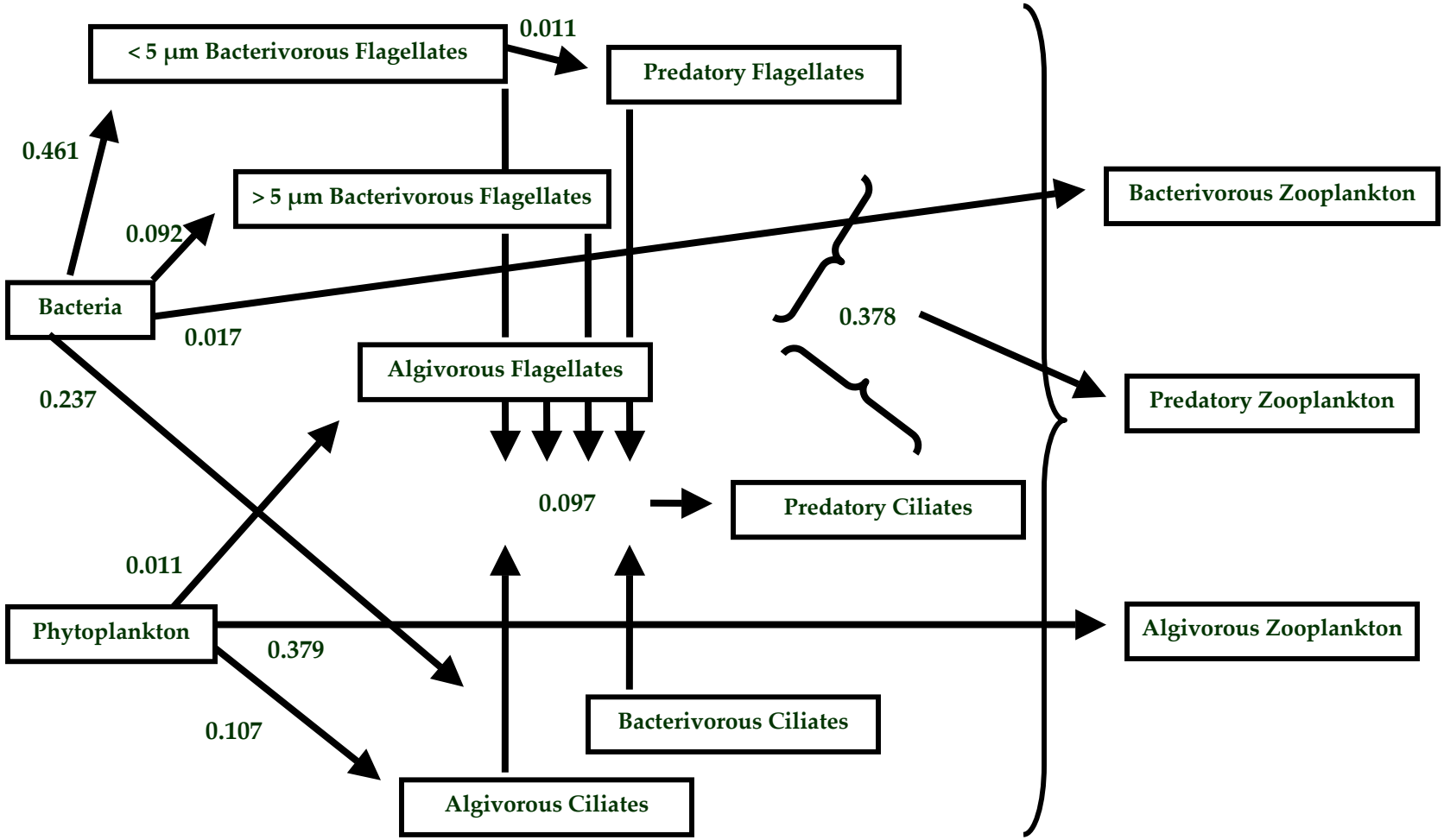

Figure 24. Hypothetical pathways for carbon flow (g C·m^{-2}·d^{-1}) in Napoleon Gulf on July 11, 2002 based on minimal carbon consumption requirements for each guild (Tables 43, 45 and 46). Carbon consumption is based on 50% carbon conversion efficiency.

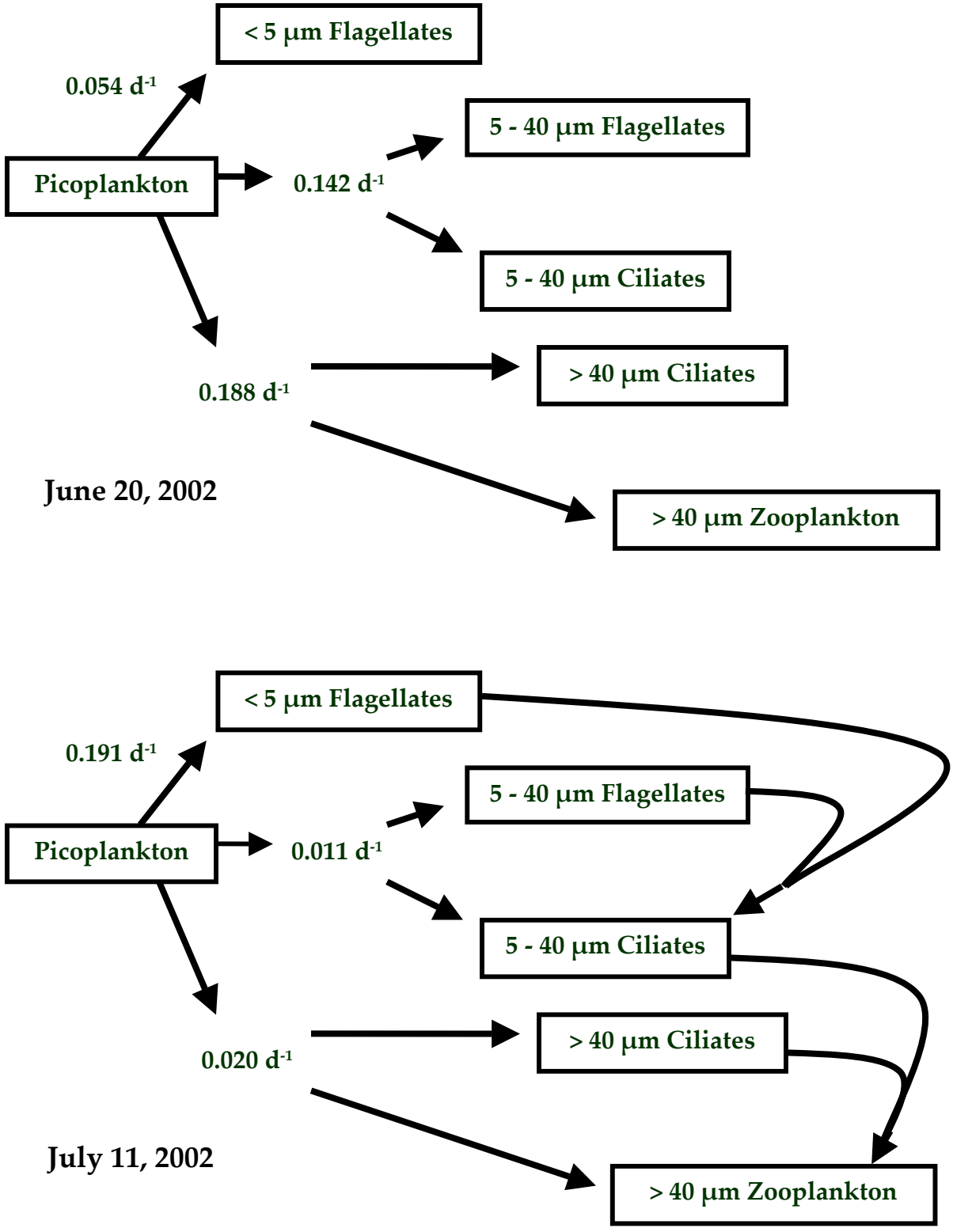

Figure 25. Pathways of carbon flow based on size fractions experiments on June 20 and July 11, 2002 (Tables 26, 27 and 29).

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Appendix

Table 49. Chlorophyll *a* (± 95% C.I.) at discrete depths between May and August 2002. Calculated according to Talling and Driver (1963). Based on 3 replicates except in 2 cases (N = 2) marked by *.

Date (Day of Year)	Depth (m)	Chlorophyll *a* > 0.7 μm ($\mu g \cdot L^{-1}$)
16/05/02 (136)	1-1.5	36.3
23/05/02 (143)	1	22.4
	5	25.9
	10	20.0
30/05/02 (150)	2	37.1
	5	26.9
	10	17.1
06/06/02 (157)	2	31.9
	5	31.5
	10	23.7
13/06/02 (164)	0	28.7
	2	30.0
	5	28.5
	10	25.9
20/06/02 (171)	0	30.4
	2	29.1
	5	24.7*
	10	19.3
27/06/02 (178)	0	39.5
	2	35.6
	5	34.7
	10	26.5
04/07/02 (185)	0	32.2
	2	29.5
	5	26.1
	10	21.5
11/07/02 (192)	0	32.2
	2	33.7
	5	29.1
	10	23.2
01/08/02 (213)	0	20.1
	2	22.8*
	5	20.4
	10	20.5

Table 50. Ciliate biovolume (x 10^3 μm^3 ± C.I.) on each of the three grazing experiment dates. R = replicate; N.A. = not applicable (N < 2); N.D. = not determined.

Genus	R	May		June		July	
Stentor A	A	438.07 ±	561.35 *	438.07 ±	561.35 *	438.07 ±	561.35 *
	B						
Stentor B	A	48.69 ±	9.97 *	44.76 ±	8.36**	48.69 ±	9.97 *
	B						
Askenasia	A	3.40 ±	2.05 *	3.40 ±	2.05 *	3.40 ±	2.05 *
	B						
Didinium	A	38.18 ±	N.A. *	38.18 ±	N.A. *	38.18 ±	N.A. *
	B						
Dileptus	A	105.89 ±	520.11 *	105.89 ±	520.11 *	105.89 ±	520.11 *
	B						
Lagenophrya A	A	1.14 ±	0.19**	1.00 ±	0.23**	0.88 ±	0.22**
	B						
Lagenophrya B	A	3.04 ±	0.47 *	2.46 ±	0.83**	3.51 ±	0.67**
	B						
Lagenophrya C	A	32.02 ±	15.63 *	32.02 ±	15.63 *	32.02 ±	15.63 *
	B						
Mesodinium A	A	0.32 ±	0.02 *	0.30 ±	0.03 •	0.31 ±	0.05 •
	B			0.35 ±	0.06 •	0.28 ±	0.06 •
Mesodinium B	A	2.07 ±	0.37 *	2.06 ±	0.42**	2.07 ±	0.37 *
	B						
Monodinium	A	1.07 ±	0.16 *	1.07 ±	0.16 *	0.97 ±	0.22**
	B						
Unknown	A	0.51 ±	0.05 *	0.53 ±	0.08**	0.49 ±	0.12 •
	B					0.52 ±	0.07 •
Pleuronema	A	2.40 ±	0.40 *	2.67 ±	0.80**	2.40 ±	0.40 *
	B						
Scuticociliate A	A	1.24 ±	0.23 •	1.28 ±	0.18 •	1.09 ±	0.23 •
	B	1.42 ±	0.31 •	1.32 ±	0.22 •	1.24 ±	0.18 •
Scuticociliate B	A	0.35 ±	0.04 •	0.28 ±	0.03 •	0.31 ±	0.08 •
	B	0.39 ±	0.07 •	0.33 ±	0.10 •	0.33 ±	0.05 •
Scuticociliate C	A	0.51 ±	0.08 •	0.54 ±	0.06 *	0.54 ±	0.06 *
	B	0.55 ±	0.09 •				
Vorticella A	A	2.05 ±	0.20 •	1.78 ±	0.33**	1.98 ±	0.24**
	B	2.41 ±	0.20 •				
Vorticella B	A	4.88 ±	1.36 •	5.84 ±	2.07**	9.41 ±	2.78 •
	B	8.51 ±	2.04 •			6.02 ±	1.84 •
Vorticella C	A	43.27 ±	7.01**	46.73 ±	6.11 *	49.88 ±	10.64**
	B						
Vorticella D	A	N.D. ±	N.A. *	N.D. ±	N.A. *	N.D. ±	N.A. *
	B						
Vorticella E	A	1.09 ±	0.89 *	1.09 ±	0.89 *	1.09 ±	0.89 *
	B						
Dysteria	A	1.32 ±	0.18 •	1.50 ±	0.73**	1.04 ±	0.10 •
	B	1.37 ±	0.23 •			1.07 ±	0.17 •

Genus	R	May		June		July	
Periacineta	A	N.D. ±	N.A. *	N.D. ±	N.A. *	N.D. ±	N.A. *
	B						
Phascolodon	A	5.41 ±	0.91 *	6.38 ±	1.01**	5.02 ±	1.80**
	B						
Sphaerophrya	A	7.13 ±	7.81 *	7.13 ±	7.81 *	7.13 ±	7.81 *
	B						
Suctorian	A	11.32 ±	N.A. *	11.32 ±	N.A. *	11.32 ±	N.A. *
	B						
Coleps	A	4.28 ±	1.00**	3.39 ±	0.58 •	4.23 ±	1.49 •
	B			3.92 ±	0.98 •	4.00 ±	1.14 •
Unknown	A	0.20 ±	0.04 *	0.17 ±	0.04**	0.22 ±	0.07 *
	B						
Urotricha	A	0.41 ±	0.26 •	0.52 ±	0.18 •	0.41 ±	0.13 •
	B	0.33 ±	0.07 •	0.45 ±	0.15 •	0.45 ±	0.14 •
Halteria A	A	0.95 ±	0.08 •	0.73 ±	0.09**	0.69 ±	0.07 •
	B	0.72 ±	0.06 •			0.71 ±	0.05 •
Halteria B	A	2.31 ±	0.23 •	1.50 ±	0.23 •	1.64 ±	0.24 •
	B	1.66 ±	0.21 •	2.10 ±	0.25 •	1.67 ±	0.21 •
Halteria C	A	4.67 ±	1.63**	5.22 ±	2.20**	4.06 ±	1.05 •
	B					3.44 ±	0.27 •
Halteria D	A	161.43 ±	N.A. *	161.43 ±	N.A. *	161.43 ±	N.A. *
	B						
Strobilidium A	A	0.73 ±	0.12 •	0.82 ±	0.15 •	0.68 ±	0.13 •
	B	0.80 ±	0.12 •	0.76 ±	0.11 •	0.60 ±	0.08 •
Strobilidium B	A	0.69 ±	0.19**	0.74 ±	0.07 •	0.61 ±	0.06 •
	B			0.60 ±	0.05 •	0.63 ±	0.06 •
Strobilidium C	A	13.88 ±	6.07**	4.18 ±	1.17 •	6.52 ±	2.14 •
	B			10.82 ±	5.29 •	8.72 ±	3.86 •
Strombidium A	A	11.05 ±	1.25**	14.31 ±	2.10 •	9.21 ±	1.42 •
	B			12.40 ±	1.61 •	10.75 ±	1.56 •
Strombidium B	A	34.54 ±	5.82**	28.58 ±	4.90**	28.48 ±	8.02**
	B						
Strombidium C	A	46.16 ±	9.09**	46.93 ±	5.85 *	46.93 ±	5.85 *
	B						
Tinntinidium A	A	3.95 ±	0.45**	4.46 ±	0.70**	4.40 ±	0.42 •
	B					4.86 ±	0.44 •
Tinntinidium B	A	3.34 ±	0.32 *	3.42 ±	0.74**	3.11 ±	0.52 •
	B					3.56 ±	0.78 •
Tinntinidium C	A	11.30 ±	26.98 *	11.30 ±	26.98 *	11.30 ±	26.98 *
	B						
Unknown A	A	53.88 ±	27.45 *	53.88 ±	27.45 *	53.88 ±	27.45 *
	B						
Unknown B	A	2.47 ±	0.64 •	1.73 ±	0.53 •	3.09 ±	1.00 •
	B	2.84 ±	1.12 •	3.18 ±	1.55 •	2.84 ±	0.71 •
Unknown C	A	0.31 ±	0.04 •	0.32 ±	0.03 •	0.36 ±	0.04 •
	B	0.30 ±	0.05 •	0.36 ±	0.05 •	0.32 ±	0.04 •

*Biovolume determined by averaging biovolume values from the 3 grazing dates
**Biovolume determined by averaging values from replicates on respective grazing dates
•Biovolume values determined by averaging values from individual replicates on respective grazing dates

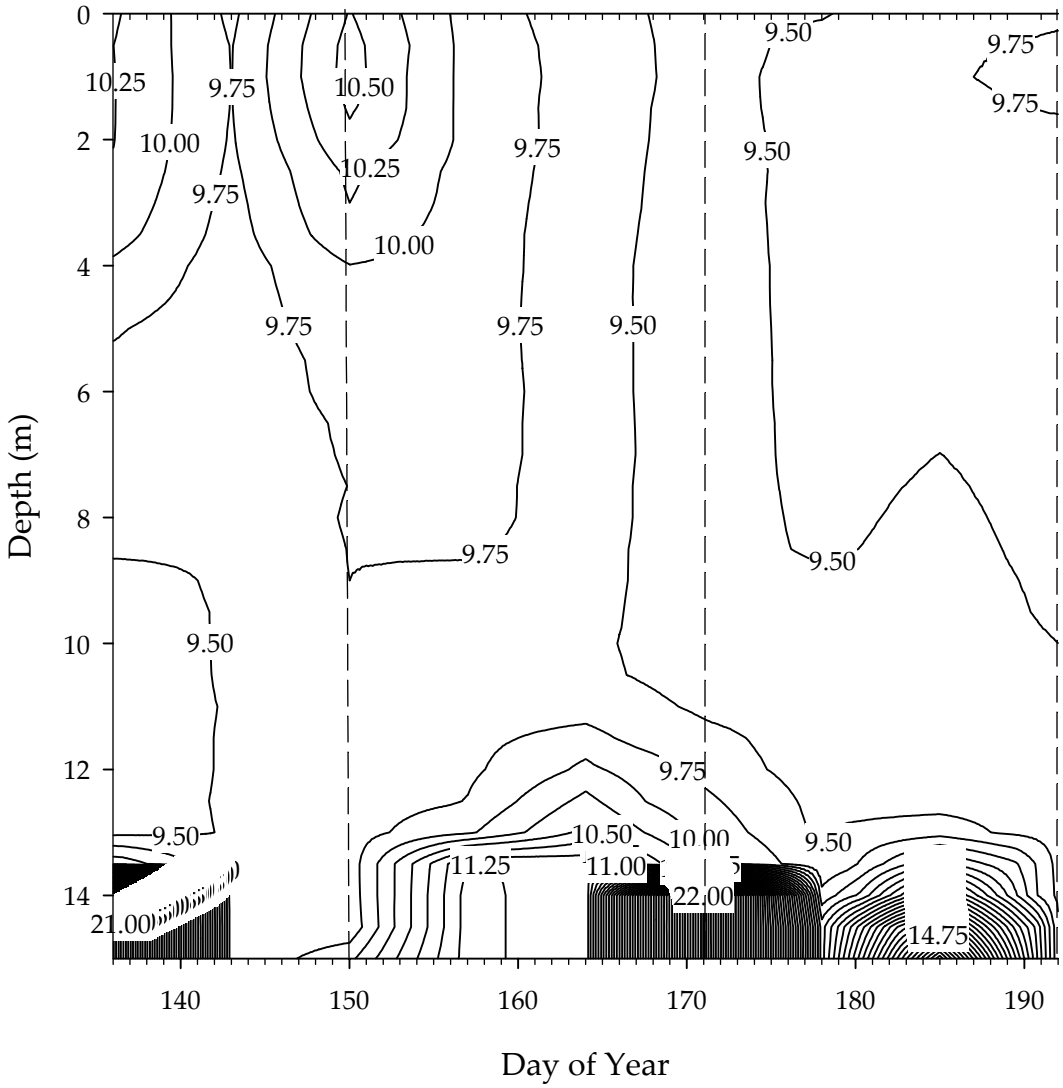

Figure 26. Water column conductivity (μS·mm^{-1}) during the period of sample collection, 2002; based on weekly sampling. Dates when grazing experiments were performed are marked with dashed lines.