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The role of ciliates, heterotrophic dinoflagellates and copepods in structuring spring plankton communities at Helgoland Roads, North Sea

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Abstract Mesocosm experiments coupled with dilution grazing experiments were carried out during the phytoplankton spring bloom 2009. The interactions between phytoplankton, microzooplankton and copepods were investigated using natural plankton communities obtained from Helgoland Roads (54°11.3′N; 7°54.0′E), North Sea. In the absence of mesozooplankton grazers, the microzooplankton rapidly responded to different prey availabilities; this was most pronounced for ciliates such as strombidiids and strobilids. The occurrence of ciliates was strongly dependent on specific prey and abrupt losses in their relative importance with the disappearance of their prey were observed. Thecate and athecate dinoflagellates had a broader food spectrum and slower reaction times compared with ciliates. In general, high microzooplankton potential grazing impacts with an average consumption of 120% of the phytoplankton production (P_p) were measured. Thus, the decline in phytoplankton biomass could be mainly attributed to an intense grazing by microzooplankton. Copepods were less important phytoplankton grazers consuming on average only 47% of P_p. Microzooplankton in turn contributed a substantial part to the copepods' diets especially with decreasing quality of phytoplankton food due to nutrient limitation over the course of the bloom. Copepod grazing rates exceeded microzooplankton growth, suggesting their strong top-down control potential on microzooplankton in the field.

Selective grazing by microzooplankton was an important factor for stabilising a bloom of less-preferred diatom species in our mesocosms with specific species (*Thalassiosira* spp., *Rhizosolenia* spp. and *Chaetoceros* spp.) dominating the bloom. This study demonstrates the importance of microzooplankton grazers for structuring and controlling phytoplankton spring blooms in temperate waters and the important role of copepods as top-down regulators of microzooplankton.

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Introduction

Since Azam et al. (1983) introduced the term "microbial loop", microzooplankton has received ever increasing attention as an important structural and functional group in planktonic ecosystems. Indeed, microzooplankton is one of the major functional groups in microbial food webs (Landry and Calbet 2004) and links the smaller planktonic unicellular organisms with higher metazoan trophic levels (Sherr et al. 1986; Gifford and Dagg 1988; Stoecker and Capuzzo 1990). It contributes substantially to mesozooplankton diets (Kleppel 1993). Furthermore, microzooplankton facilitates the rapid recycling of nutrients back to primary producers (Calbet and Saiz 2005; Irigoien et al. 2005). Microzooplankton is both prey and competitor for mesozooplankton. A literature synthesis by Landry and Calbet (2004) revealed that microzooplankton grazing can account for 60–75% of the mortality of phytoplankton production across a spectrum of open ocean and coastal systems and therefore may exert a stronger grazing pressure on phytoplankton than copepods (Sherr and Sherr 2007). During bloom events, unicellular microzooplankton can respond quickly to increasing phytoplankton availability (Johansson et al. 2004; Aberle et al. 2007) with cell division rates in the same range as those of its prey. The

combination of its faster metabolism and higher production compared to mesozooplankton (Fenchel and Finlay 1983; Müller and Geller 1993; Montagnes and Lessard 1999) with no egg and larval stages allows microzooplankton a rapid and direct response to prey availability when compared to mesozooplankton competitors.

The success of any phytoplankton species depends on having a gross growth rate that exceeds the losses due to physical (e.g. advection, mixing) and biological factors (notably predation). In combination with abilities that allow competitive advantage against other phytoplankters (e.g. higher maximum growth rate, higher substrate affinities, higher photosynthetic efficiency) even small differences in any of these factors can have profound effects explaining competitive advantage in growth capacity (Flynn 2008).

Irigoien et al. (2005) proposed that phytoplankton blooms occur when an external perturbation (e.g. more light and nutrients) breaks down the equilibrium in the formerly stable system by promoting better growth conditions and opens a "loophole" in the microbial loop. The improved growth conditions at the onset of a bloom allow phytoplankton species to escape predation pressure by microzooplankton. At this time, stocks and total grazing rates of herbivorous protists are not sufficiently high enough to suppress bloom formation (Sherr and Sherr 2009). In fact, total exclusion from grazing is not required for a particular phytoplankton species for the formation of a bloom; only a positive difference between growth rate and grazing rate resulting in positive net growth, while phytoplankton competitors may remain controlled by zooplankton grazing.

According to Irigoien et al. (2005), these loopholes for phytoplankton blooms are widened by the combined effects of (1) mesozooplankton predation on microzooplankton and (2) inter-microzooplankton predatory activity and thus grazing reduction on phytoplankton (trophic cascade effect) and (3) defence mechanisms (e.g. size, colony–formation, toxicity, spines) and (4) bad nutritional status of the algae and thus consequently predator avoidance (de-selection effect). The latter presupposes that predators can actively choose their prey and show preference or avoidance tactics for specific prey items.

Foraging strategies are fundamental to trophic ecological considerations, e.g., trophic cascade effects, and some copepod species, for example, are known to choose specific food actively related to taxonomic differences of the prey (Gentsch et al. 2009), prey size (Paffenhöfer 1988), nutrient composition of the prey (Cowles et al. 1988) and related to their own life stages (Mauchline 1998). There is also evidence for selective feeding by microzooplankton species (Verity 1991) regarding particle size or taxonomic differences of the prey (Fenchel 1980; Stoecker et al. 1981; Jonsson 1986; Hansen 1992; Hamels et al. 2004). However,

our knowledge on microzooplankton food selectivity is scarce in contrast to knowledge on selective feeding of mesozooplankton. This is attributed to methodological difficulties associated with ecological work on planktonic microzooplankton. Most microzooplankton species are fragile, not easy to handle and difficult to culture (Gifford 1985). Hence, laboratory investigations on feeding behaviour have focused on easily cultivable species.

Given the diverse feeding modes even within the microzooplankton community (Tillmann 2004), food preference and selectivity are also likely to be highly diverse in this group of grazers. As there is still only little knowledge on the cumulative influence of those factors on phytoplankton bloom assemblages (Brussaard et al. 1995; Aberle et al. 2007), investigations on microzooplankton grazing under conditions as close to nature as possible are imperative. In this context, special emphasis should be placed on interspecific interactions in the plankton as well as the total effect of changes in selectivity of the present grazers.

Our investigations focused on North Sea spring plankton communities at Helgoland Roads. Although this station has been sampled for plankton since 1962, the microzooplankton has only recently been investigated more thoroughly (Löder 2010). With their year-round occurrence and high biomass in the plankton at Helgoland Roads (Löder et al. 2011), heterotrophic protists can be expected to play an important role as phytoplankton grazers. In this study, we hypothesise that: (1) microzooplankton with its various feeding modes can have a considerable impact on phytoplankton spring blooms, which is potentially higher than the impact of copepods, (2) selective grazing by microzooplankton leads to blooms of less-preferred phytoplankton species, (3) microzooplankton succession in spring can be directly linked to the availability of different prey and (4) microzooplankton contributes substantially to copepods' diets, and copepods are therefore an important top-down control factor for herbivorous protists.

Materials and methods

We conducted a mesocosm experiment and simulated a natural spring bloom using in situ plankton communities from Helgoland Roads. Top-down control (e.g. copepod grazing) on microzooplankton can be severe (Sherr and Sherr 2009), especially in a restricted mesocosm environment, and can cause strong trophic cascade effects (Sommer et al. 2003; Sommer and Sommer 2006; Zöllner et al. 2009), thus hindering exclusive investigations on the direct effects of microzooplankton grazing on phytoplankton. We therefore excluded mesozooplankton grazers from the incubations. By relaxing microzooplankton from the grazing pressure of mesozooplankton, we could explicitly

examine the role of microzooplankton grazing on phytoplankton communities during the bloom. Grazing experiments for detailed investigations on microzooplankton grazing and selectivity were conducted at four defined points of the phytoplankton spring bloom: pre-bloom (exponential growth phase = experiment 1), bloom peak (biomass maximum = experiment 2), early post-bloom (1 week after biomass maximum = experiment 3) and later post-bloom (2 weeks after biomass maximum = experiment 4). The role of copepods in structuring the spring phyto- and microzooplankton community was also examined via measuring copepod grazing and selectivity during these distinct bloom phases.

Sampling site

Helgoland is located in the German Bight (Southern North Sea). It is subject to both coastal influences from the shallow Wadden Sea as well as marine influences from the open North Sea. Since 1962, water samples are taken workdaily as part of a long-term monitoring for plankton and nutrients at the "Kabeltonne" site at Helgoland Roads (54°11.3′N; 7°54.0′E) (Wiltshire et al. 2008). Water for the mesocosm experiment was taken at this site.

Set-up

The aim of the mesocosm experiment was to follow a typical spring plankton succession under near-natural conditions. The mesocosm experiment took place from mid-March until mid-April 2009 in a constant temperature room with a starting temperature of 4.2°C and a quick rise towards the end temperature of ∼6.8°C within a few days. The tanks were heated by the increasing room temperature. Start and end temperatures were close to in situ conditions (4.2°C/6.7°C). In contrast to the field where temperature increased almost linearly, the rise in temperature in the mesocosms was somewhat faster and 6.5°C were reached on day four of the experiment.

Three cylindrical mesocosms with a volume of 750 L each were filled with natural seawater from Helgoland Roads. Water was first repeatedly scooped from the water surface using an open 850-L container suspended from the crane of the research vessel Uthörn, and three 1,000-L containers were subsequently filled by hose via gravity feed. In order to remove mesozooplankton but to allow for the passage of chain-forming diatoms and microzooplankton, the water was screened over the feed using a 200-μm gauze bag connected to the end of the hose, which floated in the container during filling. Back on land, this water was transferred to the mesocosms again via gravity feed. Pumps were not used to ensure the survival of the whole plankton community and particularly delicate

organisms (Löder et al. 2010). The even distribution of the water from each container to the three mesocosms was ensured by an interconnected triple-split hose distributor mounted on the main hose. Thus, after the filling of each mesocosm, they contained identical over-wintering/spring populations of bacteria, phytoplankton and zooplankton smaller than 200 μm (microzooplankton).

The mesocosms were gently stirred by a propeller (107.5 rpm, 15 min on, then 15 min off). The propeller produced currents similar to that found in the field at Helgoland Roads (mean 0.6 m s^{-1}, max 1.2 m s^{-1}), ensured the continuous mixing of the water column and avoided sedimentation of the plankton. Light was provided by computer-controlled light units (Profilux II, GHL Groß Hard- and Software Logistics, Kaiserslautern, Germany) operated via an external control computer (Programme 'Prometheus', GHL, modified version 'Copacabana'). The light units were equipped with two different fluorescent tubes to obtain full light spectra ('Solar Tropic' and 'Solar Nature', JBL, Neuhofen, Germany), enabling the simulation of triangular light curves (see Sommer et al. 2007 for details). The light cycle and intensity was adjusted daily by the computer to account for changes in the photoperiod (same light cycle as in the field) during the experimental run according to the geographical position of Helgoland following the model by Brock (1981). A light intensity of 60% of surface irradiance without cloud cover was chosen, simulating the intensity of light at 1.50 m water depth with a light attenuation coefficient of 0.34 (5 m Secchi depth) under in situ conditions. Calculation of the light intensity was done via equations given by Tyler (1968) and Poole and Atkins (1929).

Stocking with natural inocula

During early seasonal succession, many planktonic organisms hatch from cysts, resting eggs or other resting stages at different times. Inoculating the mesocosms with one start community only would preclude the effects of later excystment or hatching. Therefore, to render similar successive patterns of the plankton in the mesocosms as in the field possible, we introduced a small inoculum of natural seawater from Helgoland Roads on a weekly basis. Five litres of 200 μm screened seawater was added to each mesocosm. An additional 15 L of filtered seawater (0.2 μm) were added to the mesocosms to compensate for evaporation and water removal due to the sampling for monitoring and experiments.

Sampling the mesocosms

Daily measurements of temperature, pH and in vivo fluorescence (chlorophyll *a*) (Algae Analyser, BBE

Moldaenke, Kiel, Germany) were conducted between 08:00 and 09:00 h. In addition to the daily measurements, three litres of each mesocosm were sampled and analysed every Monday, Wednesday and Friday and as well as on days with grazing experiments.

Silicate, phosphate and DIN (nitrite, nitrate and ammonia) were determined colorimetrically after filtration of at least 0.3 L of sample through 0.45-µm nylon filters (Falcon) following the methods of Grasshoff et al. (1999).

For the determination of phytoplankton species composition during the course of the experiment, 100 mL of the sample were subsampled into amber bottles and immediately fixed with neutral Lugol's iodine solution (final conc. 0.5%) (Throndsen 1978). For the determination of the microzooplankton, 250 mL were fixed with acid Lugol's iodine solution immediately (final conc. 2%) (Throndsen 1978). Samples were stored cool and dark. For phytoplankton species determination 25 mL and for microzooplankton 50 mL of the sample were settled in sedimentation chambers (HYDRO-BIOS) for 24 h, and one replicate per mesocosm (total n = 3) was counted under a Zeiss Axiovert 135 inverted microscope using the Utermöhl method (Utermöhl 1958).

Counting procedure for the samples of the grazing experiments was principally the same as for the succession in the mesocosms but with higher replication, i.e., the whole set of incubation bottles (see detailed description below) was sampled and one subsample of each sample was counted.

Phytoplankton (diatoms, phytoflagellates except dinoflagellates) and microzooplankton (ciliates, dinoflagellates and others) were identified where possible to genus or species level or, otherwise, pooled into size-dependent groups or "morphotypes" (see taxa in the detailed tables of the "Appendix"). It is known that most chloroplast-bearing dinoflagellates are capable of mixotrophic nutrition via phagotrophy (Du Yoo et al. 2009). Therefore, all dinoflagellate species were considered potentially heterotrophic and were assigned to the microzooplankton. For microzooplankton, the whole surface of the sedimentation chamber was counted at 200-fold magnification to reduce counting biases against rare species. Phytoplankton was counted according to the standard method applied for the Helgoland Roads long-term phytoplankton data archive (Wiltshire and Dürselen 2004; Wiltshire et al. 2008). The whole surface of the chamber, or at least 100 cells or chains per abundant taxon, were counted when enumeration was "in tracks". The identification of phytoplankton and dinoflagellates was primarily based on Dodge (1982), Tomas (1996) and Hoppenrath et al. (2009). Ciliates were determined based on Kahl (1932), Carey (1992) and Montagnes (2003).

Phytoplankton and microzooplankton net growth rates in the mesocosms were calculated using the exponential growth model and the abundance values from the monitoring (see section "Growth and grazing calculations").

Grazing experiments

Dilution experiments on microzooplankton grazing (Landry 1993; Landry and Hassett 1982) and bottle incubations with the copepod *Temora longicornis* were carried out simultaneously at four different times (as described earlier) of the phytoplankton bloom (Fig. 1c).

Microzooplankton grazing set-up

A stock of water for the purpose of dilution was collected at the same time as the mesocosms were filled. Water was filtered at low pressure through a pre-washed 0.45 + 0.2-µm sterile inline membrane filter capsule (Sartobran® 300, 300 cm²) after pre-filtering with a combination of 3-µm GFF + 0.2-µm membrane filter. The sterile water was stored in the dark in the thermo-constant room together with the mesocosms. Particle freeness was checked via flow cytometry (FACS Calibur, Becton & Dickinson) before each experiment started. Three exact dilutions of 10, 25, 50 and 100% of undiluted seawater from each mesocosm were prepared in carboys (Landry 1993). For the incubation, three 2.3-L polycarbonate bottles were gently filled with water from each dilution carboy (n = 36: 3 mesocosms × 4 dilution levels × 3 replicates). The Funnel-Transfer-Technique appropriate for ciliates (Löder et al. 2010) was used for filling purposes as these organisms are very sensitive to destruction by vigorous filling and mixing procedures (Landry 1993).

To prevent nutrient limitation biases in the microzooplankton grazing bottles, sterile filtered nutrient solutions (F/2 medium, Guillard and Ryther 1962) were added to the dilution series (Landry and Hassett 1982; Landry 1993) $(8 \times 10^{-4} \text{ mNO}_3, 1.3 \times 10^{-5} \text{ mPO}_4 \text{ and } 2.4 \times 10^{-5} \text{ mSiO}_2$, experiment 1 + 2 no SiO$_2$). One bottle of undiluted water per mesocosm was incubated without the addition of nutrients to serve as control for the nutrient addition.

Samples for initial concentrations of microzooplankton and phytoplankton (250 mL, acid Lugol's iodine solution, final conc. 2%) in the dilution experiments were obtained from the premix carboys of the dilution series in triplicate; after incubation for 24 h, each incubation bottle was sampled. Microzooplankton and phytoplankton concentration in the samples was estimated as described earlier.

Copepod grazing set-up

The best method to the objective of this study for the quantification of feeding rates of mesozooplankton on both
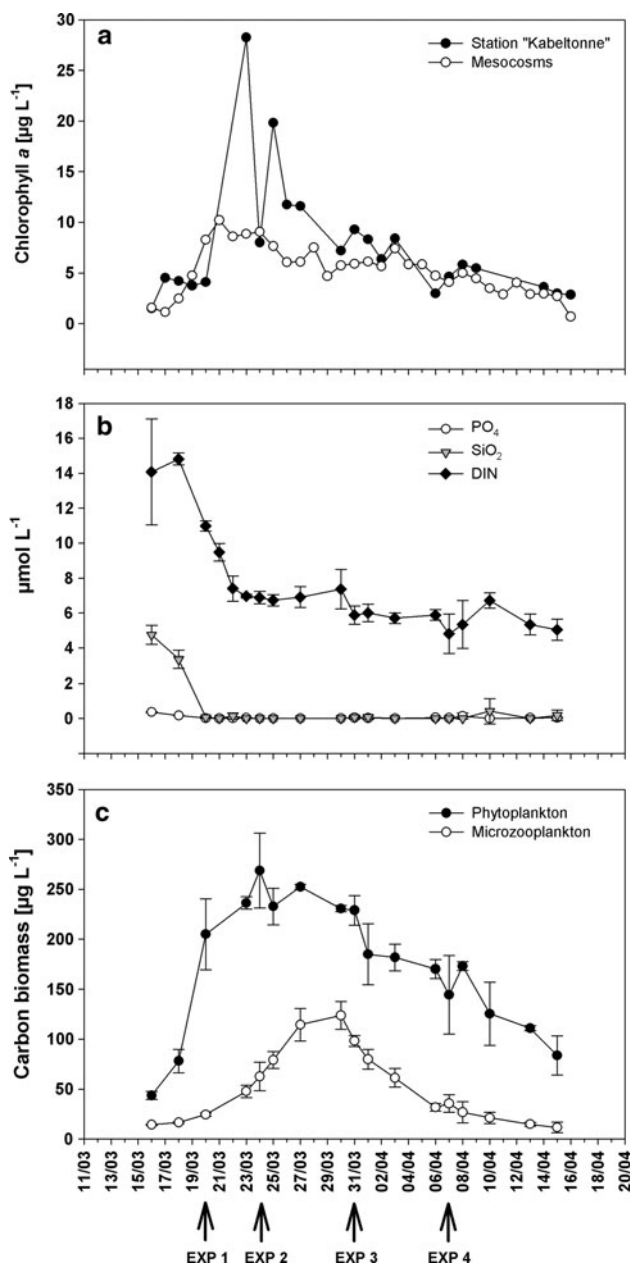
Fig. 1 Mean values of chlorophyll *a* (in situ fluorescence) in the mesocosms as compared to the field station "Kabeltonne" (**a**), development of nutrients in the mesocosms (**b**) as well as the development of phytoplankton and microzooplankton biomass during the mesocosm experiment (**c**), dates at which the grazing experiments were performed are marked with *arrows*, *error bars* correspond to one standard deviation ($n = 3$)

phytoplankton and non-pigmented microzooplankton was the analysis of particle removal in bottle incubations (Båmstedt et al. 2000). Because of interferences with microzooplankton grazing activity, especially when both micro- and mesozooplankton prey upon the same species, it is necessary to simultaneously estimate the microzooplankton grazing rates in separate dilution experiments

(Nejstgaard et al. 1997, 2001). Thus, for copepod grazing experiments three 2.3-L bottles per mesocosm (100% undiluted water with added nutrients) were filled from carboys prepared along with the dilutions, and 25 female copepods of the species *Temora longicornis* were added to each bottle (~ 11 copepod L^{-1}) ($n = 9$: 3 mesocosms $\times$ 3 replicates). This copepod concentration was at the upper limit of in situ densities in the period March–April (Greve et al. 2004).

The copepods were caught by vertical net hauls at Helgoland Roads and transferred to the laboratory immediately. Only actively swimming females of *T. longicornis* were sorted and acclimated to the mesocosm conditions for 24 h prior to the experiments.

Pre-condition of the copepods took place at the same temperature and light conditions as for the mesocosms in 3-L glass beakers containing mesocosm water. The 100% undiluted bottles in the dilution series served as a control for the *T. longicornis* grazing experiments. Sampling for plankton concentrations took place at the beginning of the *T. longicornis* grazing experiments and after 24 h as described for the microzooplankton grazing set-up. Plankton concentration in the samples was estimated as described earlier.

The whole set of incubation bottles (39 dilution series + 9 *T. longicornis* = 48 bottles) was incubated for 24 h on two plankton wheels (0.8 rpm) under the same light and temperature conditions as the mesocosms.

Biovolume and carbon calculation

Biovolume of each plankton species was calculated from the measurement of cell dimensions using geometric formulae according to Hillebrand et al. (1999). The cell volume was converted into carbon (C) according to the equations given by Menden-Deuer and Lessard (2000) for diatoms (pgC $cell^{-1} = 0.288 \times V^{0.811}$), dinoflagellates ($pgC$ $cell^{-1} = 0.760 \times V^{0.819}$) and all other protist plankton except ciliates (pgC $cell^{-1} = 0.216 \times V^{0.939}$), whereby V refers to cell volume in μm^3. Ciliate carbon was calculated using a conversion factor of 0.19 pgC μm^{-3} (Putt and Stoecker 1989). Rotifer carbon was estimated according to McCauley (1984) and Park and Marshall (2000): After a calculation of the biovolume by means of geometric formulae, this biovolume was converted to wet weight assuming a specific gravity of 1. Wet weight was then converted to dry weight by a factor of 0.1 and 50% of dry weight was assumed to be carbon. Carbon values for the copepod species *T. longicornis* were derived from measurements with an elemental analyser (EA 1110 CHNS-O, Thermo-Finnigan). The mean spring carbon content (10 μg carbon female^{-1}, March/April 2007,

n = 12; Schoo, K. L. unpublished data) of this copepod was used in this study.

Growth and grazing calculation: microzooplankton

Growth rates of phytoplankton species and grazing rates of the microzooplankton community were calculated using linear regressions of apparent phytoplankton growth (calculated at a taxon level, for phytoplankton groups as well as for the total phytoplankton community) against the dilution factor (Landry and Hassett 1982; Landry 1993). Start values for the diluted samples were calculated from the 100% undiluted samples according to their dilution factor. The growth of phytoplankton (day^{-1}) was described by the exponential growth model in Eq. (1):

$$C_{t_{24}} = C_{t_0} \times e^{(k-g) \times \Delta t} \tag{1}$$

whereby C_{t0} is the concentration of phytoplankton biomass at the beginning of the experiment, C_{t24} after 24 h, k is the phytoplankton growth coefficient, g is the microzooplankton grazing coefficient and Δt is the incubation time in days.

Where in our experiments nonlinearity induced by saturated feeding of microzooplankton (Gallegos 1989) was seen, especially in experiments 1 and 4 where predator abundance was low, only the diluted samples (10, 25, 50%) were used for regression analysis (Paterson et al. 2008). The obtained value of apparent phytoplankton growth was used to calculate the grazing coefficient at 100% undiluted seawater level. For comparisons between microzooplankton and mesozooplankton grazing, we normalised grazing parameters according to predator carbon concentration:

Daily carbon-specific grazing rates g_c, filtration rates F_c and ingestion rates I_c of the microzooplankton community were calculated for average (during the time interval t_0–t_{24}) prey carbon concentrations [C_{prey}] after Frost (1972) with g and k obtained from the dilution experiments. F_c and I_c was adjusted for the growth of predators using mean predator carbon concentration [$C_{predator}$] according to Heinbokel (1978) with Eqs. (2)–(5):

$$F_c = g \times [C_{predator}]^{-1} \tag{2}$$

$$I_c = F_c \times [C_{prey}] \tag{3}$$

$$[C_{prey}] = \frac{C_{t_0} \times (e^{(k-g) \times \Delta t} - 1)}{(k-g) \times \Delta t} \tag{4}$$

$$[C_{predator}] = \left(\frac{C_{predator,t_{24}} - C_{predator,t_0}}{\ln C_{predator,t_{24}} - \ln C_{predator,t_0}} \right) \tag{5}$$

The instantaneous (natural) growth rate of phytoplankton μ_0 was calculated by adding grazing mortality to values of apparent phytoplankton growth obtained from the incubation bottles without added nutrients (Landry 1993;

Caron 2000); negative values of g were set to zero for calculation. Based on the coefficients obtained for μ_0 and g applied on the initial phytoplankton biomass C_{t0}, the loss (%) of phytoplankton standing crop per day P_i and the loss (%) of potential phytoplankton production P_p of each species were calculated according to Eqs. (6) and (7) (Quinlan et al. 2009).

$$P_i = \frac{C_{t_0} \times (e^g - 1)}{C_{t_0}} \times 100 \tag{6}$$

$$Pp = \frac{C_{t_0} \times [(e^{\mu_0} - 1) - (e^{(\mu_0 - g)} - 1)]}{C_{t_0} \times (e^{\mu_0} - 1)} \times 100 \tag{7}$$

Copepod grazing: correcting for trophic cascade effects

The uncorrected grazing coefficient $g_{cop,p}$ of T. longicornis was calculated for all prey types p (taxon level, phytoplankton/microzooplankton groups, total phytoplankton/microzooplankton community) after Frost (1972) at average prey concentrations, whereby the undiluted seawater incubation bottles of the dilution experiments served as control. As bottle incubations, containing several trophic levels (phytoplankton, microzooplankton and mesozooplankton), face the problem of insignificant, low or even statistically significant negative grazing rates (Nejstgaard et al. 1997, 2001), significance of grazing was tested after correction for trophic cascade effects.

The corrected copepod grazing coefficient ($g_{corr,p}$, Eq. 8) was calculated following the general method of Nejstgaard (2001) by adding a correction factor k_p for reduced microzooplankton grazing rates due to predation on micrograzers by T. longicornis to $g_{cop,p}$:

$$g_{corr,p} = g_{cop,p} + k_p \tag{8}$$

$$k_p = g_{micro,p} \times \left(\frac{[C_{predator}] - [C_{predator}]*}{[C_{predator}]} \right) \tag{9}$$

whereby [$C_{predator}$] in Eq. (9) is the mean microzooplankton carbon concentration in the undiluted seawater from the dilution series and [$C_{predator}$]* is the mean microzooplankton carbon concentration in the T. longicornis bottles. Only significant microzooplankton grazing rates (linear regression analysis, $P < 0.05$) were used for the correction, negative grazing rates were set to zero. We calculated rates of filtration (F_i) and ingestion (I_i) per individual of T. longicornis. To allow for comparisons with the microzooplankton, carbon-specific grazing (g_c) and filtration rates (F_c) and carbon-specific ingestion rates (I_c) (phytoplankton and microzooplankton prey) of the added T. longicornis were calculated as described earlier for the microzooplankton. Contrary to the growth of phytoplankton microzooplankton growth was assumed not to be influenced by nutrient addition, and therefore, values of k obtained for microzooplankton growth k from the 100% undiluted

seawater incubation bottles were taken to calculate P_i and P_p instead of μ_0.

Sometimes negative P_i and P_p values were found in our grazing experiments. These resulted from either negative g (for P_i) or μ_0/k (mortality in the control without grazer) (for P_p) and thus were set to zero. The same was done for positive P_p values resulting from negative g and μ_0.

Selectivity and electivity

Prey selectivity α of the microzooplankton community and *T. longicornis* was calculated for each prey type (see above) according to Chesson (1978, 1983) (Eq. 10):

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j} \tag{10}$$

whereby r_i is the frequency of prey i in the diet and n_i is the frequency of prey in the environment, divided by the sum of all relationships between the frequency of prey in the diet and in the environment. Negative *T. longicornis* ingestion rates were set to zero for the calculation of the frequency of prey in the diet according to Nejstgaard (2001). We chose Chesson's case 1 equation (n_i assumed to be constant) (Chesson 1983) because our values of ingestion and percentage of prey in the environment were obtained by averaged prey concentrations and phytoplankton initial stocks were high, so that a strong depletion of food was unlikely.

Values of α were used to calculate the electivity index E^* according to Vanderploeg and Scavia (1979a, b) (Eq. 11).

$$E^* = \frac{\alpha_i - \frac{1}{n}}{\alpha_i + \frac{1}{n}} \tag{11}$$

(n = total number of prey types).

Values of E^* cover a range from -1 to 1. E^* values of 0 indicate non-selective feeding, values >1 indicate preference, values <1 indicate discrimination against a prey type.

Data analysis

To monitor possible negative effects of our set-up technique on abundances, we statistically compared (t tests) microzooplankton communities at the start of the experiments in the mesocosms with the communities in the experimental bottles for differences. Insignificance was a requirement for applying the results of the experiments to the mesocosms. Regression analyses for the determination of k and g in the dilution experiments were conducted using "SigmaPlot 9.0" (SYSTAT Software); further statistical analyses were conducted using the software "Statistica 7.1" (StatSoft). Values of g, k, F, I and E^* obtained in the *T. longicornis* grazing experiments were tested against zero

using two-tailed t tests (Köhler et al. 1995). Significance levels of 0.05 were chosen in our analyses.

Results

Developments in the mesocosms

Nutrients

In the first 4 days of bloom development phosphate (start 0.36 µmol L^{-1}) and silicate (start 4.75 µmol L^{-1}) decreased rapidly to values below detection limit (<0.01 µmol L^{-1}) and no relaxation from nutrient limitation could be observed during the course of the experiment. Dissolved inorganic nitrogen (DIN) dropped from around 14 µmol L^{-1} to around 7 µmol L^{-1} after the first week and remained at a level between 5 and 7 µmol L^{-1} during the rest of the experiment (Fig. 1b).

General development of the spring bloom

Starting with 44 µgC L^{-1} phytoplankton biomass, similar to the bloom development in the field, the mesocosm spring bloom was initiated immediately and reached its maximum at 269 µgC L^{-1} (chlorophyll *a*: 9 µg L^{-1}, Fig. 1a) within the first 8 days of the experiment (24.03.09) (Fig. 1c). At this exponential phase, phytoplankton had a maximal net growth rate of 0.48 day^{-1} (18.–20.03.09) and a mean net growth rate of 0.23 day^{-1} (16.–24.03.09). During the following 3 weeks, the biomass decreased at a mean rate of -0.05 day^{-1} to a final value of 84 µgC L^{-1}.

Microzooplankton, starting with 14 µgC L^{-1}, followed the phytoplankton bloom with a delay of roughly one week and peaked on the 30.03.09 with 124 µgC L^{-1} (Fig. 1c). Microzooplankton reached growth rates of up to 0.27 day^{-1} (23.–24.03.09) but grew at a mean rate of 0.16 day^{-1}. Until the end of the experiment, microzooplankton biomass decreased at a mean rate of -0.15 day^{-1} to 12 µgC L^{-1}, i.e. close to the starting value.

Phytoplankton composition

The spring bloom was dominated by diatoms and small flagellates (five size classes of 5–25 µm length, details in the "Appendix") (Fig. 2a, b). While flagellates contributed 34% to phytoplankton biomass at the start, they played only a minor role during the bloom phase. The bloom itself was principally build up by the same taxa as in the field (Löder et al., unpublished data) and was dominated by diatoms (96%) of the genera *Chaetoceros* (*C. danicus* and other *Chaetoceros* spp. of different size classes), *Thalassiosira* (*T. rotula* and *T. nordernskjoeldii*) and *Rhizosolenia* (*R. stylisformis/hebetata* group and *R. pungens*), each
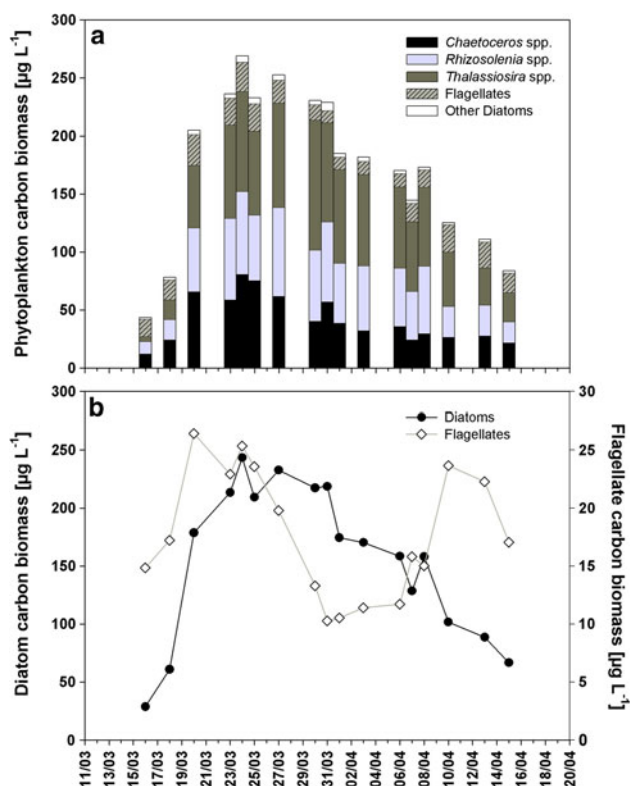
Fig. 2 Phytoplankton species succession (**a**) and development of diatom and flagellate carbon biomass (**b**) during the mesocosm experiment, mean values of the three mesocosms

Fig. 3 Microzooplankton species succession during the mesocosm experiment (**a** ciliates, **b** dinoflagellates and **c** other microzooplankton), mean values of the three mesocosms

genus contributing roughly one-third. In the later bloom phase, *Thalassiosira* became more dominant and contributed up to 49% to the phytoplankton carbon. The category 'other diatoms' (*Pseudonitzschia* spp., *Navicula* spp., *Asterionellopsis glacialis* and others) contributed only 1–4% to the phytoplankton biomass. Flagellate biomass peaked 4 days earlier than the diatoms and showed a steeper decline. Along with decreasing diatom shares, it increased again contributing around 20% to the total phytoplankton carbon in the last week of the experiment.

Microzooplankton composition

Microzooplankton (Fig. 3) comprised four groups: dinoflagellates, ciliates, rotifers and thecate amoebae, whereby ciliates and dinoflagellates dominated during the first 3 weeks of the experiment. Due to their very low abundances, other metazoans like copepod nauplii or polychaete larvae were detected only sporadically and were neglected in our analyses.

Ciliate community

After a week of stability ($\sim$6 µgC L^{-1}), ciliate biomass increased at rates of around 0.36 day^{-1} from 23.03.09

onwards reaching a peak on 30.03.09 (96 µgC L^{-1}) (Fig. 3a). Afterwards, it decreased rapidly to a final 5 µgC L^{-1}. Ciliates contributed 27–46% to the total microzooplankton biomass and dominated the bloom (up to 78%). A clear succession was found in the community. Until the end of March, *Strombidium* spp. (*S. capitatum*, *S.* cf. *emergens*, *S.* cf. *epidemum*, *Laboea strobila*, *Tontonia gracillima* and others) dominated. The most important species was *S. capitatum* contributing 92% to the strombidiids and 64% to the total ciliate biomass at the ciliate peak. Co-occurring strobilids (*Rimostrombidium* sp., *Lohmanniella oviformis*, *Leegaardiella* sp., *Strombidinopsis* sp. and others) contributed 6–21% to the ciliate biomass until the 31.03.09. After the maximum, both genera declined to values below 5% of total ciliate biomass and strombidiids finally disappeared. Simultaneously, the big haptorid *Cyclotrichium* sp. started to dominate until the end at 40–67% of the total

biomass. Cyclotrichids (*Myrionecta rubra*, *Mesodinium* sp. and *Askenasia* sp.) only initially played a major role. During the final 10 days, the category 'other ciliates' (mainly *Acineta* sp. and *Euplotes* spp.) became more important (up to 55% of ciliate biomass).

Dinoflagellate community

Dinoflagellate biomass increased directly after the start ($\sim$7 µgC L^{-1}) at lower rates than those for ciliates (mean 0.15 day^{-1}) but peaked already 5 days earlier (28 µgC L^{-1}, 25.03.09) (Fig. 3b). During the following 8 days, it fluctuated on a high level (20–25 µgC L^{-1}) and declined afterwards to a final 4 µgC L^{-1}. Dinoflagellates contributed 21–62% to the total microzooplankton biomass with a more pronounced role before and after the ciliate peak. *Gyrodinium* spp. dominated the community at 38–52% in the first 10 days and thereafter increased to 66-87% reaching a maximum of 21 µgC L^{-1} on the 03.04.09. Different *Protoperidinium* species (*P. ovatum*, *P. thorianum*, *P. pellucidum*, *P.* cf. *leonis*, *P. bipes*, *P. brevipes*. *P.* cf *pyriforme* and others) contributed 2–23% to the total dinoflagellate biomass. The group 'athecate dinoflagellates' (*Warnowia* sp., *Torodinium* sp., *Katodinium* sp. and small athecate dinoflagellates < 15 µm) contributed 2–19% to the total biomass until 27.03.09 and thereafter declined below 1%. 'Thecate dinoflagellates' (*Diplopsalis* sp., *Dinophysis* sp., small thecate dinoflagellates < 15 µm and others) contributed 27–48% to total biomass until the 25.03.09, but declined afterwards to only 6%. The decline in the last two groups was caused mainly by the loss of the smallest dinoflagellates (<15 µm).

Other microzooplankton

Beside ciliates and dinoflagellates, a thecate amoeba and a rotifer (*Synchaeta* sp.) occurred in the microzooplankton community (Fig. 3c). Both species together contributed 4–30% to the total microzooplankton biomass with values over 13% during the last 10 days of the experiment when *Synchaeta* sp. became more abundant, whereas the parasitic thecate amoeba (mainly attached to *Chaetoceros* spp.) dominated this group until the end of March.

Microzooplankton grazing and selectivity

The microzooplankton community showed carbon-specific grazing rates g_c between 0.006 and 0.014 (µgC predator)$^{-1}$ day^{-1} during the grazing experiments (Fig. 4). All groups of phytoplankton were grazed, while we detected different selectivity patterns for different taxa. Detailed information is given in Tables 1, 2 and on prey taxon level in the "Appendix".
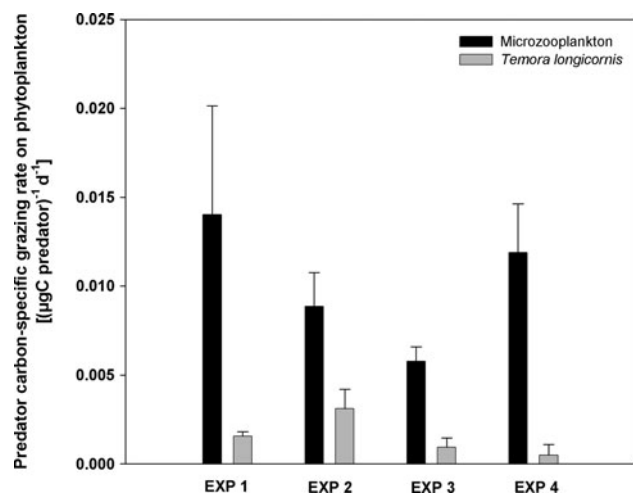
Fig. 4 Predator carbon-specific grazing rates g_c of microzooplankton and *Temora longicornis* grazing on phytoplankton during the four experiments, *error bars* correspond to one standard error ($n = 36$ for microzooplankton, $n = 9$ for *T. longicornis*)

Before the bloom (experiment 1), dinoflagellates dominated the grazer biomass (62%) followed by ciliates (27%). They displayed maximal growth rates of $\sim$0.3 day^{-1}. Saturated feeding was detected in 12 out of 20 phytoplankton prey species accompanied by low grazer biomass (30 µg L^{-1}) ("Appendix", Table 5). However, microzooplankton showed a total grazing rate g of 0.43 day^{-1} (Table 1) and the highest carbon-specific ingestion rate I_c of 1.57 µgC prey µgC predator^{-1} day^{-1} on total phytoplankton among the four experiments, leading to a total daily ingestion I_{total} of 47.65 µgC L^{-1} day^{-1} (Table 2) on the community level. Microzooplankton grazed 53% of the phytoplankton initial stock (P_i) and 223% of the total potential production (P_p) (Table 1) due to the lowest instantaneous growth μ_0 (0.17 day^{-1}) of prey in our four experiments. Based on the index E^* microzooplankton clearly selected the groups *Chaetoceros* spp. and *Thalassiosira* spp. (Table 2).

At the phytoplankton peak (experiment 2), total grazer biomass (74 µg L^{-1}) was more than twice as high as during the pre-bloom experiment and shares of dinoflagellate and ciliate biomass were almost equal. Ciliates displayed the highest growth rates of 0.37 day^{-1} in this phase. The community showed a total I_c of 1.00 µgC prey µgC predator^{-1} day^{-1} (Table 2) on all phytoplankton and a total grazing rate g of 0.66 day^{-1} (Table 1). As μ_0 (0.77 day^{-1}) was higher than g, 93% of P_i and 90% of P_p (Table 1) were grazed. Food selectivity reflected the high grazer diversity and was spread over all categories of phytoplankton resulting in a total daily ingestion I_{total} of 74.58 µgC L^{-1} day^{-1} (Table 2). On group level microzooplankton selected flagellates and *Chaetoceros* spp. (Table 2).

The early post-bloom phase (experiment 3) was characterised by the highest grazer biomass of all experiments

Table 1 Microzooplankton grazing g (day^{-1}), phytoplankton growth rates k (day^{-1}) and instantaneous growth rate values μ_o (day^{-1}) from bottles without added nutrients, percentage of initial stock P_i (%) and potential production P_p (%) grazed as determined in four dilution experiments for different phytoplankton groups

Phytoplankton	Microzooplankton												
	Experiment 1 (MMC 30.33 µgC L^{-1})						Experiment 2 (MMC 74.47 µgC L^{-1})						
	k	P	g	P	μ_0	P_i	P_p	k	P	g	P	μ_0	P_i	P_p
Chaetoceros spp.	*0.46*		*0.60*	*	*0.40*	*83*	*139*	1.15	****	1.27	****	1.50	256	92
Rhizosolenia spp.	*0.25*		*0.28*	**	*−0.01*	*32*	*0*	0.70	****	0.76	****	0.78	114	98
Thalassiosira spp.	0.53	****	0.56	**	0.42	75	124	0.60	****	0.63	****	0.85	88	82
Flagellates	*0.21*		*0.19*	**	*−0.47*	*21*	*0*	0.58	***	0.84	*	0.74	132	109
Other diatoms	0.02		−0.10	*	−0.47	0	0	0.35	****	0.41	**	0.27	51	141
Total phytoplankton	0.41	*	0.43	*	0.17	53	223	0.80	****	0.66	***	0.77	93	90

	Experiment 3 (MMC 93.82 µgC L^{-1})						Experiment 4 (MMC 33.12 µgC L^{-1})						
Chaetoceros spp.	*0.49*	***	0.52	*	*0.41*	68	*121*	0.80	****	0.70	****	1.27	102	70
Rhizosolenia spp.	0.43	****	0.42	****	0.65	52	72	0.51	****	0.49	****	0.76	64	73
Thalassiosira spp.	0.14	***	0.15	*	0.19	16	78	0.68	****	0.69	****	0.89	100	85
Flagellates	0.58	****	0.53	***	0.72	70	81	−0.20		0.10		−0.47	10	0
Other diatoms	0.38	***	0.37	*	0.32	45	114	0.72	****	0.71	****	0.98	103	81
Total phytoplankton	0.39	****	0.54	****	0.65	72	87	0.41	****	0.39	***	0.52	48	80

Food saturation given in italic values; negative P_i and P_p values resulting from negative g (P_i) or μ_o (P_p) were set to zero, also positive P_p values resulting from negative g and μ_o

MMC mean microzooplankton carbon biomass

P values from linear regression analysis of apparent phytoplankton growth against dilution factor ($n = 36$), * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 2 Microzooplankton carbon-specific filtration rates F_c (mL µgC predator^{-1} day^{-1}) and carbon-specific ingestion rates I_c (µgC prey µgC predator^{-1} day^{-1}), total ingestion rates of the microzooplankton community I_{total} (µgC prey L^{-1} day^{-1}) and electivity $E*$ ($-$) for different phytoplankton groups

Phytoplankton	Microzooplankton									
	Experiment 1 (MMC 30.33 µgC L^{-1})					Experiment 2 (MMC 74.47 µgC L^{-1})				
	F_c	P	I_c	P	$E*$	F_c	P	I_c	P	$E*$
Chaetoceros spp.	19.88	*	0.30	*	*0.30*	17.04	****	0.16	****	*0.24*
Rhizosolenia spp.	9.11	**	0.33	**	−0.08	10.22	****	0.41	****	−0.01
Thalassiosira spp.	18.50	**	0.73	**	*0.26*	8.46	****	0.35	****	−0.11
Flagellates	6.35	**	0.10	**	−0.26	11.31	*	0.11	*	*0.04*
Other diatoms	−3.46	*	−0.02	*	−1.00	5.49	**	0.03	**	−0.31
Total phytoplankton	14.02	*	1.57	*		8.85	***	1.00	***	
Related to total microzooplankton C L^{-1}		I_{total}	47.65				I_{total}	74.58		

	Experiment 3 (MMC 93.82 µgC L^{-1})					Experiment 4 (MMC 33.12 µgC L^{-1})				
Chaetoceros spp.	5.53	*	0.08	*	*0.13*	21.19	****	0.17	****	*0.13*
Rhizosolenia spp.	4.48	****	0.16	****	*0.03*	14.93	****	0.39	****	−0.04
Thalassiosira spp.	1.59	*	0.08	*	−0.46	20.94	****	0.49	****	*0.13*
Flagellates	5.68	***	0.09	***	*0.14*	2.92		0.06		−0.70
Other diatoms	3.98	*	0.01	*	−0.03	21.45	****	0.02	****	*0.14*
Total phytoplankton	5.77	****	0.62	****		11.89	***	0.97	***	
Related to total microzooplankton C L^{-1}		I_{total}	58.02				I_{total}	32.13		

Positive selection given in italic values

MMC mean microzooplankton carbon biomass

P values are the same as for the grazing rates of microzooplankton, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

(94 µg L^{-1}) and ciliates clearly dominated the community (69%). Microzooplankton grazed 72% of P_i and 87% of P_p of the total phytoplankton community at a rate of 0.54 day^{-1} (g) (Table 1). Phytoplankton displayed a higher instantaneous growth rate μ_0 (0.65 day^{-1}) than in the fertilised incubation bottles ($k = 0.39$ day^{-1}). I_c (0.62 µgC prey µgC predator^{-1} day^{-1}) on total phytoplankton was the lowest detected in our experiments leading to a total daily ingestion I_{total} of 58.02 µgC L^{-1} day^{-1} of the microzooplankton (Table 2). Microzooplankton selected for flagellates (except flagellates 5 µm, see "Appendix"), *Rhizosolenia* spp. and *Chaetoceros* spp. (Table 2).

In the late post-bloom phase (experiment 4), grazer biomass (33 µg L^{-1}) was as low as before the bloom and saturated feeding in 5 phytoplankton species was detected ("Appendix", Table 5). Besides the now dominating dinoflagellates, rotifers became as important as ciliates. The community grazed 48% of P_i and 80% of P_p at a rate of 0.39 day^{-1} (g) (Table 1). I_c (0.97 µgC prey µgC predator^{-1} day^{-1}) increased to a value similar to experiment 2 resulting in a total daily ingestion I_{total} of 32.13 µgC L^{-1} day^{-1}. Again instantaneous growth μ_0 (0.52 day^{-1}) of the phytoplankton exceeded the growth in fertilised bottles (0.41 day^{-1}) (Table 1). Selectivity was similar to experiment 1, whereas also the category 'other diatoms' was selected.

Temora longicornis grazing and selectivity

The *T. longicornis* (108.7 µgC L^{-1}) biomass added was always higher than the microzooplankton biomass in the experiments. Even so, the copepod species had a much lower grazing impact on the phytoplankton community (Fig. 4) than the microzooplankton (g_c: 0.0005–0.003 (µgC predator)$^{-1}$ day^{-1}). During the course of the experiments, *T. longicornis* switched its diet gradually from a phytoplankton-dominated towards a microzooplankton-dominated diet (Fig. 5a; Table 4). This was reflected in E^* values and a positive selection for microzooplankton in general when compared to phytoplankton prey, with the exception of the phytoplankton peak experiment (Fig. 5b; Table 4). However, on a taxon level some phytoplankters were also positively selected (see "Appendix" for details). Detailed information on individual and carbon-based grazing parameters of *T. longicornis* is given on prey group level in Tables 3, 4.

Before the bloom (experiment 1), the copepods showed a grazing rate of 0.17 day^{-1} (Table 3) and ingested 17.87 µgC L^{-1} day^{-1} of the total phytoplankton community (I_{total}) at a carbon-specific ingestion rate I_c of 0.16 µgC prey µgC predator^{-1} day^{-1} (Table 4) leading to 18% reduction of P_i and 100% of P_p (Table 3). Per capita filtration rate F_i was 15.51 mL Ind.$^{-1}$ day^{-1} and one copepod ingested 1,644 ngC Ind.$^{-1}$ day^{-1} of phytoplankton
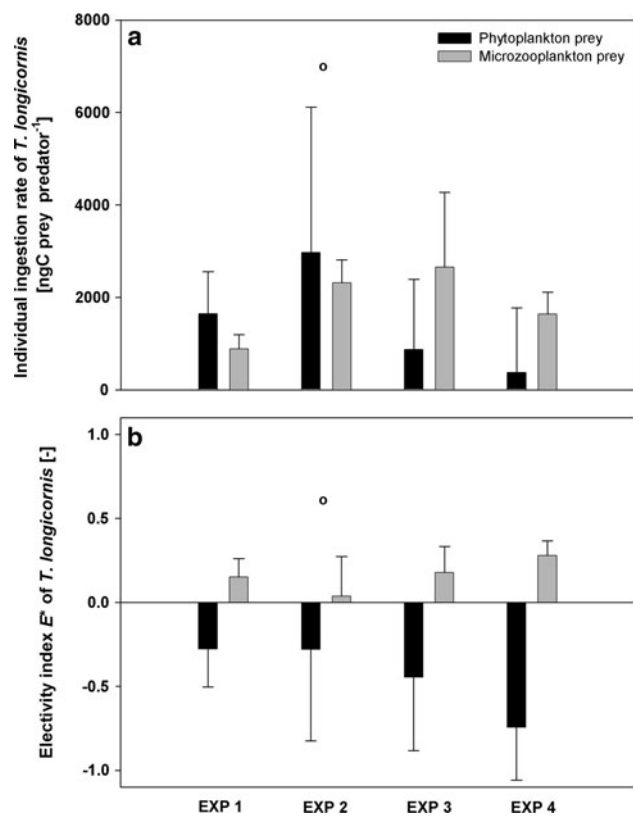
Fig. 5 a Individual ingestion rate I_i and **b** electivity index E^* of *Temora longicornis* for phytoplankton and microzooplankton prey, 'o' marks experiment with insignificant differences of I_i and E^* between both prey groups, *error bars* correspond to one standard deviation ($n = 9$)

(I_i, Table 4). Due to the lower biomass of microzooplankton prey, the copepods reached a higher g (0.40 day^{-1}) and they ingested 9.58 µgC L^{-1} day^{-1} (I_{total}) of the microzooplankton community at an I_c of 0.09 µgC prey µgC predator^{-1} day^{-1}, leading to a 49% decrease of P_i and 174% of P_p (Table 3). One copepod cleared 36.72 mL Ind.$^{-1}$ day^{-1} and ingested 881 ngC Ind.$^{-1}$ day^{-1} in form of microzooplankton (Table 4).

Only at the bloom peak (experiment 2), electivity for microzooplankton prey was insignificant (Fig. 5). The copepods ingested the highest amount of biomass during our experiments (57.50 µgC L^{-1} day^{-1}, I_{total} phytoplankton + microzooplankton, Table 4) and showed grazing rates of 0.34 day^{-1} for phytoplankton and 0.43 day^{-1} for microzooplankton (Table 3), at carbon-specific ingestion rates I_c of 0.30 and 0.23 µgC prey µgC predator^{-1} day^{-1}, respectively (Table 4). Copepods grazed 40% of phytoplankton P_i (highest value for *T. longicornis*) and 54% of its P_p and 53% of the microzooplankton P_i and 147% of its P_p. Per capita filtration rate F_i was 31.21 mL Ind.$^{-1}$ day^{-1} for phytoplankton and 39.33 mL Ind.$^{-1}$ day^{-1} for microzooplankton and an individual ingested 2,974 ngC Ind.$^{-1}$ day^{-1} phytoplankton and 2,316 ngC Ind.$^{-1}$ day^{-1} microzooplankton.

Table 3 *Temora longicornis* grazing g (day^{-1}), phytoplankton and microzooplankton growth rates k (day^{-1}) and phytoplankton instantaneous growth rate values μ_o (day^{-1}) from bottles without added nutrients, percentage of initial stock P_i (%) and potential production P_p (%) grazed as determined in four grazing experiments for different prey groups

| | *Temora longicornis* (TC 108.70 µgC L^{-1}) | | | | | | | | | | | | | |
| | Experiment 1 | | | | | | | Experiment 2 | | | | | | |
	k	P	g	P	μ_0	P_i	P_p	k	P	g	P	μ_0	P_i	P_p
Phytoplankton														
Chaetoceros spp.	−0.13		0.34	***	0.40	40	88	0.24	*	0.47	*	1.50	60	48
Rhizosolenia spp.	−0.02		0.13	*	−0.01	14	0	0.01		0.20		0.78	23	34
Thalassiosira spp.	0.00		0.21	**	0.42	23	54	0.31	**	0.56	*	0.85	74	74
Flagellates	0.01		0.05		−0.47	5	0	−0.26	*	0.08		0.74	8	14
Other diatoms	0.11		−0.05		−0.47	0	0	−0.16		0.02		0.27	2	9
Total phytoplankton	−0.01		0.17	***	0.17	18	100	0.13	*	0.34	*	0.77	40	54
Microzooplankton														
Gyrodinium spp.	−0.02		1.11	**		203	0	0.32	****	0.27	***		31	86
Protoperidinium spp.	0.20		1.32	***		275	406	0.21		0.33	**		39	150
other athecate dinoflagellates	0.03		0.18			20	497	−0.01		0.27	*		30	0
other thecate dinoflagellates	0.39	****	−0.03			0	0	−0.43	****	0.20	*		23	0
Strombidium spp.	0.30	*	1.18	***		224	267	0.46	****	0.79	****		121	148
Strobilidium spp.	0.26		0.92	*		150	262	0.66	***	0.36	**		43	62
Cyclotrichids	0.18		0.95	**		158	374	−0.32		0.16			18	0
Haptorids	−0.28		0.93	*		154	0	0.39		0.35			42	91
Other ciliates	−0.03		0.04			4	0	0.17		0.58	*		79	289
Thecate amoeba sp.	0.16		0.32	***		38	191	0.25	**	0.23	*		26	93
Rotifers	0.00		–			–	–	–		–			–	–
Total microzooplankton	0.21	****	0.40	****		49	174	0.27	****	0.43	****		53	147
	Experiment 3							Experiment 4						
Phytoplankton														
Chaetoceros spp.	−0.02		0.23	*	0.41	25	61	0.28	*	0.21		1.27	23	26
Rhizosolenia spp.	−0.09		0.03		0.65	3	5	0.13		0.11		0.76	12	20
Thalassiosira spp.	−0.35		−0.03		0.19	0	0	0.08		0.21	*	0.89	24	32
Flagellates	−0.06		0.23	**	0.72	26	40	−0.28	**	−0.24	***	−0.47	0	0
Other diatoms	−0.14		0.40	*	0.32	49	120	0.23	**	0.21	*	0.98	24	31
Total phytoplankton	−0.18		0.10		0.65	11	20	0.04		0.05		0.52	6	13
Microzooplankton														
Gyrodinium spp.	0.05		0.21	***		24	425	−0.11		0.66	**		93	0
Protoperidinium spp.	0.12		0.76	**		114	487	−0.06		0.53	**		70	0
Other athecate dinoflagellates	0.05		0.22			25	418	–		–			–	–
Other thecate dinoflagellates	−0.14		0.14			15	0	−0.35		0.07			7	0
Strombidium spp.	−1.61	****	0.15			16	0	1.30		0.32			37	37
Strobilidium spp.	−0.61	****	0.22			25	0	−0.21		0.40			50	0
Cyclotrichids	0.01		0.59	*		80	3066	−0.46		0.49			63	0
Haptorids	0.87	**	0.54	**		72	72	−0.52		2.48			1097	0
Other ciliates	0.54		0.44			56	85	−0.11		0.10			11	0
Thecate amoeba sp.	−0.11		0.13	*		13	0	−0.05		0.25	***		29	0
Rotifers	0.02		0.33			39	1183	0.03		1.84	***		529	3,349
Total microzooplankton	0.07		0.38	***		46	478	−0.04		0.78	****		118	0

Negative P_i and P_p values resulting from negative g (P_i) or μ_o/k (P_p) were set to zero, also positive P_p values resulting from negative g and μ_o/k

TC total *T. longicornis* carbon biomass

P values derived from t tests against zero, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 4 *Temora longicornis* individual filtration F_i (mL Ind.$^{-1}$ day^{-1}) and ingestion rates I_i (ngC Ind.$^{-1}$ day^{-1}) as well as carbon-specific filtration rates F_c (mL µgC predator^{-1} day^{-1}) and carbon-specific ingestion rates I_c (µgC prey µgC predator^{-1} day^{-1}), total ingestion rates I_{total} (µgC prey L^{-1} day^{-1}) and electivity $E*$ (−) for different prey groups

| | *Temora longicornis* (TC 108.70 µgC L^{-1}) | | | | | | | | | | | | | | | |
| | Experiment 1 | | | | | | | | Experiment 2 | | | | | | | |
	F_i	F_c	P	I_i	I_c	P	E*	P	F_i	F_c	P	I_i	I_c	P	E*	P
Phytoplankton																
Chaetoceros spp.	31.19	3.12	***	403.04	0.0403	**	−0.21		43.29	4.33	*	333.07	0.0333	*	−0.03	
Rhizosolenia spp.	11.94	1.19	*	425.53	0.0426	*	−0.57	**	18.74	1.87		688.94	0.0689		−0.30	
Thalassiosira spp.	18.89	1.89	**	689.01	0.0689	**	−0.40	**	51.06	5.11	*	1784.99	0.1785	*	−0.01	
Flagellates	4.24	0.42		32.41	0.0032		−0.65	**	7.09	0.71		61.63	0.0062		−0.61	**
Other diatoms	−4.97	−0.50		−23.11	−0.0023		−0.80	***	1.92	0.19		27.57	0.0028		−0.62	**
Total phytoplankton	15.51	1.55	***	1643.64	0.1644	***	−0.28	**	31.21	3.12	*	2973.72	0.2974	*	−0.28	
Related to total copepod C L^{-1}				I_{total}	17.87							I_{total}	32.32			
Microzooplankton																
Gyrodinium spp.	102.01	10.20	**	263.25	0.0263	**	0.18		24.77	2.48	***	330.25	0.0330	***	−0.19	
Protoperidinium spp.	121.70	12.17	***	79.97	0.0080	****	0.38	**	30.13	3.01	**	91.86	0.0092	*	−0.19	
Other athecate dinoflagellates	16.51	1.65		20.68	0.0021		−0.48	**	24.45	2.45	*	26.73	0.0027	*	−0.23	
Other thecate dinoflagellates	−2.36	−0.24		−21.03	−0.0021		−0.89	****	18.72	1.87	*	136.85	0.0137	*	−0.39	*
Strombidium spp.	108.29	10.83	***	251.16	0.0251	****	0.36	**	72.78	7.28	****	1101.16	0.1101	****	0.38	****
Strobilidium spp.	84.30	8.43	*	42.07	0.0042	*	0.05		32.78	3.28	**	190.64	0.0191	**	−0.10	
Cyclotrichids	87.07	8.71	**	179.21	0.0179	****	0.25	**	14.87	1.49		51.04	0.0051		−0.31	
Haptorids	85.78	8.58	*	7.02	0.0007	*	−0.06		32.07	3.21		2.06	0.0002		−0.12	
Other ciliates	3.25	0.33		−1.51	−0.0002		−0.36		53.47	5.35	*	9.76	0.0010	*	0.02	
Thecate amoeba sp.	29.76	2.98	***	60.68	0.0061	***	−0.26		21.60	2.16	*	142.56	0.0143	*	−0.27	
Rotifers	–	–		–	–		–		–	–		–	–		–	
Total microzooplankton	36.72	3.67	****	880.91	0.0881	****	0.15	**	39.33	3.93	****	2316.33	0.2316	****	0.04	
Related to total copepod C L^{-1}				I_{total}	9.58							I_{total}	25.18			

| | Experiment 3 | | | | | | | | Experiment 4 | | | | | | | |
	F_i	F_c	P	I_i	I_c	P	E*	P	F_i	F_c	P	I_i	I_c	P	E*	P
Phytoplankton																
Chaetoceros spp.	20.86	2.09	*	254.93	0.0255	*	−0.34		18.89	1.89		131.90	0.0132		−0.45	**
Rhizosolenia spp.	2.32	0.23		58.91	0.0059		−0.68	***	10.45	1.05		233.08	0.0233		−0.57	*
Thalassiosira spp.	−2.83	−0.28		−259.38	−0.0259		−0.71	**	19.57	1.96	*	427.66	0.0428	*	−0.32	
Flagellates	21.36	2.14	**	304.11	0.0304	**	−0.26		−22.44	−2.24	***	−441.30	−0.0441	***	−1.00	
Other diatoms	36.43	3.64	*	43.37	0.0043	*	−0.27		19.45	1.94	*	18.68	0.0019	*	−0.36	
Total phytoplankton	9.34	0.93		866.25	0.0866		−0.45	*	4.97	0.50		370.16	0.0370		−0.74	***
Related to total copepod C L^{-1}				I_{total}	9.42							I_{total}	4.02			
Microzooplankton																
Gyrodinium spp.	19.63	1.96	***	320.35	0.0320	***	−0.23	*	60.35	6.04	**	432.87	0.0433	****	0.15	
Protoperidinium spp.	70.08	7.01	**	102.51	0.0103	**	0.23		48.58	4.86	**	67.71	0.0068	*	0.07	
Other athecate dinoflagellates	20.41	2.04		1.57	0.0002		−0.55		–	–		–	–		–	
Other thecate dinoflagellates	12.98	1.30		6.20	0.0006		−0.29		6.13	0.61		2.30	0.0002		−0.58	*
Strombidium spp.	13.65	1.36		−169.88	−0.0170		−0.52		29.25	2.93		–	–		–	
Strobilidium spp.	20.27	2.03		85.21	0.0085		−0.33		37.08	3.71		1.23	0.0001		−0.17	
Cyclotrichids	54.17	5.42	*	52.98	0.0053		0.07		45.00	4.50		−7.01	−0.0007		−0.08	

Table 4 continued

	Experiment 3								Experiment 4							
Haptorids	49.72	4.97	**	1116.13	0.1116		−0.08		228.35	22.83		198.93	0.0199		*0.23*	
Other ciliates	40.91	4.09		3.93	0.0004		*0.01*		9.39	0.94		29.68	0.0030		−0.58	**
Thecate amoeba sp.	11.55	1.16	*	46.54	0.0047	*	−0.44	*	23.21	2.32	***	39.28	0.0039	***	−0.29	
Rotifers	30.5535	3.06		47.86	0.0048		−0.16		169.13	16.91	***	706.47	0.0706	***	*0.55*	**
Total microzooplankton	35.02	3.50	***	2649.93	0.2650	**	*0.18*	*	71.61	7.16	****	1635.56	0.1636	****	*0.28*	****
Related to total copepod C L^{-1}				I_{total}	28.80							I_{total}	17.78			

Positive selection given in italic values

TC total *T. longicornis* carbon biomass

P values derived from *t* tests against zero,* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

In the early post-bloom phase (experiment 3), the total amount of carbon ingested by the copepods dropped again to 38.22 µgC L^{-1} day^{-1} (Table 4, I_{total} phytoplankton + microzooplankton). They had a grazing rate of 0.10 day^{-1} on phytoplankton and 0.38 day^{-1} on microzooplankton (Table 3) at an I_c of 0.09 and 0.27 µgC prey µgC predator^{-1} day^{-1}, respectively (Table 4). On individual level, a *T. longicornis* cleared 9.34 mL Ind.$^{-1}$ day^{-1} for phytoplankton and 35.02 mL Ind.$^{-1}$ day^{-1} for microzooplankton. Ingestion was 866 ngC Ind.$^{-1}$ day^{-1} for phytoplankton and 2,650 ngC Ind.$^{-1}$ day^{-1} for microzooplankton. The impact of the copepods on the phytoplankton community was once again lower with 11% of P_i and 20% of P_p grazed. On the other hand, *T. longicornis* grazed 46% of microzooplankton P_i and 478% of its P_p.

During the late post-bloom (experiment 4) I_{total} of the copepods for phytoplankton and microzooplankton further dropped to 21.80 µgC L^{-1} day^{-1} (Table 4). While the copepods had only a grazing rate of 0.05 day^{-1} (g) on phytoplankton at a carbon-specific ingestion rate I_c of 0.04 µgC prey µgC predator^{-1} day^{-1}, the grazing rate for microzooplankton was 0.78 day^{-1} (g) at an I_c of 0.16 µgC prey µgC predator^{-1} day^{-1} (Table 3, 4). This led in turn to a reduced impact on the phytoplankton community (P_i: 6%, P_p: 13%) and an even more pronounced impact on the microzooplankton biomass (P_i: 118%, P_p: not defined). Per capita filtration rate of *T. longicornis* on phytoplankton was 4.97 mL Ind.$^{-1}$ day^{-1} and one copepod ingested 370 ngC Ind.$^{-1}$ day^{-1} in form of phytoplankton (I_i, Table 4). The highest filtration rate (71.61 mL Ind.$^{-1}$ day^{-1}) measured during our experiments led to an I_i of 1,636 ngC Ind.$^{-1}$ day^{-1} for microzooplankton prey.

Microzooplankton predator–prey relationships in the mesocosms

We observed a direct coupling between ciliate and flagellate biomass. This resulted in a strong suppression of flagellate biomass from 26 to 10 µgC coincident with the ciliate peak (Fig. 6a). It was most pronounced for thecate and athecate dinoflagellates < 15 µm, which disappeared totally during the S*trombidium capitatum* bloom (Fig. 6b). Simultaneously, with the disappearance of both dinoflagellate groups *S. capitatum* started to form cysts and its population collapsed totally within 1 week. With the break down of strombidiid and strobilid biomass at the end of March, a relaxation from grazing pressure enabled the flagellates to regenerate again.

The majority of dinoflagellate species we found in the mesocosms are reported to prefer diatom prey. As diatoms hardly changed in composition, dinoflagellate succession in the mesocosms was not as pronounced as for the ciliates. While two groups disappeared during the first half of our experiment due to predation by ciliates as described earlier, the remaining dinoflagellate community composition remained relatively constant until the end of the experiment.

We also found a strong predator–prey relationship between a thecate amoeba and *Chaetoceros* spp. The "apparently" parasitic amoeba was found attached only to cells of this genus and followed the bloom development of its host closely, thus declining towards the end of the experiment.

Discussion

The aim of this study was to explicitly examine the role of microzooplankton grazing on phytoplankton communities during a spring bloom in temperate waters. As waters around Helgoland are subject to strong water column mixing by tidal currents (Hickel et al. 1993), it was necessary to bring a defined water body into the laboratory giving us the opportunity to study the wax and wane of the "same" spring bloom under controlled conditions. Using our mesocosm set-up and excluding mesozooplankton

Fig. 6 a General development of ciliate and flagellate biomass in the mesocosms, *error bars* correspond to one standard deviation (*n* = 3), **b** close predator–prey relationship: development of small dinoflagellates and their predator *Strombidium capitatum* and *Strombidium capitatum* cysts, mean values of the three mesocosms
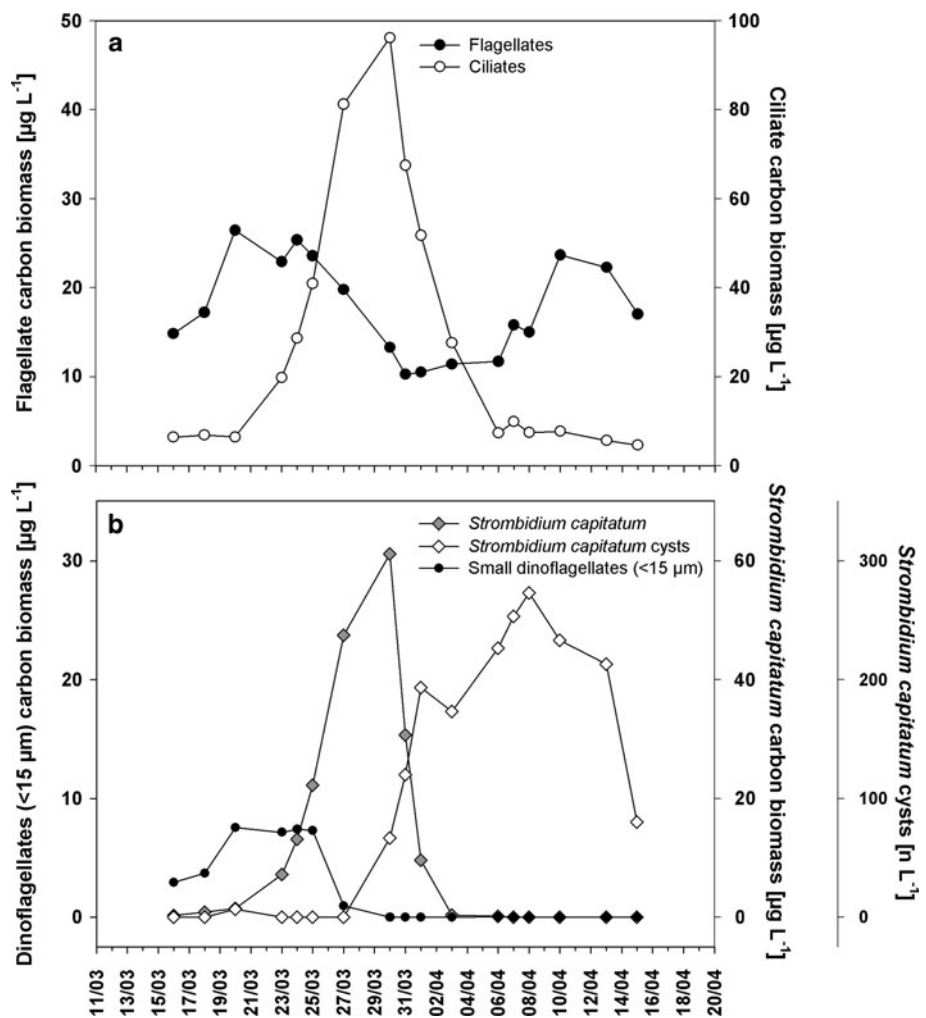
grazers allowed us to follow the plankton spring succession, focusing on top-down control mechanisms on phytoplankton by microzooplankton solely. Furthermore, it allowed us to conduct grazing experiments with microzooplankton as well as copepods at defined points of the phytoplankton spring bloom.

Problems with the estimation of the grazing impact by the dilution technique have been recently discussed (Dolan and McKeon 2005; Landry and Calbet 2005) and the discussion showed that if the restrictions of the dilution technique are recognised, the method has the fundamental advantage of barely altering natural prey and grazer communities and only excluding larger zooplankton. Thus, natural grazing interactions within the microplankton community, as these were our main target, are included in dilution experiments.

Microzooplankton dilution experiments, as applied here, provide us with an alternative to determine grazing rates of microzooplankton by indirect, labour-intensive, and taxonomically selective techniques (Landry and

Hassett 1982; Calbet and Landry 2004). However, methodological restrictions do have to be taken into account (Gallegos 1989; Landry et al. 1995; Dolan et al. 2000; Moigis 2006; Teixeira and Figueiras 2009) most of which are related to the theoretical assumptions (Landry and Hassett 1982) the dilution method is based on. For example, to overcome nonlinear feeding responses due to food saturating conditions, a modified protocol can be used (Paterson et al. 2008; this study). To prevent nutrient limiting conditions in the experimental vessels, often dialysis bags are incubated in situ (Landry 1993; Sommer et al. 2005a, b; Aberle et al. 2007) or nutrients are added in excess to the dilution series (Landry 1993; Fonda Umani et al. 2005; First et al. 2009) in bottle incubations. As we wanted to keep conditions in microzooplankton und copepod grazing experiments comparable, we chose the second alternative (bottle incubations), that was also necessary for correction of trophic cascade effects in the copepod grazing set-up (Nejstgaard et al. 1997, 2001; Fonda Umani et al. 2005).

Another factor has to be kept in mind when using bottle incubations for studies on microzooplankton. Microzooplankton species, especially ciliates, are highly fragile and sensitive to handling. Filling and mixing procedures during experiments (Gifford 1985; Landry 1993; Broglio et al. 2003) can cause considerable losses, and a high mortality of, e.g., ciliates had been reported previously (up to 80%, Tiselius 1989). This would have, in this study, caused severe underestimations in grazing rates of microzooplankton and also of *T. longicornis* on microzooplankton. To prevent mortality, we applied the new filling method of Löder et al. (2010). Furthermore, microzooplankton survival in the bottles was proven by comparing the microzooplankton communities in the bottles with the mesocosms (see section on "Data analysis"). Although there was always some mortality on a taxon level during incubation, we generally detected positive growth rates (0.07–0.21 day^{-1}, Table 3) for the microzooplankton community and only a very low mortality was detected at the decline of the bloom (−0.04 day^{-1}, Table 3, experiment 4). This allowed us to determine realistic grazing estimations and feeding preferences of the microzooplankton community and *T. longicornis* during the mesocosm spring bloom.

Microzooplankton and *T. longicornis* grazing impact on the phytoplankton bloom

Microzooplankton had a higher grazing potential on phytoplankton throughout the whole period of the phytoplankton spring bloom 2009 in the mesocosms, while copepods only played a secondary role as phytoplankton grazers, which confirms the results of previous studies (e.g., Maar et al. 2004; Fonda Umani et al. 2005). The role of copepods has to be seen in the context of the densities we used in our experiments, which reflect the highest abundance of spring concentrations in the field at Helgoland Roads (Greve et al. 2004) and should thus have represented the maximal expectable grazing impact.

T. longicornis is known to be a selective (Koski et al. 2005) and omnivorous grazer feeding on phytoplankton and microzooplankton (Kleppel et al. 1991; Kleppel 1993; Gentsch et al. 2009) of a wide size range in natural assemblages (O'Connors et al. 1980; Tackx et al. 1989, 1990). Furthermore, field populations of *T. longicornis* can have a substantial grazing impact on phytoplankton (Dam and Peterson 1993). At Helgoland Roads, the growth of phytoplankton in spring is followed by a drastic population increase of small calanoid copepods, while other mesozooplankton does not play a significant role (Greve et al. 2004). A new revision of long-term data on mesozooplankton (March/April 1975–2002) revealed that the group 'small calanoid copepods' represented 90% of the adult

copepod community at the time of our experiments. Within the group, *T. longicornis* contributed up 60% to adult calanoid copepod numbers (mean 28%, Kong, S.-M., unpublished). Given this fact, *T. longicornis* can be considered as an important copepod species in the North Sea planktonic food web in spring, and therefore, it was selected as representative copepod grazer in our experiments.

Low impacts on spring bloom development by copepods have been reported previously (Dagg et al. 1982; Dam et al. 1993), where the removal of daily primary production by copepods accounted for less than 25% of P_p. Although *T. longicornis* selected for microzooplankton in three out of four experiments, phytoplankton was always present in its diet (18–65%). Furthermore, the maximum impact of copepods we detected in this study was 100%, suggesting a structuring potential by copepods under certain conditions. Similar to the maximum values found by Dam and Peterson (1993), the average grazing impact of *T. longicornis* on the potential phytoplankton production we detected was 47% and therefore slightly higher than the 10–40% given by Calbet (2001) for copepods on a global scale. The range of per capita filtration rates of *T. longicornis* on phytoplankton we measured (5–31 mL $Ind.^{-1}$ day^{-1}) is comparable to the values found by Dam (1986) in laboratory experiments (1–46 mL $Ind.^{-1}$ day^{-1}). We found maximum filtration rates in our experiments at the phytoplankton bloom peak, which were around twice as high as reported for *T. longicornis* feeding on natural phytoplankton at comparable chlorophyll *a* concentrations (Dam 1986). This difference may result from differences in phytoplankton assemblages but unfortunately information about the species composition is lacking in the study of Dam (1986). The highest ingestion rates of *T. longicornis* were also measured at the phytoplankton bloom peak. One copepod ingested 2.9 µgC $Ind.^{-1}$ day^{-1} in the form of phytoplankton, which is comparable to reported ingestion rates (2.2 µgC $Ind.^{-1}$ day^{-1}) on diatom prey at similar chlorophyll *a* concentrations (Dam 1986). In our experiment, we assumed all dinoflagellates, also mixotrophic species, to be heterotrophic. Consequently, we potentially underestimated copepod herbivory. However, the percentage of mixotrophic dinoflagellates in the microzooplankton community of the mesocosms was low (0.2–3.1% of microzooplankton total carbon) and *T. longicornis* did not preferentially feed on them; thus, the underestimation of herbivory should have been low also.

Although the total carbon-specific ingestion rates (0.20–0.53, phytoplankton + microzooplankton prey) of *T. longicornis* were similar to results reported in previous studies (0.15–0.20: Daro 1985; 0.40–2.2: Koski et al. 2005), microzooplankton showed an almost sevenfold

higher carbon-specific ingestion rate (I_c) when preying on phytoplankton in contrast to the copepods. The total ingestion of microzooplankton we measured showed a mean of 53 µgC L^1 day^{-1}, which is close to the mean value of 60 µgC L^1 day^{-1} found during late winter and spring by Fonda Umani et al. (2005). They registered a mean impact of microzooplankton on potential phytoplankton production of 123%. Similarly, in our experiments microzooplankton grazed on average 120% of the potential phytoplankton production. This is around two-fold higher than results reported by Landry and Calbet (2004). They found an average grazing impact of 59–75% of P_p by microzooplankton across a spectrum of open ocean and coastal systems, whereas the lower border was found for estuarine systems with chlorophyll *a* values similar to those of our experiment. In this study, the high availability of food during the bloom situation combined with a release from grazing pressure by metazoans allowed the development of a high microzooplankton grazer biomass in the mesocosms. Our results should therefore represent the maximum in microzooplankton grazing impact on phytoplankton in coastal regions under spring bloom conditions and has to be seen as the potential grazing impact of microzooplankton when top-down control by mesozooplankton is lacking.

Spring bloom dynamics in the North Sea around Helgoland are, of course, additionally subject to factors other than grazing (e.g., hydrography, salinity fluctuations, storm events and nutrient fluxes on a daily basis), which our mesocosm environment could not mimic. However, the close resemblance of chlorophyll *a* development (and also composition of microzooplankton and phytoplankton assemblages, Löder et al., unpublished data) in our mesocosms to the natural situations (where mesograzers were present) suggests that microzooplankton drives the spring bloom dynamics of the phytoplankton community in waters around Helgoland (compare Fig. 1a).

Optimal bloom exploitation through different feeding strategies of microzooplankton

Different feeding strategies are recorded among heterotrophic dinoflagellates including direct engulfment, pallium- and peduncle- or tube feeding (Jacobson and Anderson 1986; Gaines and Elbrächter 1987). Ciliates are categorised as suspension, raptorial, deposit and diffusion feeders (Müller and Weisse 1994). Depending on the predators' feeding mode different prey is selected. Therefore, depending on the zooplankton community present at specific times of the year, feeding habits are directly mirrored by food selectivity patterns. Grazing selectivity itself also structures the phytoplankton composition (Irigoien et al.

2005). In our experiments, the microzooplankton community showed a large variety of food preferences and preferred food size spectra according to grazer species, grazer size and feeding mode.

Generally, dinoflagellates can feed on a wide range of prey (Jeong 1999) and are likely to be more quantitatively significant consumers of bloom-forming diatoms than copepods (Sherr and Sherr 2007). Athecate *Gyrodinium* spp. (20–120 µm length) and thecate *Protoperidinium* spp. (15–75 µm diameter) dominated the dinoflagellate grazer assemblage in our mesocosm study. Both genera are mainly associated with diatom blooms (Sherr and Sherr 2007). Dinoflagellates can feed and grow on variable predator to prey size ratios between 5.2:1 and 0.15:1 (Naustvoll 2000a, b). The upper limit of prey size reported by Naustvoll (2000a, b) is probably not reached by naked phagotrophs such as *Gyrodinium* spp. as they prefer food of their own size (Hansen 1992), but rather by thecate, pallium-feeding dinoflagellates like *Protoperidinium* spp. With regard to their size and feeding abilities, the present dinoflagellate taxa were able to feed on the biggest diatoms in the mesocosms.

Ciliates feed mainly on nanoplankton in an optimal size at approximately 1/10 of their own size (Spittler 1973; Heinbokel 1978; Jonsson 1986). However, it is reported that they can feed on prey items sometimes larger than themselves (Smetacek 1981; Kahl 1932; Gifford 1985; Johansson et al. 2004). Ciliates are thus at times in direct feeding competition with copepods (Aberle et al. 2007) and dinoflagellates (Hansen 1992; Sherr and Sherr 2007). *Strombidium capitatum,* the dominating strombidiid is known to feed on small flagellates of different groups (Stoecker and Silver 1990; Crawford and Stoecker 1996). Other *Strombidium* and *Strobilidium* species as present in our experiment are considered to consume phytoplankton fractions ranging from 2 to 15 µm (Christaki et al. 1998; Sime-Ngando et al. 1999; Aberle et al. 2007). Xu et al. (2005) found a big *Cyclotrichium* species, similar to the species present in the second half of the mesocosm bloom, feeding on different algae including diatoms. The main prey of ciliates in the mesocosm should, however, have been flagellates and smaller diatoms.

We found a highly diverse microzooplankton community during the spring bloom. Species of different size classes with different feeding modes were always present. It is therefore not surprising that microzooplankton grazed on all possible components of the phytoplankton ranging from smallest flagellates to large diatoms. Microzooplankton was even able to graze on very large bloom-forming diatoms like *Rhizosolenia* spp. In our mesocosms we did not investigate factors such as cell death, cyst

formation, sedimentation, parasitism or viral lysis that can lead to a decay of phytoplankton blooms. Senescence of cells and cell death as a consequence of nutrient depletion were, however, factors that certainly played an important role in our mesocosms, although one can argue about the remineralisation of nutrients due to microzooplankton grazing activity (Sherr and Sherr 2002). Nevertheless, the measured consumption of all available phytoplankton species should have been one of the most important factors for the decay of the bloom since it led to a strong suppression of phytoplankton and contributed to an almost complete decline within 3 weeks after the bloom peak.

Bloom stabilisation of less-favoured species due to selective grazing by microzooplankton

Phytoplankton blooms occur when external perturbations (improved light conditions in our study) promote improved growth conditions and open a loophole in the microbial loop (Irigoien et al. 2005). The species that are able to escape predation pressure by microzooplankton and have competitive advances compared to other phytoplankton (Flynn 2008) can benefit from improved growth conditions at the onset of a bloom thus enabling these species to form mass occurrences. As a consequence of rapidly dividing phytoplankton, the total exclusion from grazing is not required, only a difference in grazing rate resulting in a positive net growth. While phytoplankton competitors remain controlled by zooplankton grazing, the advance in net growth rate enables a particular phytoplankton species to form a bloom. Although microzooplankton is usually not able to prevent phytoplankton blooms under natural conditions (Sherr and Sherr 2009), its grazing can have at least a structuring influence and this circumstance has also been observed in previous studies (Riegman et al. 1993; Fonda Umani et al. 2005).

Irigoien et al. (2005) pointed out that among other factors, defence mechanisms (e.g. large cell sizes, colonies or spine formation) and selective predation of microzooplankton open a loophole for phytoplankton blooms of less edible, unfavoured species. As food selectivity is a constant process a pre-selection of phytoplankton species will have been already taken place in the field prior to the filling of our mesocosms. In early spring, total grazing rates of microzooplankton at the start of our experiment were not sufficiently high enough to suppress a spring bloom formation (see also Sherr and Sherr 2009). However, one can assume some directive influence of microzooplankton.

Flagellates made up one-third of the phytoplankton community at the start of the experiment. As they lost importance towards the end of March, we assume that the growth of flagellates was controlled by selective predation

of microzooplankton thus hindering flagellates to form a bloom. By contrast, shortly after the onset of the bloom, the phytoplankton community in our mesocosms was dominated by three diatom genera: *Rhizosolenia*, *Thalassiosira* and *Chaetoceros*. *Rhizosolenia* was the largest diatom genus (mean length 288 µm) occurring in the mesocosms. Although *Rhizosolenia* was grazed to some extent, electivity values showed that it was less-preferred compared to other phytoplankton. It thereby had an advantage resulting in a relatively constant biomass value of ∼27% of the total phytoplankton biomass throughout the experiment. A good example for the opening of loopholes via selective grazing is the genus *Thalassiosira*. Two species occurred during the experiments, *T. rotula* and *T. nordenskjoeldii*, whereas the latter one dominated the total *Thalassiosira* spp. biomass with up to 92% and its dominance increased with the duration of the bloom. Both *Thalassiosira* species are able to form long chains but, in addition, *T. nordenskjoeldii* possesses spines. During our experiment, *T. nordenskjoeldii* was always a less-preferred prey item resulting in an increase in *Thalassiosira* spp. from 10 to 49% of total phytoplankton biomass. The other spine-possessing and chain-forming genus *Chaetoceros* showed a more ambivalent picture. It consisted of species of different size classes (10–40 µm diameter per cell). While the small *Chaetoceros* spp. (10 µm) totally disappeared due to grazing, others, especially the bigger ones with long spines, were grazed less and remained as a constant fraction of the phytoplankton. Even if some bloom dynamics were observed, the consumption and selective grazing by microzooplankton stabilised the phytoplankton assemblage and widened the loophole for the bloom of three less-favoured diatom taxa.

Microzooplankton species succession: a direct response to different food availability

The general succession pattern and species composition of the microzooplankton in the mesocosms was comparable to the patterns previously observed in the field at Helgoland Roads. In early spring, ciliates are the major group of microzooplankton grazers as they respond rapidly to increasing phytoplankton availability and dinoflagellates follow the ciliate bloom with some delay (Löder et al. 2011).

In the mesocosms, ciliates showed a direct response and distinct succession patterns in relation to food availability which was most pronounced in the genera *Strombidium* and *Strobilidium*. Their abundance was directly coupled with the availability of flagellate prey and resulted in a strong suppression of flagellates during the ciliate peak. With the disappearance of their predators due to food shortage the

relaxation from grazing pressure re-enabled a positive net growth of flagellates. The fact that they did not disappear completely due to grazing is most probably due to selective predation on specific flagellate species. This predator–prey relationship was most obvious in *Strombidium capitatum*, which is known to be directly dependent on flagellate prey (Stoecker and Silver 1990) and forms cysts as soon as unfavourable conditions occur (Kim et al. 2008). Simultaneously with the disappearance of its potential prey (dinoflagellates < 15 μm) *S. capitatum* started to form cysts and its population collapsed within 1 week. After the decrease of strombidiids and strobilids, *Cyclotrichium* sp. a ciliate which also feeds on diatoms (Xu et al. 2005) started to dominate and towards the end of the bloom bacterivorous ciliates (*Acineta* sp., *Euplotes* sp.) gained in importance.

In contrast, dinoflagellates showed unclear succession patterns compared to ciliates. While two groups disappeared due to predation by ciliates (thecate and athecate dinoflagellates < 15 μm), the remaining dinoflagellate community remained relatively stable until the end of the experiment. This was most likely related to the fact that diatoms, the preferred prey of dinoflagellates (Sherr and Sherr 2007), were always present. The opposing patterns found for dinoflagellates and ciliates might also be related to a contrasting ecological strategy of these groups. Dinoflagellates are considered to have lower growth rates than ciliates (Hansen 1992), and therefore, their ability to react rapidly to enhanced food availability is limited. On the other hand, dinoflagellates can prey on almost every organic particle present in the oceans (Jeong 1999; Tillmann 2004). Additionally, they have a higher starving potential (Hansen 1992; Menden-Deuer et al. 2005), and thus can survive periods of food shortage (Sherr and Sherr 2007). In contrast, ciliates can respond rapidly to enhanced food availability showing growth rates higher than those of dinoflagellates (Strom and Morello 1998) but their potential to survive starvation periods is low (Jackson and Berger 1985; Hansen 1992) and they are more restricted to certain prey items (Tillmann 2004). Thus, the succession of microzooplankton observed in the present study is mainly triggered by the availability of food and contrasting survival strategies. In this context, ciliates can be considered specialists and dinoflagellates to be more generalists. Furthermore, the close resemblance of the mesocosm succession (no top-down control by mesozooplankton) with the general spring succession patterns as observed in the field (top-down control by mesozooplankton present) (Löder et al. 2011) suggest that microzooplankton species succession is mainly triggered by food availability (bottom-up), whereas abundance in the field should be subject to a combination of the factors food availability and predation (combined effects of bottom-up and top-down control).

Potential factors determining the microzooplankton bloom in the mesocosms

Interestingly, microzooplankton biomass started to decline at a mean rate of -0.15 day^{-1} to a level close to the start value immediately after it reached its peak. The collapse started 1 week after the phytoplankton bloom peak, even though a considerable amount of phytoplankton was still available. Furthermore, neither phytoplankton composition nor grazing impact or food selectivity of microzooplankton changed greatly. However, all microzooplankton taxa, except *Strombidium* spp. and rotifers (Table 3), displayed mortality rates of -0.05 to -0.52 day^{-1}.

Besides strong predator–prey relations that lead to the death of the predator due to starvation when its prey is absent (Jackson and Berger 1985; this study) changes in the food quality of the preferred food might be a plausible explanation for the decline in microzooplankton biomass. This seems even more reasonable given the fact that prey availability was not limited. With the duration of the bloom in our mesocosms phytoplankton got increasingly nutrient-depleted (Schoo 2010), and therefore, it seems likely that phytoplankton during the post-bloom phase did not meet the nutritional needs of the microzooplankton. The effort to capture, handle, digest the prey and egest the excess carbon might have been more energy demanding than the energy benefit the prey offered resulting in low growth or even mortality.

Negative effects due to poor food have been reported (Jensen and Hessen 2007) and if predators have the choice between good and bad food they naturally choose the good one. Other microzooplankters, which feed on nutrient-limited phytoplankton, represent the better food when compared to the phytoplankton itself (Malzahn et al. 2010). Thus, an additional effect introduced by "bad quality phytoplankton" may have been predation within microzooplankton. Pronounced carnivory towards the end of phytoplankton blooms has been described by Irigoien et al. (2005) and in our experiment microzooplankton might also have switched its feeding strategy.

Towards the end of the bloom rotifers gained in importance (up to 28% of biomass). They are the only group, besides *Strombidium* spp. (unimportant from a biomass perspective) which showed positive growth rates. About 10–40% of rotifer food can consist of heterotrophic components as rotifers are efficient predators on protozoans (Arndt 1993). It is therefore most likely that the combined effect of both, predation within the microzooplankton especially by rotifers and the bad nutritional quality of the

food sources, resulted in an overall decline in microzooplankton abundance.

Copepod selective feeding and the microzooplankton fate in a real bloom

Microzooplankton is able to compete with copepods for the same food and to exploit food stocks more efficiently due to their fast metabolic abilities and growth rates (Hansen 1992; Sherr and Sherr 2007; Aberle et al. 2007). They in turn are preferred food for higher trophic levels, e.g. mesozooplankton, even if phytoplankton is available in high numbers but with a low food quality (Hansen et al. 1993). Although the degree of herbivory differs between copepod species (Maar et al. 2004), microzooplankton contributes as a substantial part to copepods' diets and it is often positively selected (Nejstgaard et al. 1997; Fileman et al. 2007). Gifford and Dagg (1988) showed for the copepod *Acartia tonsa* that even when microzooplankton was present in low concentrations (3% of total carbon) it made up to 41% of the copepods diet. Grazing on microzooplankton by copepods can result severe trophic cascade effects. The release of microzooplankton grazing pressure can promote nanoflagellates, an important prey of ciliates, and thus affect bacterial abundance negatively as bacteria are the main food source of nanoflagellates (Zöllner et al. 2009). Even more pronounced effects were reported for chlorophyll *a* concentrations: copepod grazers reduced microzooplankton biomass and led to overall higher chlorophyll *a* concentrations due to the release of small sized flagellates from microzooplankton grazing (Sommer et al. 2003, 2005a, b).

Trophic upgrading of food by heterotrophic protists (Martin-Creuzburg et al. 2005; Tang and Taal 2005; Bec et al. 2006) has been demonstrated. Data also show that protozoan grazers can compensate stoichiometric imbalances to a certain extent when they feed on low quality food (Malzahn et al. 2010). This fact, as well as their capacity to synthesise highly unsaturated fatty acids and sterols makes them good quality food from a copepod perspective (Klein Breteler et al. 1999; Tang and Taal 2005). With decreasing phytoplankton food quality in our experiments *T. longicornis* changed its diet gradually from phytoplankton-dominated to microzooplankton-dominated over the course of the bloom. Hence, we observed high positive selection for microzooplankton species, especially larger dinoflagellates and ciliates. This is in contrast to a laboratory study by Jakobsen et al. (2005) where *T. longicornis* showed no selectivity when offered mixed prey including a ciliate. Koski et al. (2005) found only a weak selectivity in *T. longicornis* during a mesocosm *Phaeocystis globosa* bloom. However, studies cited in Koski et al. (2005) provided evidence for a selective feeding capability of *T. longicornis,* especially a positive selection for microzooplankton, dinoflagellates and ciliates. Given the fact that copepod species like *T. longicornis* positively select for microzooplankton and can have a severe grazing impact on microzooplankton we assume that microzooplankton biomass can be top-down controlled by copepod grazing during spring bloom situations at Helgoland Roads if the density of predators is high enough.

Conclusions

1. Microzooplankton reacted quickly to enhanced prey availability and its high grazing rates contributed to a decrease to pre-bloom concentrations of phytoplankton.
2. Microzooplankton was the more efficient phytoplankton grazer when compared with copepods.
3. Selective grazing by microzooplankton supported a bloom of less-favoured phytoplankton species and stabilised the shares of bloom-forming species during the course of the bloom.
4. Ciliates responded with rapid growth and mortality to differences in prey availability, leading to a short but large peak. Dinoflagellates had a broader food spectrum and lower growth and mortality rates, which led to a longer duration of the dinoflagellate bloom.
5. As a substantial part of the copepods' diet microzooplankton became more important with decreasing food quality of the phytoplankton during the course of the bloom.

Appendix

See Tables 5, 6, 7, and 8.

Table 5 Microzooplankton grazing g (day^{-1}), phytoplankton growth rates k (day^{-1}) and instantaneous growth rate values μ_o (day^{-1}) from bottles without added nutrients, percentage of initial stock P_i (%) and potential production P_p (%) grazed as determined in four dilution experiments for each registered prey taxon

Phytoplankton	Microzooplankton													
	Experiment 1 (MMC 30.33 μgC L^{-1})							Experiment 2 (MMC 74.47 μgC L^{-1})						
	k	P	g	P	μ_0	P_i	P_p	k	P	g	P	μ_0	P_i	P_p
Pseudonitzschia spp. (120 μm)	0.43	***	0.62	**	0.31	86	172	0.87	****	1.04	****	1.52	183	83
Pseudonitzschia spp. (80 μm)	*0.14*		*0.29*		*−0.46*	*34*	*0*	0.57	***	0.66	*	0.85	93	84
Pseudonitzschia spp. (60 μm)	*0.44*		*1.08*		*0.51*	*195*	*164*	0.99	****	0.88	*	0.50	142	148
Navicula spp. (40 μm)	*0.66*	*	*0.39*	*	*0.16*	*48*	*220*	0.98	****	1.35	****	1.62	285	92
Navicula spp. (20 μm)	*0.08*		*−0.21*		*−0.28*	*0*	*74*	0.20		0.52	*	0.23	68	199
Navicula spp. (10 μm)	*−0.32*	*	*−0.50*		*−0.39*	*0*	*135*	0.24	*	0.44	*	0.16	56	237
Chaetoceros danicus	*1.14*	**	*1.11*	****	*0.65*	*203*	*141*	0.40	**	0.16		0.30	18	58
Chaetoceros spp. (40 μm)	*0.72*	**	*1.16*	**	*0.62*	*220*	*149*	1.07	****	0.91	**	1.25	150	84
Chaetoceros spp. (30 μm)	*0.48*	**	*0.77*	**	*0.86*	*116*	*93*	0.59	***	0.54	*	0.93	71	69
Chaetoceros spp. (20 μm)	*0.41*		*0.55*	*	*0.40*	*72*	*129*	1.60	****	1.69	****	1.70	443	100
Chaetoceros spp. (10 μm)	*0.71*	*	*1.19*	*	*0.73*	*230*	*135*	1.34	***	0.75		0.66	113	109
Rhizosolenia styliformis/hebetata	*0.32*		*0.35*	**	*0.03*	*42*	*1063*		****	0.61	****	0.62	85	99
Rhizosolenia pungens/setigera	*−0.58*	*	*−0.73*	*	*0.05*	*0*	*0*	1.09	****	1.02	****	1.03	177	99
Thalassiosira nordenskioeldii	*0.50*	***	*0.50*	*	*0.33*	*65*	*141*	0.66	****	0.39	*	0.63	47	69
Thalassiosira rotula	*0.56*	****	*0.68*	**	*0.64*	*96*	*104*	−0.14		−0.29		0.16	0	0
Flagellates (25 μm)	*0.54*		*0.68*	*	*0.83*	*98*	*88*	0.49	*	0.74	*	0.78	110	97
Flagellates (20 μm)	*0.11*		*0.02*		*−0.12*	*2*	*0*	0.07		0.47	*	−0.06	60	0
Flagellates (15 μm)	*−0.52*	**	*−0.36*		*−0.47*	*0*	*0*	0.53	***	0.91	***	0.69	149	119
Flagellates (10 μm)	*0.49*	*	*0.31*	**	*−0.23*	*36*	*0*	0.46	**	0.66	**	0.58	94	109
Flagellates (5 μm)	*0.24*		*0.28*	**	*−0.61*	*32*	*0*	0.79	****	1.21	***	1.42	236	93
Total phytoplankton	*0.41*	*	*0.43*	*	*0.17*	*53*	*223*	0.80	****	0.66	***	0.77	93	90
	Experiment 3 (MMC 93.82 μgC L^{-1})							Experiment 4 (MMC 33.12 μgC L^{-1})						
Pseudonitzschia spp. (120 μm)	0.38	***	0.41	*	0.46	51	91	0.78	****	0.44	****	0.75	55	67
Pseudonitzschia spp. (80 μm)	0.91	****	0.94	***	1.26	156	85	1.08	****	1.14	***	1.82	213	81
Pseudonitzschia spp. (60 μm)	1.63	****	2.04	****	2.02	666	100	1.02	***	1.22	**	1.46	239	92
Navicula spp. (40 μm)	*1.35*	****	*1.62*	****	*0.16*	*404*	*541*	0.20		0.50	*	−0.20	66	0
Navicula spp. (20 μm)	0.15		0.52		0.45	68	111	−0.18		0.18		0.18	19	96
Navicula spp. (10 μm)	0.30		0.62	*	0.23	85	223	1.32	**	1.43	*	2.18	316	86
Chaetoceros danicus	−0.03		−0.07		−0.02	0	0	−0.28		−0.11		0.21	0	0
Chaetoceros spp. (40 μm)	1.09	****	1.42	***	1.72	313	92	1.18	****	1.00	**	1.67	173	78
Chaetoceros spp. (30 μm)	0.45	*	0.34		0.50	40	73	1.17	****	0.84	****	1.66	131	70
Chaetoceros spp. (20 μm)	0.27	*	0.51	*	0.08	66	515	0.64	****	0.16		0.68	18	31
Chaetoceros spp. (10 μm)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia styliformis/hebetata	0.41	****	0.47	****	0.73	61	73	0.50	****	0.36	**	0.65	43	63
Rhizosolenia pungens/setigera	0.64	**	0.66	*	0.74	93	92	*0.33*		*0.28*		*0.06*	*32*	*409*
Thalassiosira nordenskioeldii	0.17	**	0.49	****	0.49	63	99	0.62	****	0.58	****	0.73	79	85
Thalassiosira rotula	0.51	***	0.87	**	1.14	138	85	0.86	****	0.70	***	1.20	102	72
Flagellates (25 μm)	1.34	*	1.92	*	2.36	584	94	1.33		1.33		3.04	278	77
Flagellates (20 μm)	0.43		1.03	*	0.76	180	121	0.66	*	0.98	*	0.73	165	121
Flagellates (15 μm)	0.84	****	1.38	****	0.72	299	146	0.28		0.50		0.68	65	79
Flagellates (10 μm)	0.82	****	0.99	****	0.95	169	102	−0.49		−0.12		−0.59	0	0
Flagellates (5 μm)	0.57	****	0.54	**	0.76	72	79	*0.007*		*0.26*	*	*−0.33*	*30*	*0*
Total phytoplankton	0.39	****	0.54	****	0.65	72	87	0.41	****	0.39	***	0.52	48	80

Food saturation given in italic values; negative P_i and P_p values resulting from negative g (P_i) or μ_o (P_p) were set to zero, also positive P_p values resulting from negative g and μ_o

MMC mean microzooplankton carbon biomass

P values from linear regression analysis of apparent phytoplankton growth against dilution factor ($n = 36$), * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 6 Microzooplankton carbon-specific filtration rates F_c (mL µgC predator^{-1} day^{-1}) and carbon-specific ingestion rates I_c (µgC prey µgC predator^{-1} day^{-1}), total ingestion rates of the microzooplankton community I_{total} (µgC prey L^{-1} day^{-1}) and electivity $E*$ (−) for each registered prey taxon

Phytoplankton	Microzooplankton									
	Experiment 1 (MMC 30.33 µgC L^{-1})					Experiment 2 (MMC 74.47 µgC L^{-1})				
	F_c	P	I_c	P	$E*$	F_c	P	I_c	P	$E*$
Pseudonitzschia spp. (120 µm)	20.52	**	0.0179	**	*0.11*	13.97	****	0.0070	****	*0.16*
Pseudonitzschia spp. (80 µm)	9.58		0.0015		−0.26	8.83	*	0.0009	*	−0.06
Pseudonitzschia spp. (60 µm)	35.71		0.0003		*0.37*	11.86	*	0.0002	*	*0.08*
Navicula spp. (40 µm)	12.94	*	0.0008	*	−0.12	18.10	****	0.0018	****	*0.29*
Navicula spp. (20 µm)	−6.98		−0.0034		−1.00	7.00	*	0.0032	*	−0.18
Navicula spp. (10 µm)	−16.40		−0.0542		−1.00	5.97	*	0.0244	*	−0.26
Chaetoceros danicus	36.51	****	0.0914	****	*0.38*	2.20		0.0046		−0.64
Chaetoceros spp. (40 µm)	38.31	**	0.0301	**	*0.40*	12.28	**	0.0096	**	*0.10*
Chaetoceros spp. (30 µm)	25.33	**	0.0500	**	*0.21*	7.23	*	0.0292	*	−0.16
Chaetoceros spp. (20 µm)	17.97	*	0.1322	*	*0.04*	22.72	****	0.0673	****	*0.39*
Chaetoceros spp. (10 µm)	39.33	*	0.0826	*	*0.41*	10.12		0.0046		*0.00*
Rhizosolenia styliformis/hebetata	11.66	**	0.4002	**	−0.17	8.23	****	0.2548	****	−0.10
Rhizosolenia pungens/setigera	−24.13	*	−0.0588	*	−1.00	13.67	****	0.1286	****	*0.15*
Thalassiosira nordenskioeldii	16.48	*	0.5005	*	0.00	5.21	*	0.1975	*	−0.32
Thalassiosira rotula	22.27	**	0.2031	**	*0.15*	−3.95		−0.0396		−1
Flagellates (25 µm)	22.57	*	0.0073	*	*0.16*	9.99	*	0.0035	*	0.00
Flagellates (20 µm)	0.73		0.0006		−0.91	6.32	*	0.0092	*	−0.23
Flagellates (15 µm)	−11.72		−0.0262		−1.00	12.23	***	0.0263	***	*0.10*
Flagellates (10 µm)	10.17	**	0.0524	**	−0.24	8.89	**	0.0271	**	−0.06
Flagellates (5 µm)	9.17	**	0.0698	**	−0.28	16.26	***	0.0366	***	*0.24*
Total phytoplankton	14.02	*	1.57	*		8.85	***	1.00	***	
Related to total microzooplankton C L^{-1}	I_{total}	47.65				I_{total}	74.58			

Phytoplankton	Experiment 3 (MMC 93.82 µgC L^{-1})					Experiment 4 (MMC 33.12 µgC L^{-1})				
	F_c	P	I_c	P	$E*$	F_c	P	I_c	P	$E*$
Pseudonitzschia spp. (120 µm)	4.41	*	0.0043	*	−0.36	13.23	****	0.0105	****	−0.18
Pseudonitzschia spp. (80 µm)	10.01	***	0.0008	***	*0.03*	34.47	***	0.0021	***	*0.29*
Pseudonitzschia spp. (60 µm)	21.70	****	0.0002	****	*0.40*	36.88	**	0.0002	**	*0.32*
Navicula spp. (40 µm)	17.24	****	0.0008	****	*0.29*	15.21	*	0.0007	*	−0.11
Navicula spp. (20 µm)	5.52		0.0012		−0.26	5.36		0.0007		−0.56
Navicula spp. (10 µm)	6.56	*	0.0026	*	−0.18	43.05	*	0.0019	*	*0.39*
Chaetoceros danicus	−0.78		−0.0016		−1	−3.34		−0.0041		−1
Chaetoceros spp. (40 µm)	15.12	***	0.0117	***	*0.23*	30.30	**	0.0146	**	*0.23*
Chaetoceros spp. (30 µm)	3.59		0.0185		−0.45	25.33	****	0.0511	****	*0.14*
Chaetoceros spp. (20 µm)	5.41	*	0.0336	*	−0.27	4.94		0.0275		−0.59
Chaetoceros spp. (10 µm)	–	–	–	–	–	–	–	–	–	–
Rhizosolenia styliformis/hebetata	5.05	****	0.1467	****	−0.30	10.75	**	0.2776	**	−0.28
Rhizosolenia pungens/setigera	7.02	*	0.0321	*	−0.14	8.46		0.0192		−0.38
Thalassiosira nordenskioeldii	5.19	****	0.1874	****	−0.29	17.65	****	0.3726	****	−0.03
Thalassiosira rotula	9.24	**	0.0501	**	−0.01	21.19	***	0.0669	***	*0.06*
Flagellates (25 µm)	20.49	*	0.0013	*	*0.37*	40.18		0.0017		*0.36*
Flagellates (20 µm)	10.97	*	0.0017	*	*0.08*	29.47	*	0.0049	*	*0.22*
Flagellates (15 µm)	14.75	****	0.0020	****	*0.22*	15.09		0.0027		−0.11
Flagellates (10 µm)	10.54	****	0.0151	****	*0.06*	−3.70		−0.0284		−1
Flagellates (5 µm)	5.80	**	0.0834	**	−0.24	7.96	*	0.0857	*	−0.41
Total phytoplankton	5.77	****	0.62	****		11.89	***	0.97	***	
Related to total microzooplankton C L^{-1}	I_{total}	58.02				I_{total}	32.13			

Positive selection given in italic values

MMC mean microzooplankton carbon biomass

P values are the same as for the grazing rates of microzooplankton, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 7 *Temora longicornis* grazing g (day^{-1}), phytoplankton and microzooplankton growth rates k (day^{-1}) and phytoplankton instantaneous growth rate values μ_o (day^{-1}) from bottles without added nutrients, percentage of initial stock P_i (%) and potential production P_p (%) grazed as determined in four grazing experiments for each registered prey taxon

| | *Temora longicornis* (TC 108.70 μgC L^{-1}) | | | | | | | | | | | | | |
| | Experiment 1 | | | | | | | Experiment 2 | | | | | | |
	k	P	g	P	μ_0	P_i	P_p	k	P	g	P	μ_0	P_i	P_p
Phytoplankton														
Pseudonitzschia spp. (120 μm)	−0.11		−0.02		0.31	0	0	−0.15	*	0.02		1.52	2	2
Pseudonitzschia spp. (80 μm)	−0.25		0.07		−0.46	8	0	−0.08		−0.04		0.85	0	0
Pseudonitzschia spp. (60 μm)	−0.29		0.51		0.51	67	99	0.26		−0.03		0.50	0	0
Navicula spp. (40 μm)	0.25		0.35		0.16	42	202	−0.27		0.21		1.62	24	24
Navicula spp. (20 μm)	0.30	*	0.01		−0.28	1	0	−0.25		0.02		0.23	2	11
Navicula spp. (10 μm)	0.15		−0.06		−0.39	0	0	−0.16		0.04		0.16	4	27
Chaetoceros danicus	0.00		1.01	**	0.65	174	134	0.36		0.08		0.30	8	29
Chaetoceros spp. (40 μm)	−0.30		0.17		0.62	19	34	0.33		0.38		1.25	46	44
Chaetoceros spp. (30 μm)	−0.15		0.29		0.86	33	43	0.31		0.43		0.93	54	58
Chaetoceros spp. (20 μm)	−0.13		0.41	**	0.40	50	102	0.08		0.43	*	1.70	53	42
Chaetoceros spp. (10 μm)	−0.31		−0.10		0.73	0	0	1.29		2.06		0.66	686	180
Rhizosolenia styliformis/hebetata	−0.04		0.13		0.03	14	432	−0.06		0.11		0.62	12	23
Rhizosolenia pungens/setigera	0.17		0.29		0.05	34	500	0.20		0.42	**	1.03	52	53
Thalassiosira nordenskioeldii	0.02		0.17	*	0.33	18	55	0.34	**	0.51	*	0.63	67	86
Thalassiosira rotula	−0.07		0.30	**	0.64	35	55	0.15		0.37	*	0.16	45	212
Flagellates (25 μm)	0.03		0.99		0.83	170	112	−0.20		0.08		0.78	8	14
Flagellates (20 μm)	−0.05		0.32		−0.12	38	0	−0.36		0.37		−0.06	45	0
Flagellates (15 μm)	−0.24		0.02		−0.47	2	0	−0.38	**	0.22	**	0.69	25	40
Flagellates (10 μm)	0.14		0.31		−0.23	37	0	−0.09		0.20		0.58	22	41
Flagellates (5 μm)	−0.04		−0.14		−0.61	0	0	−0.44		−0.43		1.42	0	0
Total phytoplankton	−0.01		0.17	***	0.17	18	100	0.13	*	0.34	*	0.77	40	54
Microzooplankton														
Gyrodinium spp. (30–75 μm)	−0.05		1.12	**		207	0	0.33	****	0.24	**		27	76
Gyrodinium spp. (75–120 μm)	0.30	*	0.95	**		158	236	0.17		1.00	****		172	407
Protoperidinium spp. (20–40 μm)	0.41		−0.14			0	0	0.11		0.37	*		45	287
Protoperidinium spp. (50–80 μm)	0.17		1.15	**		217	435	0.23		0.32	*		38	136
Ceratium spp.	−0.21		1.51			354	0	0.06		0.19			21	325
Torodinium spp.	0.02		0.23			26	1047	0.15		−0.03			0	0
Other athecate dinoflagellates	0.02		0.18			19	729	−0.02		0.31	*		37	0
Other thecate dinoflagellates	0.40	****	−0.03			0	0	−0.44	****	0.21	*		23	0
Strombidium spp. (25–40 μm)	−0.12		0.39			47	0	0.34	***	0.75	**		111	181
Strombidium spp. (40–110 μm)	0.32	*	1.24	***		245	257	0.46	****	0.80	****		122	148
Strobilidium spp.	0.26		0.92	*		150	262	0.66	***	0.36	**		43	62
Myrionecta rubra	0.18		0.95	**		158	373	−0.32		0.17			18	0
Other Cyclotrichids	0.00		0.00			0	–	−0.67		–			–	–
Haptorids	−0.28		0.93	*		154	0	0.39		0.35			42	91
Tintinnids	0.11		−0.08			0	0	0.09		0.52	*		69	452
Other Ciliates	–		–			–	–	–		–			–	–
Thecate amoeba sp.	0.16		0.32	***		38	191	0.25	**	0.23	*		26	93
Rotifers	0.00		–			–	–	–		–			–	–
Total microzooplankton	0.21	****	0.40	****		49	174	0.27	****	0.43	****		53	147

Table 7 continued

	Experiment 3							Experiment 4						
Phytoplankton														
Pseudonitzschia spp. (120 µm)	−0.04		0.34		0.46	41	78	0.38	***	0.13		0.75	14	23
Pseudonitzschia spp. (80 µm)	−0.05		0.14		1.26	15	18	0.06		0.88	**	1.82	140	70
Pseudonitzschia spp. (60 µm)	−0.37		0.09		2.02	9	10	−0.24		0.57		1.46	78	57
Navicula spp. (40 µm)	−0.28		0.74	***	0.16	109	353	−0.47		0.23		−0.20	26	0
Navicula spp. (20 µm)	−0.46		−0.01		0.45	0	0	−0.36	*	−0.11		0.18	0	0
Navicula spp. (10 µm)	−0.39	*	0.45	**	0.23	56	175	−0.08		0.20		2.18	22	20
Chaetoceros danicus	0.02		0.18		−0.02	19	0	−0.19		0.43		0.21	53	182
Chaetoceros spp. (40 µm)	−0.23		0.35		1.72	42	36	0.23		0.48		1.67	61	47
Chaetoceros spp. (30 µm)	0.19		−0.10		0.50	0	0	0.32	*	0.24		1.66	28	27
Chaetoceros spp. (20 µm)	−0.16		0.56	***	0.08	75	555	0.38		−0.10		0.68	0	0
Chaetoceros spp. (10 µm)	–		–		–	–	–	–		–		–	–	–
Rhizosolenia styliformis/hebetata	−0.09		0.02		0.73	2	4	0.14		0.04		0.65	4	7
Rhizosolenia pungens/setigera	0.06		0.15		0.74	16	27	0.03		0.42	**	0.06	52	569
Thalassiosira nordenskioeldii	−0.36	*	0.04		0.49	5	11	0.06		0.17	*	0.73	19	30
Thalassiosira rotula	−0.34		−0.02		1.14	0	0	0.21		0.24		1.20	27	30
Flagellates (25 µm)	−0.28		1.40		2.36	305	83	0.00		−1.05		3.04	0	0
Flagellates (20 µm)	−0.51	*	0.07		0.76	7	12	−0.21		0.24		0.73	28	42
Flagellates (15 µm)	−0.39	*	0.42		0.72	53	67	−0.10		−0.11		0.68	0	0
Flagellates (10 µm)	−0.15		−0.07		0.95	0	0	−0.36	****	−0.16		−0.59	0	0
Flagellates (5 µm)	−0.04		0.27	**	0.76	32	45	−0.20		−0.18	*	−0.33	0	0
Total phytoplankton	−0.18		0.10		0.65	11	20	0.04		0.05		0.52	6	13
Microzooplankton														
Gyrodinium spp. (30–75 µm)	0.02		0.15	**		16	593	−0.22	*	0.42	**		52	0
Gyrodinium spp. (75–120 µm)	0.20	*	0.68	****		98	276	0.18		1.23	***		242	439
Protoperidinium spp. (20–40 µm)	0.03		0.24			27	802	−0.25		0.15			16	0
Protoperidinium spp. (50–80 µm)	0.14		0.91	**		149	467	−0.05		0.68	*		98	0
Ceratium spp.	0.26		0.50			65	170	−0.30		−0.39			0	0
Torodinium spp.	0.27		0.22			25	85	–		–			–	–
Other athecate dinoflagellates	–		–			–	–	–		–			–	–
Other thecate dinoflagellates	−0.26		−0.02			0	0	−0.47	*	0.06			6	0
Strombidium spp. (25–40 µm)	−0.15		1.34			284	0	–		–			–	–
Strombidium spp. (40–110 µm)	−1.61	****	0.15			16	0	0.61		0.19			20	37
Strobilidium spp.	−0.61	****	0.22			25	0	−0.21		0.40			50	0
Myrionecta rubra	−1.09	***	0.34	*		40	0	−0.72		0.49			63	0
Other Cyclotrichids	0.96	*	0.83			129	91	–		–			–	–
Haptorids	0.87	**	0.54	**		72	72	−0.52		2.48			1097	0
Tintinnids	0.26		0.69			100	216	–		–			–	–
Other Ciliates	0.32		0.27			31	87	−0.11		0.10			11	0
Thecate amoeba sp.	−0.11		0.13	*		13	0	−0.05		0.25	***		29	0
Rotifers	0.02		0.33			39	1183	0.03		1.84	***		529	3349
Total microzooplankton	0.07		0.38	***		46	478	−0.04		0.78	****		118	0

Negative P_i and P_p values resulting from negative g (P_i) or μ_c/k (P_p) were set to zero, also positive P_p values resulting from negative g and μ_c/k

TC total *T. longicornis* carbon biomass

P values derived from t tests against zero, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$

Table 8 *Temora longicornis* individual filtration F_i (mL Ind.$^{-1}$ day^{-1}) and ingestion rates I_i (ngC Ind.$^{-1}$ day^{-1}) as well as carbon-specific filtration rates F_c (mL µgC predator^{-1} day^{-1}) and carbon-specific ingestion rates I_c (µgC prey µgC predator^{-1} day^{-1}), total ingestion rates I_{total} (µgC prey L^{-1} day^{-1}) and electivity E^* (−) for each registered prey taxon

| | *Temora longicornis* (TC 108.70 µgC L^{-1}) | | | | | | | | | | | | | | | |
| | Experiment 1 | | | | | | | | Experiment 2 | | | | | | | |
	F_i	F_c	P	I_i	I_c	P	E^*	P	F_i	F_c	P	I_i	I_c	P	E^*	P
Phytoplankton																
Pseudonitzschia spp. (120 µm)	−1.48	−0.15		−1.65	−0.0002		−0.80	***	1.75	0.17		1.16	0.0001		−0.71	***
Pseudonitzschia spp. (80 µm)	6.80	0.68		−0.52	−0.0001		−0.56	*	−3.24	−0.32		−0.31	0.0000		−0.52	*
Pseudonitzschia spp. (60 µm)	46.91	4.69		0.44	0.0000		−0.52		−2.48	−0.25		−0.33	0.0000		−0.48	
Navicula spp. (40 µm)	32.58	3.26		1.12	0.0001		−0.22		19.66	1.97		0.98	0.0001		−0.49	*
Navicula spp. (20 µm)	1.01	0.10		0.90	0.0001		−0.58	**	2.10	0.21		3.57	0.0004		−0.60	***
Navicula spp. (10 µm)	−5.31	−0.53		−18.19	−0.0018		−0.82	***	3.86	0.39		26.02	0.0026		−0.59	*
Chaetoceros danicus	92.80	9.28	**	122.09	0.0122	**	0.21		7.30	0.73		4.94	0.0005		−0.65	**
Chaetoceros spp. (40 µm)	15.82	1.58		4.50	0.0004		−0.40		34.98	3.50		17.82	0.0018		−0.18	
Chaetoceros spp. (30 µm)	26.53	2.65		47.82	0.0048		−0.34		40.01	4.00		32.18	0.0032		−0.01	
Chaetoceros spp. (20 µm)	37.28	3.73	**	219.95	0.0220	**	−0.21		39.20	3.92	*	101.04	0.0101		−0.13	
Chaetoceros spp. (10 µm)	−9.38	−0.94		−24.59	−0.0025		−0.86	****	189.72	18.97		65.33	0.0065		0.51	
Rhizosolenia styliformis/hebetata	11.88	1.19		398.88	0.0399		−0.60	**	10.15	1.02		316.50	0.0316		−0.46	*
Rhizosolenia pungens/ setigera	26.92	2.69		70.84	0.0071		−0.01		38.36	3.84	**	290.95	0.0291	**	−0.16	
Thalassiosira nordenskioeldii	15.47	1.55	*	439.49	0.0439	*	−0.52	***	47.27	4.73	*	1311.92	0.1312	*	−0.07	
Thalassiosira rotula	27.63	2.76	**	222.88	0.0223	**	−0.32	*	33.88	3.39	*	254.22	0.0254	*	−0.15	
Flagellates (25 µm)	91.50	9.15		28.93	0.0029		0.12		7.19	0.72		−14.08	−0.0014		−0.42	
Flagellates (20 µm)	29.59	2.96		11.03	0.0011		−0.12		34.13	3.41		36.32	0.0036		−0.31	
Flagellates (15 µm)	2.25	0.22		8.44	0.0008		−0.44	**	20.61	2.06	**	38.86	0.0039	*	−0.34	*
Flagellates (10 µm)	28.70	2.87		82.87	0.0083		−0.29		18.39	1.84		45.95	0.0046		−0.43	
Flagellates (5 µm)	−13.28	−1.33		−134.07	−0.0134		−0.82	****	−39.27	−3.93		−79.18	−0.0079		−0.87	****
Total phytoplankton	15.51	1.55	***	1643.64	0.1644	***	−0.28	**	31.21	3.12	*	2973.72	0.2974	*	−0.28	
Related to total copepod C L^{-1}				I_{total}	17.87							I_{total}	32.32			
Microzooplankton																
Gyrodinium spp. (30–75 µm)	103.21	10.32	**	236.46	0.0236	**	0.10		22.17	2.22	**	281.39	0.028	**	−0.27	
Gyrodinium spp. (75–120 µm)	87.07	8.71	**	27.29	0.0027	**	0.34		91.98	9.20	****	52.12	0.0052	***	0.41	***
Protoperidinium spp. (20–40 µm)	−13.29	−1.33		−0.56	−0.0001		−0.67	**	34.31	3.43	*	9.84	0.0010		−0.23	
Protoperidinium spp. (50–80 µm)	106.09	10.61	**	81.36	0.0081	**	0.31		29.62	2.96	*	82.35	0.0082	*	−0.20	
Ceratium spp.	139.27	13.93		10.68	0.0011		0.56		17.68	1.77		2.68	0.0003		−0.43	
Torodinium spp.	21.37	2.14		0.04	0.0000		−0.33		−2.91	−0.29		−0.39	0.0000		−0.70	**
Other athecate dinoflagellates	16.30	1.63		19.47	0.0019		−0.50	**	28.82	2.88	*	27.43	0.0027	*	−0.16	
Other thecate dinoflagellates	−2.59	−0.26		−23.41	−0.0023		−0.88	****	19.22	1.92	*	139.51	0.0140	*	−0.40	*
Strombidium spp. (25–40 µm)	35.67	3.57		3.97	0.0004		−0.25		68.57	6.86	**	9.15	0.0009	**	0.19	
Strombidium spp. (40–110 µm)	113.94	11.39	***	242.60	0.0243	****	0.37	**	73.24	7.32	****	1091.25	0.1091	****	0.34	***

Table 8 continued

| | Temora longicornis (TC 108.70 µgC L⁻¹) | | | | | | | | | | | | | | | |
| | Experiment 1 | | | | | | | | Experiment 2 | | | | | | | |
	F_i	F_c	P	I_i	I_c	P	$E*$	P	F_i	F_c	P	I_i	I_c	P	$E*$	P
Strobilidium spp.	84.30	8.43	*	42.07	0.0042	*	0.04		32.78	3.28	**	190.64	0.0191	**	−0.15	
Myrionecta rubra	87.06	8.71	**	179.10	0.0179	****	0.23	*	15.47	1.55		52.50	0.0052		−0.33	
Other Cyclotrichids	0.00	0.00		–	–		–		–	–		–	–		–	
Haptorids	85.78	8.58	*	7.02	0.0007	*	−0.08		32.07	3.21		2.06	0.0002		−0.16	
Tintinnids	−7.09	−0.71		−0.47	0.0000		−0.40		48.19	4.82	*	11.43	0.0011	**	0.08	
Other Ciliates	–	–		–	–		–		–	–		–	–		–	
Thecate amoeba sp.	29.76	2.98	***	60.68	0.0061	***	−0.26	*	21.60	2.16	*	142.56	0.0143	*	−0.30	
Rotifers	–	–		–	–		–		–	–		–	–		–	
Total microzooplankton	36.72	3.67	****	880.91	0.0881	****	0.15	**	39.33	3.93	****	2316.33	0.2316	****	0.04	
Related to total copepod C L⁻¹				I_{total}	9.58							I_{total}	25.18			

| | Experiment 3 | | | | | | | | Experiment 4 | | | | | | | |
	F_i	F_c	P	I_i	I_c	P	$E*$	P	F_i	F_c	P	I_i	I_c	P	$E*$	P
Phytoplankton																
Pseudonitzschia spp. (120 µm)	31.39	3.14		18.01	0.0018		−0.31		11.74	1.17		8.78	0.0009		−0.54	**
Pseudonitzschia spp. (80 µm)	12.71	1.27		0.57	0.0001		−0.49	*	80.56	8.06	**	3.13	0.0003	**	0.16	
Pseudonitzschia spp. (60 µm)	8.16	0.82		0.07	0.0000		−0.60		52.85	5.28		0.23	0.0000		0.00	
Navicula spp. (40 µm)	68.03	6.80	***	2.20	0.0002	**	0.22		21.06	2.11		0.61	0.0001		−0.37	
Navicula spp. (20 µm)	−0.48	−0.05		−2.95	−0.0003		−0.65	**	−10.07	−1.01		−2.23	−0.0002		−0.68	**
Navicula spp. (10 µm)	41.17	4.12	**	13.65	0.0014	*	−0.10		18.42	1.84		−0.36	0.0000		−0.54	
Chaetoceros danicus	16.32	1.63		23.65	0.0024		−0.42		39.14	3.91		35.57	0.0036		−0.16	
Chaetoceros spp. (40 µm)	32.00	3.20		14.46	0.0014		−0.35		43.83	4.38		10.20	0.0010		−0.27	
Chaetoceros spp. (30 µm)	−9.08	−0.91		−93.07	−0.0093		−0.76	****	22.52	2.25		26.28	0.0026		−0.41	
Chaetoceros spp. (20 µm)	51.58	5.16	***	259.00	0.0259	**	0.09		−8.80	−0.88		−91.85	−0.0092		−0.72	***
Chaetoceros spp. (10 µm)	–	–		–	–		–		–	–		–	–		–	
Rhizosolenia styliformis/hebetata	1.92	0.19		48.73	0.0049		−0.73	***	3.27	0.33		21.17	0.0021		−0.72	**
Rhizosolenia pungens/setigera	13.87	1.39		40.93	0.0041		−0.45	*	38.32	3.83	**	54.55	0.0055	*	−0.14	
Thalassiosira nordenskioeldii	4.11	0.41		10.62	0.0011		−0.66	**	15.73	1.57	*	303.59	0.0304	*	−0.42	*
Thalassiosira rotula	−1.52	−0.15		−24.78	−0.0025		−0.60	*	21.93	2.19		54.55	0.0055		−0.48	*
Flagellates (25 µm)	128.74	12.87		18.61	0.0019		0.56		−97.03	−9.70		−12.83	−0.0013		−1.00	
Flagellates (20 µm)	6.06	0.61		1.18	0.0001		−0.41		22.41	2.24		4.36	0.0004		−0.19	
Flagellates (15 µm)	39.00	3.90		5.40	0.0005		−0.15		−10.54	−1.05		−4.98	−0.0005		−0.70	**
Flagellates (10 µm)	−6.63	−0.66		−5.42	−0.0005		−0.82	***	−14.91	−1.49		−113.03	−0.0113		−0.86	****
Flagellates (5 µm)	25.29	2.53	**	310.09	0.0310	**	−0.28		−16.17	−1.62	*	−223.63	−0.0224	*	−0.95	****
Total phytoplankton	9.34	0.93		866.25	0.0866		−0.45	*	4.97	0.50		370.16	0.0370		−0.74	***
Related to total copepod C L⁻¹				I_{total}	9.42							I_{total}	4.02			
Microzooplankton																
Gyrodinium spp. (30–75 µm)	13.89	1.39	**	206.51	0.0207	**	−0.47	***	38.68	3.87	**	229.15	0.0229	***	−0.15	
Gyrodinium spp. (75–120 µm)	62.84	6.28	****	106.13	0.0106	****	0.24	**	113.01	11.30	***	175.73	0.0176	****	0.44	***

Table 8 continued

| | *Temora longicornis* (TC 108.70 μgC L^{-1}) | | | | | | | | | | | | | | | |
| | Experiment 1 | | | | | | | | Experiment 2 | | | | | | | |
	F_i	F_c	P	I_i	I_c	P	E*	P	F_i	F_c	P	I_i	I_c	P	E*	P
Protoperidinium spp. (20–40 μm)	22.11	2.21		2.04	0.0002		−0.46		13.45	1.34		0.65	0.0001		−0.52	*
Protoperidinium spp. (50–80 μm)	83.79	8.38	**	99.18	0.0099	**	*0.25*		62.94	6.29	*	61.92	0.0062	*	*0.02*	
Ceratium spp.	46.21	4.62		4.47	0.0004		−0.06		−36.28	−3.63		−12.94	−0.0013		−1.00	
Torodinium spp.	20.41	2.04		1.43	0.0001		−0.54		–	–		–	–		–	
Other athecate dinoflagellates	–	–		–	–		–		–	–		–	–		–	
Other thecate dinoflagellates	−1.89	−0.19		−7.54	−0.0008		−0.34		5.39	0.54		0.14	0.0000		−0.63	*
Strombidium spp. (25–40 μm)	123.67	12.37		5.06	0.0005		*0.42*		–	–		–	–		–	
Strombidium spp. (40–110 μm)	13.41	1.34		−173.09	−0.0173		−0.53		17.03	1.70		–	–		–	
Strobilidium spp.	20.27	2.03		85.21	0.0085		−0.38		37.08	3.71		1.23	0.0001		−0.18	
Myrionecta rubra	30.94	3.09	*	15.96	0.0016		−0.20		45.00	4.50		−7.01	−0.0007		−0.14	
Other Cyclotrichids	76.40	7.64		18.11	0.0018		0.00		–	–		–	–		–	
Haptorids	49.72	4.97	**	1116.13	0.1116		−0.10		228.35	22.83		198.93	0.0199		*0.19*	
Tintinnids	63.73	6.37		5.65	0.0006		*0.24*		–	–		–	–		–	
Other Ciliates	24.86	2.49		−2.36	−0.0002		−0.05		9.3870	0.94		29.6777	0.0030		−0.58	**
Thecate amoeba sp.	11.55	1.16	*	46.54	0.0047	*	−0.52	**	23.21	2.32	***	39.28	0.0039	***	−0.33	*
Rotifers	30.55	3.06		47.86	0.0048		−0.22		169.13	16.91	***	706.47	0.0706	***	*0.53*	***
Total microzooplankton	35.02	3.50	***	2649.93	0.2650	**	*0.18*	*	71.61	7.16	****	1635.56	0.1636	****	*0.28*	****
Related to total copepod C L^{-1}				I_{total}	28.80							I_{total}	17.78			

Positive selection given in italic values

TC total *T. longicornis* carbon biomass

P values derived from *t* tests against zero,* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

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