

Calanoid copepod grazing affects plankton size structure and composition in a deep, large lake

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Cultural oligotrophication is expected to shift lake zooplankton to become dominated by calanoid copepods. Hence, understanding the influence of calanoids on the taxonomic and size structure of the lower plankton food web is crucial for predicting the effects of oligotrophication on energy fluxes in these systems. We studied the effect of an omnivorous calanoid, *Eudiatomus gracilis*, on the lower planktonic food web using an *in situ* incubation approach in large and deep Lake Constance. We show that *E. gracilis* significantly reduced ciliate, phytoplankton, rotifer, but increased bacteria biovolume. Highest clearance rates were observed for ciliates whose biovolume declines may have caused a release of predation pressure on bacteria. *E. gracilis* grazing shifted the size structure of the phytoplankton community by reducing mean phytoplankton cell size (directional selection) and simultaneously increasing cell size variance (disruptive selection). Ciliate cell sizes experienced a similar selective regime in one of the experiments, whereas in the other two experiments, no change of size structure was detected. Results suggest strong influences of *E. gracilis* grazing on the lower plankton food web and a significant shift in phytoplankton size structure. For evaluating detailed effects of omnivorous consumers on plankton size structure, cascading interactions need to be considered.

KEYWORDS: directional and disruptive selection; omnivory; food web interactions; community structure; cascading interactions

INTRODUCTION

Body size is considered as a master trait in planktonic food webs because it is correlated with many physiological and life-history traits of organisms (Litchman *et al.*, 2007; Gianuca *et al.*, 2016). Body size controls growth, nutrient uptake and sedimentation as well as the vulnerability of organisms to predation (Sommer *et al.*, 2017). Hence, it is a key factor for energy transfer and nutrient regeneration within ecosystems (Hildrew *et al.*, 2007; Arhonditsis *et al.*, 2018).

In aquatic habitats, predator–prey relationships have been shown to be highly size-dependent (Hansen *et al.*, 1994; Scharf *et al.*, 2000; Emmerson and Raffaelli, 2004; Folke *et al.*, 2004). Usually, consumers prefer specific cell or body sizes of prey organisms resulting in predator–prey body size ratios based on the predator's feeding behaviour, e.g. foraging tactics, mode of ingestion or food preferences (Hansen *et al.*, 1994, 1997; Brose *et al.*, 2006). Amongst other factors, size-specific predation might play an important role for seasonal plankton succession (DeMott, 1989; Gliwicz and Pijanowska, 1989).

Numerous lakes in Europe and Northern America are currently undergoing oligotrophication, resulting in changes in the composition of planktonic food webs. (Søndergaard *et al.*, 1990; Jeppesen *et al.*, 2002, 2005; Van Donk *et al.*, 2008; Bunnell *et al.*, 2014; Watkins *et al.*, 2015). Copepods are key components within these food webs and calanoid copepods in particular dominate the crustacean zooplankton biomass in oligotrophic waters (Straile and Geller, 1998). Consequently, the relative importance of calanoid copepods is likely to increase in lakes which currently experience declines in nutrients, i.e. (re-) oligotrophication (Barbiero *et al.*, 2012, 2014; Rudstam *et al.*, 2015; Straile, 2015).

Calanoid copepods are known to switch their feeding mode from passive suspension feeding to ambush feeding depending on the concentration of prey (Vanderploeg and Paffenhöfer, 1985). This allows calanoid species to feed on a broad size range and high diversity of prey organisms (Stoecker and Egloff, 1987; Carrick *et al.*, 1991; Fessenden and Cowles, 1994; Adrian and Schneider-Olt, 1999; Šorf and Brandl, 2012). Several studies indicate size- and taxon-specific ingestion by small calanoid copepods. For instance, small calanoids similar in size to *Eudiaptomus gracilis* (e.g. *Boeckella* spp., *Diaptomus minutus*, *Diaptomus pygmaeus*, *Epischura baikalensis*, *Epischura lacustris*, *Eudiaptomus graciloides*) have been shown to highly select for ciliates with preference for smaller ciliates (size range: 10–20 µm) over smaller-sized algae (≤10 µm) as well as large ciliates (>20 µm) (Burns and Gilbert, 1993; Burns and Schallenberg, 1996; Burns and Schallenberg, 1998; Adrian and Schneider-Olt, 1999; Burns and

Schallenberg, 2001). Less is known about small calanoid predation effects on rotifers (Williamson and Butler, 1986; Dhanker *et al.*, 2012). In contrast, large calanoids (*Calanus propinquus*, *D. pallidus*, *E. lacustris*, *E. nevadensis*, *Limnocalanus macrurus*) feed primarily on larger animal prey such as rotifers and small crustaceans in addition to phytoplankton (Warren, 1985; Wong and Chow-Fraser, 1985; Schulze and Folt, 1990; Pasternak and Schnack-Schiel, 2001; Doubek and Lehman, 2014). Thus, both predator and prey sizes control the selective feeding behaviour of calanoids and therefore the structure of the prey community.

In many deep, peri-alpine European lakes, the calanoid copepod *Eudiaptomus gracilis* is abundant throughout the year (e.g. Anneville *et al.*, 2007; Seebens *et al.*, 2007). *E. gracilis* was long considered as a herbivorous species and therefore, many experimental studies were performed using algal dietary sources (Muck and Lampert, 1980; Horn, 1985a, b). Amongst phytoplankton, *E. gracilis* predominantly feeds on larger species and hence has been termed a 'macro-filtrator' (Horn, 1985a, b). However, *E. gracilis* also feeds on small algae groups such as *Scenedesmus* (~200 µm³) with enhanced filtering rates (Muck and Lampert, 1980). More recently, there is evidence for carnivorous feeding with studies showing preference for ciliates (Adrian and Schneider-Olt, 1999; Yoshida *et al.*, 2001) and rotifers up to 260 µm in body length and a body volume of 340 000 µm³, respectively (Brandl, 2005; Šorf and Brandl, 2012). Thus, *E. gracilis* seems to be an omnivorous consumer able to prey on primary producers (phytoplankton) but also on primary consumers (herbivorous ciliates and rotifers) and secondary consumers, e.g. predatory ciliates (Müller *et al.*, 1991). This suggests the potential for complex and cascading effects of this copepod's feeding on the structure and size of plankton communities.

Recently, Vellend proposed his 'theory of ecological communities' in which he advocated to organize community ecology into four high-level processes in analogy to evolutionary biology (natural selection theory): drift, selection, dispersal and speciation (Vellend, 2010, 2016). Using this framework, the grazing impact of a herbivore on a multispecies community may be conceptualized as selection of species resulting in changes in species and trait composition within a community. Accordingly, directional selection will change the mean of the prey size frequency distribution inducing a shift towards one end of the size spectrum; stabilising selection will decrease the variance of the size frequency distribution, whereas disruptive selection will increase the variance of the size frequency distribution (Coutinho *et al.*, 2016).

In this study, we analyse the direct and indirect influence of one of Europe's most common calanoid copepods, *E. gracilis*, on a natural plankton community

(rotifers, ciliates, heterotrophic flagellates, phytoplankton and bacteria) using an experimental approach in Lake Constance. We assess the impact of *E. gracilis* on the size structure and composition of the lower plankton food web during autumn as long-term data from this lake indicated that the copepod's abundance increases during this season (Seebens *et al.*, 2007).

More specifically, we test the following four hypotheses:

- 1) The grazing impact of *E. gracilis* is prey-size dependent resulting in largest clearance rates for rotifers, followed by ciliates and phytoplankton,
- 2) Grazing of *E. gracilis* results in cascading trophic interactions, i.e. high clearance rates for ciliates (large prey) will release bacteria (small prey) from predation,
- 3) Size-selective copepod feeding within taxonomic prey groups (phytoplankton, ciliates and rotifers) will result in smaller average body sizes (directional selection) and reduced body size variances (stabilising selection) within those groups, and
- 4) The effect of *E. gracilis* on the biovolume and the mean and variance of body size of plankton groups does show short-term (within weeks) temporal variation.

METHOD

Study system

To examine the grazing impact of *E. gracilis* and its short-term variability, we conducted three bottle experiments during a 3-week period in autumn 1998 in Überlinger See, a fjord-like basin of Upper Lake Constance (47° 45' N, 9° 08' E). Briefly, Upper Lake Constance is a large (473 km²), deep (maximum depth: 252 m), warm-monomictic peri-alpine lake bordering Germany, Switzerland and Austria, which experienced reoligotrophication during the last decades (Jochimsen *et al.*, 2013). During the study year, the lake was mesotrophic with a total phosphorus concentration of 0.55 µmol P L⁻¹ in September.

Incubation experiments

On the day before each of the three experiments (Experiment 1: 21 September; Experiment 2: 28 September and Experiment 3: 05 October 1998), specimens of *E. gracilis* were collected with a HYDROBIOS plankton net (38.5 cm diameter, 55 µm mesh size) in four vertical tows from 0 to 25 m depth and kept overnight in filtered lake water (0.45 µm pore size) at 17.2°C. Most of the copepods were adult egg-sac bearing females. Environmental conditions during the overall study period were rather stable

with Secchi depths slightly increasing from 5.8 (Experiment 1) to 7.4 m (Experiment 2), and 8.4 m (Experiment 3) and epilimnetic water temperatures (measured in 2 m depth) varying ~14°C (Experiment 1: 14°C, Experiment 2: 14.7°C and Experiment 3: 13.8°C).

On the first day of each experiment, eight transparent PVC bottles of ~1250 mL volume were filled *in situ* with lake water from a depth-integrated sample (0–20 m) gently mixed and filtered through a 55 µm mesh (Experiment 3: 100 µm) to remove mesozooplankton. Samples from the filtered lake water were directly taken as duplicates to define the initial microplankton composition (S) at the starting point of the study. Subsequently, four bottles (E1–E4) were populated with 30 adult individuals of *E. gracilis* individually, the remaining four bottles without copepods served as control/no copepod treatment (C1–C4). Similar densities of *E. gracilis* were reported for natural lake habitats, e.g. up to 22 ind L⁻¹ in Lake Balaton (Zánkai and Ponyi, 1986) and up to 9 ind L⁻¹ in Lake Constance (Stich, 1989). Also, the chosen copepod density lay within the density ranges used in previous mesocosm studies and was likely to trigger trophic cascading effects (Adrian and Schneider-Olt, 1999; Sommer *et al.*, 2001; Sommer *et al.*, 2004; Zöllner *et al.*, 2009). All bottles were incubated in 2 m water depth for 72 h to allow the microbial community to respond to multi-level grazing whilst minimising enclosure effects, e.g. algal growth on enclosure walls (c.f. Burns and Schallenberg, 1996). Also, in 2 m depth, the bottles were affected by wind driven water movement, which generated turbulence and reduced sedimentation of immobile plankton. The total exposure time until plankton fixation amounted to 74 h.

Plankton cell concentrations and biomass

To quantify changes in pico- and microplankton due to feeding of *E. gracilis*, we estimated the abundances (cells/mL) of the different plankton groups in the control (C) and *Eudiatomus* (E) bottles at the end of each experiment. In addition, plankton densities at the start of each experiment (S), i.e. from the water used to fill the experimental bottles, were examined and used as a reference to illustrate temporal dynamics in both control and predator treatment. After fixation in Lugol's acid solution + sodium acetate (100 mL sample volume per replicate), phytoplankton species were counted following Utermöhl (1958). Individual samples (250 mL sample volume per replicate) of both ciliates and rotifers were fixed in Lugol's acid solution + 10% glacial ethanoic acid and counted as combined samples. Subsamples of 100 mL were counted until 200 individuals of the most common taxon were obtained (only small ciliate taxa < 35 µm) or the whole sedimentation chamber

was analysed (larger ciliate taxa > 35 µm and rotifers). Heterotrophic nanoflagellates (HNF) and bacteria were fixed in concentrated formal solution (~2% final solution) with 10 mL sample volume per replicate. For cell counting with the epifluorescence microscope, 3 mL subsamples were filtered over 0.2 µm pore-sized black nuclepore filters (CORNING; 25 mm diameter), which were subsequently stained with 4,6-diamidino-2-phenylindol (DAPI). A minimum of 100 (400x magnification) and 400 cells per filter (1000x magnification) were counted for HNF and bacteria, respectively.

Phytoplankton, ciliate and rotifer biovolumes were calculated using taxon-specific body volumes as previously established for Lake Constance (Kümmerlin and Bürgi, 1989; Müller *et al.*, 1991; Pauli, 1989). The mean cell volume of HNF and bacteria used for biovolume calculation was 15.09 (Børsheim and Bratbak, 1987) and 0.036 µm³ (Simon, 1987), respectively.

Statistical analysis

Differences in biovolumes between treatments and experiments for the individual plankton groups were analysed using two-way ANOVA (factor 1: Treatment; levels: E, C; factor 2: Experiment; levels: 1–3) and type II sum of squares. To ensure homogeneity of variance, data were log₁₀-transformed prior to statistical analyses.

Taxon- (Supplementary Table SI) and group-specific clearance rates of *E. gracilis* were calculated from prey concentrations in C and E bottles at the end of the incubation (Rigler, 1971; Båmstedt *et al.*, 2000), i.e. assuming exponential dynamics (i.e. growth or possibly declines due to microzooplankton grazing and/or bottle effects) of prey concentrations in the C bottles:

$$F = \ln \frac{C}{E_i} * \frac{V}{t * n}$$

where F is the clearance rate [mL*animal⁻¹*h⁻¹], C is the geometric mean biovolume of each group in the control/no copepod treatments, E_i is the biovolume of each group in replicate i of treatment E , V is the bottle volume [mL], t is the experimental duration [h] and n is the number of adult *Eudiatomus* in replicate i of treatment E at the end of the experiments (for detailed explanation and derivation of this formula, see Supplementary text T1). This number ranged between 26 and 30 individuals, i.e. average mortality of *Eudiatomus* during the experiment was low (7.7%). For each experiment separately, differences between mean clearance rates of prey groups were examined using one-way mixed effects ANOVA. Here, replicates were used as a random factor in order to account for non-independence of clearance

rates on the various prey groups within each replicate. Pairwise *post-hoc* comparisons were analysed using Tukey's HSD (R package multcomp, Hothorn *et al.*, 2008). Evidently, clearance rate replicates calculated with mean control biovolumes cannot be considered independent (Jason Stockwell, personal communication). Moreover, control and grazer treatments were not paired. Thus, mixed effects ANOVA and *post-hoc* comparisons were not conducted using the clearance rates calculated from geometric mean control biovolumes, but using clearance rates for all possible combinations of control and grazer bottles (i.e. 4! = 24 combinations of four grazer and four control bottles).

The analysis of size-specific grazing impacts was conducted using three independent approaches: (1) size-specific clearance rates were calculated for distinct size classes, which were formed by rounding log₁₀-transformed body volume to the nearest integer: size class -1: 0.04–0.3 µm³ cell volume; size class 1: 4–15 µm³; size class 2: 40–300 µm³; size class 3: 350–2700 µm³; size class 4: 3200–30 000 µm³; size class 5: 32 000–279 000 µm³; size class 6: 335 000–443 000 µm³. (2) body volume distributions for control and *Eudiatomus* treatments were calculated using kernel density plots with gaussian kernels and (3) weighted mean body volume (BVM_w) and weighted body volume variance (BVV_w) of phytoplankton, ciliates and rotifers were calculated as

$$\text{BVM}_w = \frac{\sum_{i=1}^n B_i * BV_i}{\sum_{i=1}^n B_i} \text{ and}$$

$$\text{BVV}_w = \frac{\sum_{i=1}^n B_i * BV_i^2}{\sum_{i=1}^n B_i} - \text{BVM}_w^2$$

with B and BV as biovolume (body volume * concentration) and log₁₀ body volume of each taxon within the respective groups (Acevedo-Trejos *et al.*, 2018). Differences in BVM_w and BVV_w between treatments and experiments were analysed using two-way ANOVA and type II sum of squares. All calculations were conducted using the packages *car* (Fox and Weisberg, 2018) and *multcomp* (Hothorn *et al.*, 2008) with the statistical software R 3.5.0 (R Core Team, 2018).

RESULTS

A total of 55 phytoplankton, 44 ciliate and 11 rotifer taxa (including undefined ciliates and rotifers; Supporting Information Table SI) were identified. Overall and across all three experiments, *Eudiatomus gracilis* decreased the biovolume of phytoplankton (average decrease across all three experiments: 25%), ciliates (67%) and rotifers

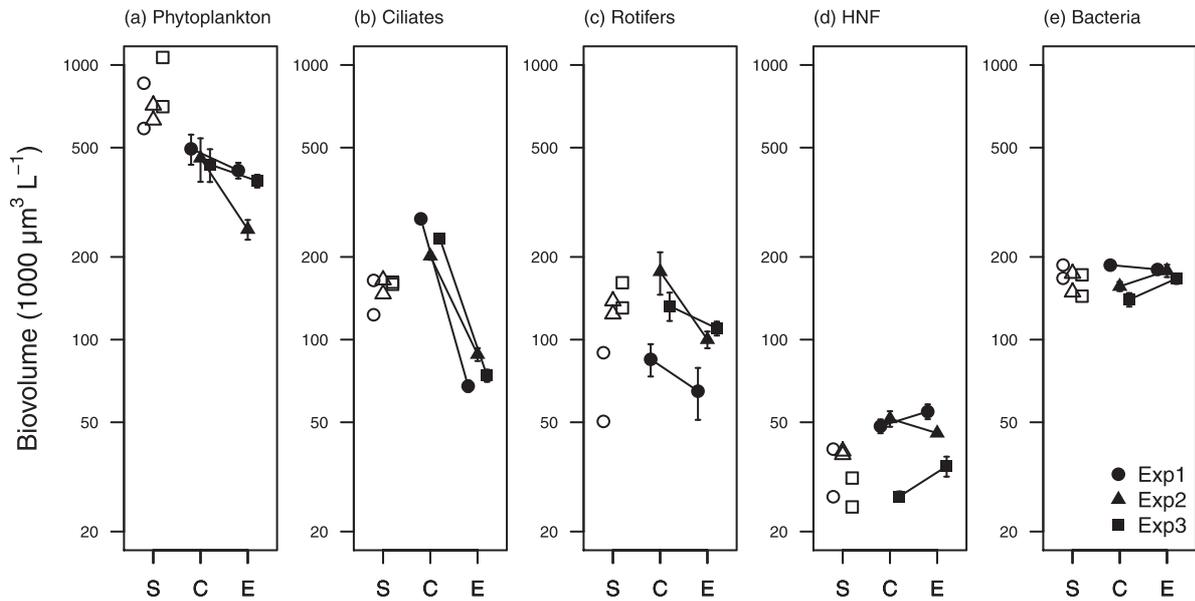


Fig. 1. Responses of biovolumes of to *Eudiatomus* grazing: (a) phytoplankton, (b) ciliates, (c) rotifers, (d) HNF and (e) bacteria. S = starting point ($n = 2$); C = control; E = copepod treatment ($n = 4$). Symbols indicate the different experiments (Circles: Experiment 1; triangles: Experiment 2 and squares: Experiment 3). Open symbols represent initial samples (S) at the starting point and filled symbols represent experimental samples (C + E) after 72 h. Error bars indicate \pm one standard error of the mean.

(28%). Whilst *E. gracilis* increased the biovolume of bacteria (9%), it did not influence HNF biovolume (Fig. 1; Table I, significant main effects of treatment). Biovolumes significantly differed between experiments for ciliates, rotifers, HNF and bacteria (significant main effect of experiment). Yet, experiment effects differed between groups. For example, rotifers biovolumes were lowest in Experiment 1, whereas HNF biovolumes were lowest in Experiment 3.

The effect of *E. gracilis* on ciliate and HNF biovolume differed significantly between experiments. (Fig. 1; Table I, significant treatment \times experiment interaction). For ciliates, this significant interaction term resulted from larger *Eudiatomus* effects in Experiment 1 (75% decline) compared to experiments 2 and 3 (56 and 68% decline, respectively). *Eudiatomus* decreased HNF biovolume in Experiment 2 (11%), but increased HNF biovolume in experiments 1 and 3 (13 and 29%, respectively). Compared to the *in situ* samples, phytoplankton biovolume was lower in both treatments whereas ciliate *in situ* biovolume was lower compared to the control but higher compared to the *Eudiatomus* treatment (Fig. 1).

We found significant differences between clearance rates on plankton groups in all experiments and all permutations performed (all $P < 0.05$). Clearance rates on ciliates were higher than those on other taxa in experiments 1 and 3 in all permutations (Fig. 2). In Experiment 2, all permutations revealed that clearance rates on

phytoplankton, ciliates and rotifers were larger than those on bacteria (Fig. 2). Other differences between groups were not consistently observed across all permutations.

Size class-specific clearance rates were low up to size class 2 and high for all groups (i.e. phytoplankton and ciliates) in size classes 3 and 4, but were group-specific in size classes 5 and 6. Ciliate clearance rates were also high in the latter two size groups whereas those for phytoplankton (size class 5, *Ceratium hirundinella*) and rotifers (size classes 5 and 6, various species) were low (Fig. 3).

As a consequence of the various size- and group-specific clearance rates, *Eudiatomus* grazing led to decreased biovolumes between $\sim 10^3$ and $10^5 \mu\text{m}^3$ (Fig. 4). This is mainly as a result of high clearance rates of abundant species, such as e.g. the algae *Cryptomonas ovata*, *Gymnodinium helveticum* and *Stephanodiscus medius* as well as the ciliates *Histobalantium* spp., *Strobilidium lacustris* and *Pelagostrombidium* spp. (Supplementary Table SI). The large biovolume declines in the 10^3 and $10^5 \mu\text{m}^3$ size ranges resulted in the relative increases of biovolumes (between 10^1 and $10^3 \mu\text{m}^3$), specifically in *Ochromonas* sp., *Rhodomonas minuta* and *Rhodomonas minuta* v. *nannoplanctica*.

Eudiatomus grazing reduced phytoplankton BVM_w , increased phytoplankton BVV_w , but had no effect on rotifer BVM_w and BVV_w (Fig. 5, Table I). For ciliates, effects of *Eudiatomus* on BVM_w and BVV_w were experiment-specific: In Experiment 1, *Eudiatomus* grazing decreased BVM_w and increased BVV_w , whereas

Table I: Analysis of variance (type II ANOVA) of the effects of treatment, experiment (Exp) and the interaction between treatment and experiment (treatment \times exp) on biovolumes, weighted mean body volume (BVM_w) and weighted body volume variance (BVV_w) of the five plankton groups.

Factor	df	Biovolume		BVM_w		BVV_w	
		F value	P value	F value	P value	F value	P value
Phytoplankton							
Treatment	1, 18	7.5130	0.0134*	7.1757	0.0153*	7.2572	0.0148*
Exp	2, 18	1.8742	0.1822	3.0921	0.0701	23.6224	<0.001***
Treatment \times Exp	2, 18	1.2191	0.3188	0.1592	0.8540	0.5652	0.5780
Ciliates							
Treatment	1, 18	1751.944	<0.001***	0.0140	0.9072	1.1158	0.3048
Exp	2, 18	16.863	<0.001***	35.4563	< 0.001***	35.5919	< 0.001***
Treatment \times Exp	2, 18	50.848	<0.001***	3.5835	0.0490*	5.4844	0.0138*
Rotifers							
Treatment	1, 18	8.7624	0.0084**	0.1224	0.7305	0.0248	0.8767
Exp	2, 18	7.9682	0.0033**	3.6808	0.0457*	16.0122	<0.001***
Treatment \times Exp	2, 18	1.8979	0.1787	0.3101	0.7372	0.4919	0.6195
HNF							
Treatment	1, 18	1.6530	0.2149				
Exp	2, 18	37.6131	< 0.001***				
Treatment \times Exp	2, 18	4.1287	0.0334*				
Bacteria							
Treatment	1, 18	5.9285	0.0255*				
Exp	2, 18	9.1138	0.0018**				
Treatment \times Exp	2, 18	3.2978	0.0602				

Significance codes: ****: <0.001, ***: <0.01, **: <0.05, *: <0.1, Since variability of body volumes in HNF and bacteria was not measured, no tests of BVM_w and BVV_w were performed.

in the other two experiments (Experiments 2 and 3), there were only weak effects on ciliate BVM_w and BVV_w . Decreased ciliate BVM_w and increased BVV_w in Experiment 1 (Fig. 5b and e) resulted from lower clearance rates in size class 3 (Fig. 3).

DISCUSSION

Our experiments revealed strong effects of a calanoid copepod species on the taxonomic and size structure of a plankton community. *Eudiaptomus gracilis* grazing resulted in significant declines of phytoplankton, ciliate and rotifer biovolumes. However, our first hypothesis assuming size-related differences between clearance rates for all prey groups was only partially confirmed. This is mainly due to relatively higher clearance rates on ciliates than those on phytoplankton. Yet, clearance rates on rotifers were lower than those on ciliates and similar to those on phytoplankton. Regarding phytoplankton, our results (mean clearance rate: 0.19 mL animal⁻¹ h⁻¹) are consistent with Zánkai and Ponyi (Zánkai and Ponyi, 1986) and Gulati (Gulati, 1978) who report average clearance rates of 0.12–0.24 mL animal⁻¹ h⁻¹ for female *E. gracilis*, respec-

tively. Higher clearance rates on ciliates relative to phytoplankton and of similar magnitude to our findings were also reported for other calanoid copepods, including for the closely related *Eudiaptomus graciloides* in mesotrophic Lake Großer Vätersee (0.22 mL animal⁻¹ h⁻¹ for Chl a; 1.24 mL animal⁻¹ h⁻¹ for ciliates; Adrian and Schneider-Olt, 1999). Likewise, ciliates contributed 96.9% of total carbon ingested by the copepod *Epischura baikalensis* in oligotrophic Lake Baikal (Moore et al., 2019). Overall, studies that explore the effects of smaller-sized calanoids on rotifers are rather rare. Stoecker and Eglhoff (1987) showed that the marine calanoid *Acartia tonsa* strongly preferred ciliates and rotifers over phytoplankton, but we are not aware of any study that compares feeding on rotifers versus ciliates of freshwater calanoids. Williamson and Butler (Williamson and Butler, 1986) showed that the small calanoid *Diaptomus pallidus* strongly prefers several rotifer species over phytoplankton when offered both food types at similar concentrations. In contrast, *Eudiaptomus gracilis* was shown to feed on rotifers but feeding on rotifers declined strongly when the green alga *Chlamydomonas geitleri* was offered simultaneously at 0.08 mmol C L⁻¹ (Šorf and Brandl, 2012). We show that in a prey community with natural concentrations of phytoplankton

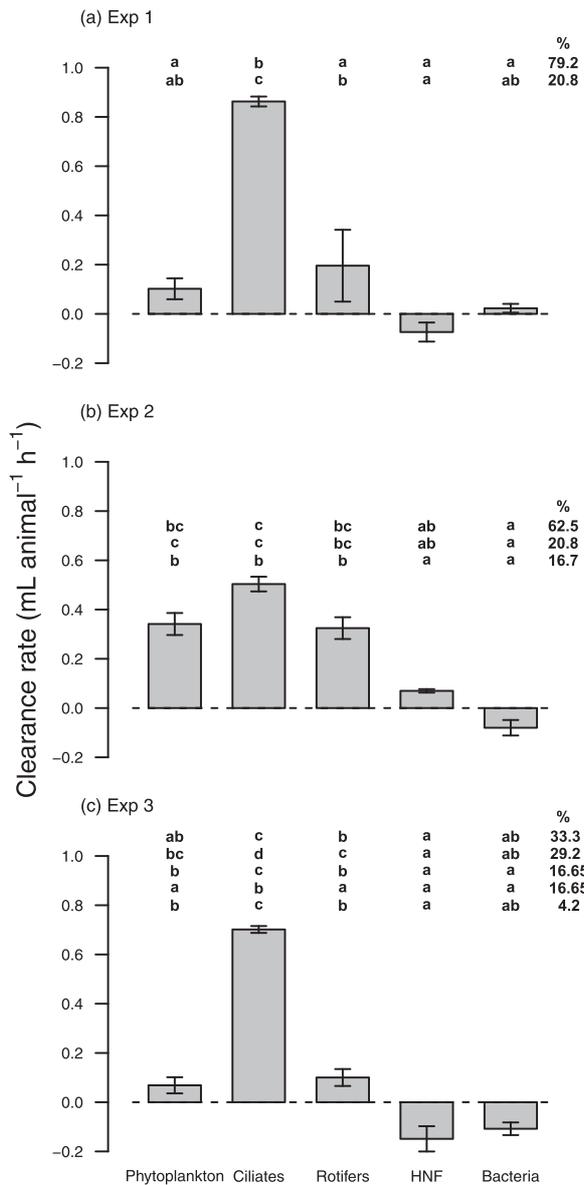


Fig. 2. Mean clearance rates of *Eudiaptomus gracilis* for the investigated plankton groups in the three experiments. Error bars indicate \pm one standard error of the mean and were calculated based on clearance rates estimated using the geometric mean control biovolumes. Letters represent the results from Tukey's *post-hoc* test calculated for all permutations of control and grazer bottles within the three experiments. Clearance rates of plankton groups differed significantly from other groups when they are flagged with a different letter ($P < 0.05$). As not all permutations revealed the same differences between clearance rates of plankton groups, all permutations results are shown for each experiment and their relative frequency is given. Note that the mean clearance rate calculated across all permutations is identical to the mean clearance rate calculated using the geometric mean of control biovolumes.

and rotifers, clearance rates on both groups were of similar magnitude. However, *Eudiaptomus* clearance rates for ciliates were considerably higher than those for rotifers in

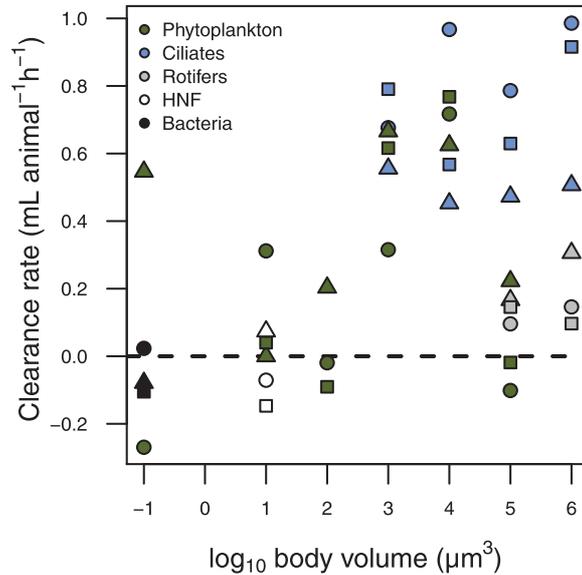


Fig. 3. Taxon- and size-specific clearance rates of *Eudiaptomus gracilis*. Clearance rates were calculated after aggregating body volumes into size classes (\log_{10} transformed biovolumes rounded to the nearest integer). See Figure 1 for explanation of the different symbols.

two out of the three experiments. Obviously, no predators of *Eudiaptomus* were included in our experiments. It is presently unclear whether predator presence might have altered foraging behaviour and thus clearance rates of the copepod.

Any ranking of clearance rates regarding different prey groups in our experiments needs to take indirect grazing effects, i.e. cascading trophic interactions, into account. Reduction of herbivorous ciliates and rotifers by *Eudiaptomus gracilis* will relieve phytoplankton from grazing pressure. In fact, it is likely that observed clearance rates on phytoplankton might underestimate true phytoplankton clearance rates of *E. gracilis*. The comparison of the *in situ* prey biovolumes (S) with the control treatment (C) also supports the presence of cascading interactions from *E. gracilis* via ciliates to phytoplankton: *in situ* phytoplankton biovolume exceeded control phytoplankton biovolume, whereas the opposite was the case for ciliates. This suggests that exclusion of *E. gracilis* and other crustacean zooplankton from the control caused biovolume increases of ciliates and declines of phytoplankton (Fig. 1). The general comparison with the *in situ* samples suggests that ciliate biovolume in Lake Constance is indeed top-down controlled, and that ciliates can control phytoplankton dynamics during specific time periods in this lake. The latter has also been suggested by steady-state carbon flow models (Gaedke and Straile, 1994) and simulation studies (Kerimoglu *et al.*, 2013).

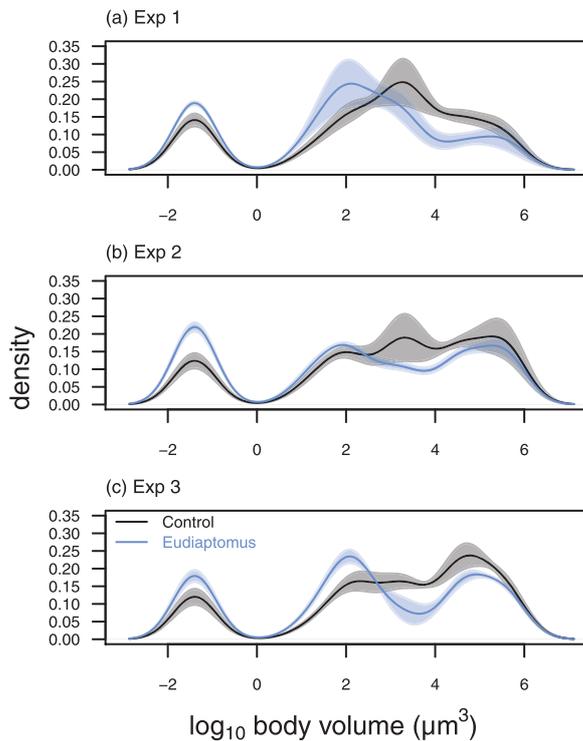


Fig. 4. Density distribution across the prey size spectrum in the control and *Eudiatomus* treatments. Lines represent the mean cell density across the four replicates; polygons depict the area within \pm one standard error of the mean.

Our results do support the second hypothesis whereby an overall increase of bacteria biovolume was observable, presumably due to cascading interactions. In addition, bacterial growth might be also stimulated by *Eudiatomus* defecation and sloppy feeding (Hygum *et al.*, 1997), although bacterial dynamics in pelagic systems have often been shown to be controlled by protozoan grazing (e.g. Bloem and Bär-Gilissen, 1989; Domaizon *et al.*, 2003). Hence, we consider it more likely that the increase of bacteria in the *Eudiatomus* treatment was caused by the observed reduction of bacterivorous ciliates (e.g. *Coleps* spp., *Cyclidium* spp.) and/or mixotrophic phytoplankton (e.g. *Gymnodinium helveticum*, *G. lantzschii*), whereas HNF which have been considered being important bacterivores in Lake Constance (Weisse and Müller, 1998; Cleven and Weisse, 2001) were not affected by *Eudiatomus gracilis*. To our knowledge, this is the first time that cascading effects of *E. gracilis* on bacteria have been reported. Hence, dominance of calanoids in oligotrophic lakes might via suppression of bacterivores partially contribute to the observed high bacteria-phytoplankton biomass ratios observed in these systems (Simon *et al.*, 1992).

Contrary to our third prediction, directional selection, i.e. a reduction of mean body sizes, was not observed in all groups, but solely in phytoplankton and in one additional experiment for ciliates. For rotifers, the size range present in the experiments was presumably too small and hence *Eudiatomus gracilis* did not lead to altered rotifer community composition based on size. The variation in clearance rates for several intermediate size classes of prey and taxonomic groups indicates that *E. gracilis* does not select its prey based solely on prey size or biovolume. There are several additional factors that may well influence copepod prey selection. These include prey motility (which triggers the ambush feeding of copepods and increases encounter rates with prey; Jonsson *et al.*, 2004), texture (aloric ciliates such as *Didinium* spp. and *Strobilidium* spp. and aloric rotifers, e.g. *Polyarthra dolichoptera* and *Synchaeta* spp., are preferred over those with a lorica; Brandl, 2005), presence/absence of escape responses (e.g. escape jumps of *Askenasia* spp. and *Strobilidium* spp.; Tamar, 1979; spines of *Keratella cochlearis*; Williamson, 1987), and even chemical properties of food items (Friedman and Strickler, 1975; DeMott, 1988).

Ciliates experienced uniformly high clearance rates across their size range providing no evidence for size selection in two of the three experiments. In all cases when directional selection was observed, there was also evidence for disruptive selection, i.e. an increase of size variance. Hence, contrary to our third hypothesis, *Eudiatomus* grazing did not result in an association of directional and stabilising selection, but in an association of directional and disruptive selection. For phytoplankton, this two-fold selective signature most likely is a combined effect of both *E. gracilis* (non-) feeding and reduced ciliate feeding. The decrease of phytoplankton BVM_w is likely due to reduced biovolumes of phytoplankton species in the 10^3 – $10^5 \mu\text{m}^3$ size range coupled to the lack of phytoplankton reduction in the 10^1 – $10^3 \mu\text{m}^3$ size range. The increase of phytoplankton BVV_w is due to the relative increase of biovolume at the lower phytoplankton size range was accompanied by a relative increase of biovolume in the higher phytoplankton size range as the largest phytoplankton species, *Ceratium hirundinella*, was also not suppressed in the *Eudiatomus* treatment. The closely related species, *Ceratium furcoides*, is defined as nutritionally poor or inadequate for egg development in *E. gracilis* (Santer, 1996). Directional selection of ciliates in Experiment 1 was mostly due to lower clearance rates and consequently higher biovolumes of small ciliates such as *Balanion planctonicum*, which shifted BVM_w to a lower value. Middle-sized ciliates such as *Coleps* spp. and *Pelagohalteria viridis* did decline in the *Eudiatomus* treatment comparatively stronger than the largest ciliates, and the BVV_w also increased.

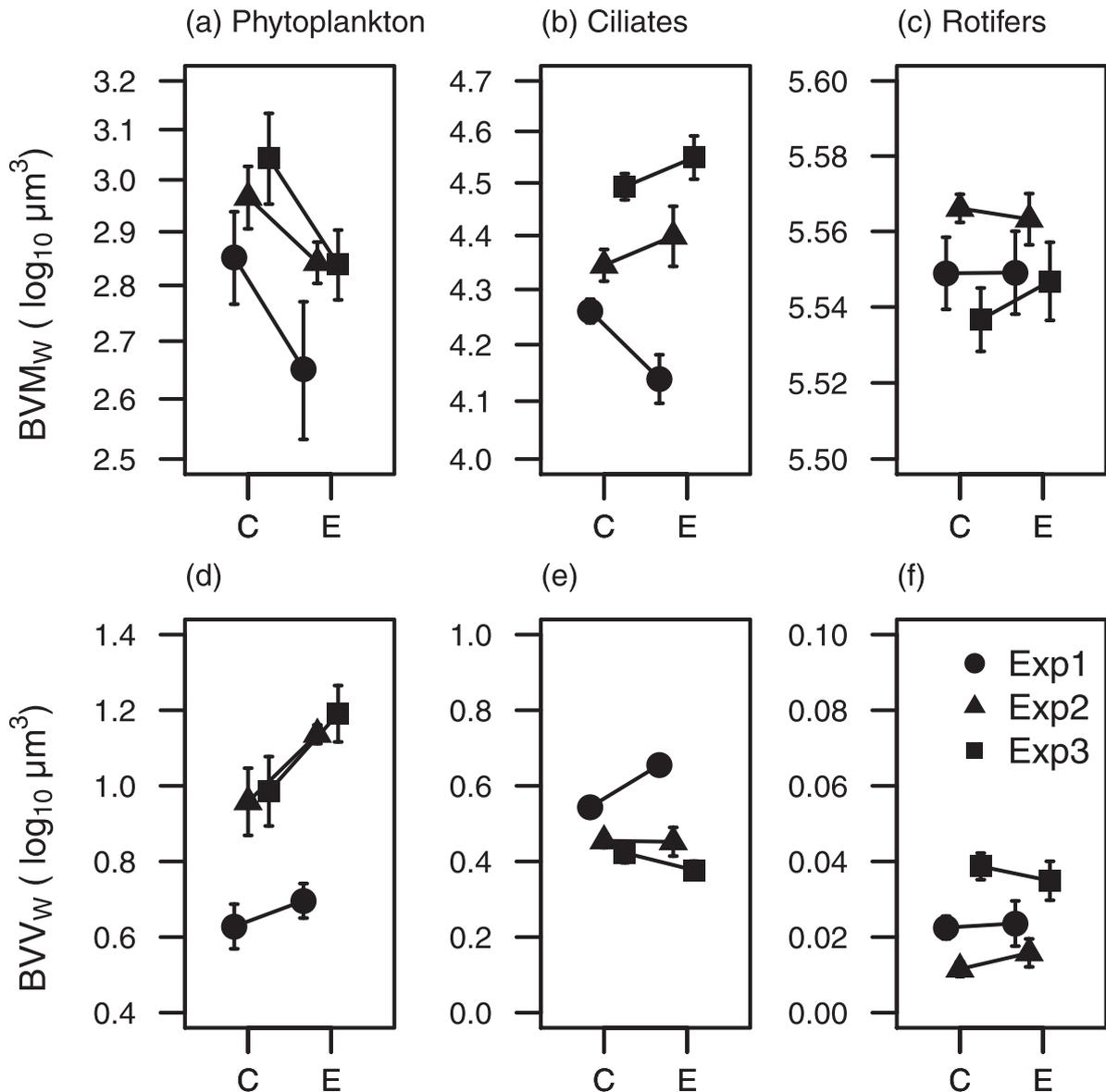


Fig. 5. Weighted mean (BVM_w) and weighted variance (BVV_w) of \log_{10} transformed body volumes in the control (C) and the copepod treatment (E) in each of the three experiments. (a, d) phytoplankton; (b, e) ciliates and (c, f) rotifers. Error bars indicate \pm one standard error of the mean.

Finally, we could reject our fourth hypothesis for phytoplankton as we found decreasing biovolume and BVM_w and increasing BVV_w in all experiments. For the biovolumes, BVM_w , and BVV_w of other groups, we observed either significant experiment effects or significant treatment \times experiment interactions (Table I). However, in case of ciliates and rotifers, *Eudiptomus* grazing resulted in reduced biovolumes in all three experiments. The observed significant experiment \times treatment interaction resulted from a different effect size of *Eudiptomus* grazing (Fig. 1) and not from the presence or absence of an

Eudiptomus effect. In contrast, for HNF and bacteria, the treatment effects seem to vary qualitatively as well. However, the reason for this is not clear and more experiments would be required to resolve the causes of short-term variability of experimental outcomes. Methodological differences between Experiment 3 versus Experiments 1 and 2 (100 versus 55 μm mesh size; see methods) are unlikely to have caused the differences between experiments as, e.g. clearance rate differences between groups were rather similar in Experiments 1 and 3, but differed from Experiment 2. In summary, we observed consistent

treatment effects in regard to the biovolumes of the main prey items, phytoplankton, ciliates and rotifers across experiments. In contrast, effects on HNF and bacteria as well as effects on group size structures (except on phytoplankton BVM_w) were less consistent and showed significant temporal variability even within a short time period of 3 weeks.

CONCLUSION

Applying an *in situ* incubation approach in large and deep Lake Constance, we obtained strong evidence that grazing of the calanoid copepod *Eudiatomus gracilis* can influence the taxonomic and size structure of the lower plankton food web. Hence, *Eudiatomus* grazing has the potential to change, e.g. trophic transfer efficiency (Carrick *et al.*, 1991) and nutrient recycling (Sailley *et al.*, 2014) in pelagic food webs. Largest clearance rates were observed for ciliates, which most likely resulted in cascading effects, i.e. an increase of bacteria biovolume and a reduced decline of smaller-sized phytoplankton. Large clearance rates of ciliates probably also contributed to the observed directional and disruptive selection on phytoplankton size. Thus, changes in phytoplankton size structure may not be understood without considering cascading interactions and the omnivory of consumers.

It is not yet clear if the observed co-occurrence of directional and disruptive selection in natural phytoplankton communities is season-specific and typical for *E. gracilis*, and whether such a coupling of selection modes exists also for grazers which are less omnivorous and may tend either to a phytoplankton diet (e.g. daphnids) or to a more ciliate-based diet (e.g. cyclopoid copepods). This suggests that there is a need for experiments in which (a) the size response of prey plankton communities to consumers differing in their degree of omnivory, and (b) seasonal variability of the selection pressure on plankton size structure is examined. Finally, controlled laboratory experiments using multiple trophic levels are needed as experiments using only trait variability at two trophic levels, e.g. phytoplankton and herbivores, will most likely only reveal an incomplete picture of selective factors affecting algal communities. Irrespective of any future work, our study suggests that the quantification of higher-level processes *sensu* Vellend (2016) might represent a promising tool to analyse predation effects on plankton communities possibly resulting in improved comparability of predator effects within and between ecosystems.

ACKNOWLEDGEMENTS

We thank Eva Lievens, Jason Stockwell and two anonymous reviewers for comments, which greatly improved the content of the manuscript.

FUNDING

This study was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation, 298726046/GRK2272).

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