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Allochthonous carbon is a major driver of the microbial food web – A mesocosm study simulating elevated terrestrial matter runoff

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ABSTRACT

Climate change predictions indicate that coastal and estuarine environments will receive increased terrestrial runoff via increased river discharge. This discharge transports allochthonous material, containing bioavailable nutrients and light attenuating matter. Since light and nutrients are important drivers of basal production, their relative and absolute availability have important consequences for the base of the aquatic food web, with potential ramifications for higher trophic levels. Here, we investigated the effects of shifts in terrestrial organic matter and light availability on basal producers and their grazers. In twelve Baltic Sea mesocosms, we simulated the effects of increased river runoff alone and in combination. We manipulated light (clear/shade) and carbon (added/not added) in a fully factorial design, with three replicates. We assessed microzooplankton grazing preferences in each treatment to assess whether increased terrestrial organic matter input would: (1) decrease the phytoplankton to bacterial biomass ratio, (2) shift microzooplankton diet from phytoplankton to bacteria, and (3) affect microzooplankton biomass. We found that carbon addition, but not reduced light levels *per se* resulted in lower phytoplankton to bacteria biomass ratios. Microzooplankton generally showed a strong feeding preference for phytoplankton over bacteria, but, in carbon-amended mesocosms which favored bacteria, microzooplankton shifted their diet towards bacteria. Furthermore, low total prey availability corresponded with low microzooplankton biomass and the highest bacteria/phytoplankton ratio. Overall our results suggest that in shallow coastal waters, modified with allochthonous matter from river discharge, light attenuation may be inconsequential for the basal producer balance, whereas increased allochthonous carbon, especially if readily bioavailable, favors bacteria over phytoplankton. We conclude that climate change induced shifts at the base of the food web may alter energy mobilization to and the biomass of microzooplankton grazers.

1. Introduction

Estuaries are among the most productive ecosystems on Earth, but their structure and function is seriously threatened by climate change (Canuel et al., 2012). They are finely balanced ecosystems that experience continually changing physicochemical conditions to which biological organisms must respond. One major future climate change prediction indicates that coastal and estuarine environments will be exposed to altered patterns of river discharge and terrestrial (allochthonous) matter export, with northerly regions in particular enduring elevated levels of rainfall (Andersson et al., 2015; Meier, 2006). Discharged terrestrial matter contains particulate and dissolved organic matter which can constitute an important source of nutrients, such as nitrogen (N), phosphorus (P) as well as carbon (C) (Meunier et al., 2016b; Richardson et al., 2010). The bioavailability of this terrestrial matter plays an important role for basal producer growth, and this bioavailability is largely related

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to the bulk nutrient composition of organic matter (for review see Findlay and Sinsabaugh, 2004). Several studies observed that bacterial production increased with increasing dissolved organic matter N content (for examples see Hunt et al., 2000; Kroer, 1993). Furthermore, allochthonous dissolved organic matter (ADOM) usually consists of an array of humic compounds that may reduce light penetration (Ask et al., 2009; Harvey et al., 2015). Since light and nutrients are important drivers of phytoplankton and bacterial production, altered abiotic conditions will have important consequences for the aquatic food web base, with implications for the productivity of higher trophic levels (Brett et al., 2017; Lefébure et al., 2013; Liess et al., 2016).

In the pelagic realm, absolute and relative light and nutrient availability determine basal productivity, phytoplankton community structure, and the relative phytoplankton to bacterial biomass (Andersson et al., 1996; Ask et al., 2009; Figueroa et al., 2016). Bacteria are superior nutrient competitors, but depend on an external C sources for growth, generally supplied through algal C exudates (Azam et al., 1983). However, the paradigm of bacterial dependence on algal exudation does not hold when an external (allochthonous) C source is available for bacterial growth (Figueroa et al., 2016). By decreasing light availability and subsidizing with allochthonous C, elevated terrestrial runoff should favor heterotrophic bacterial production over autotrophic phytoplankton production (Figueroa et al., 2016; Sandberg et al., 2004). The planktonic food web consists of two energy pathways, the photoautotrophic (phytoplankton-based) energy pathway, and the heterotrophic (bacterial-based) energy pathway (Azam et al., 1983; Meunier et al., 2016b). Phytoplankton-based food chains are generally considered to transfer energy and C more efficiently to higher trophic levels than bacteria-based food chains (Berglund et al., 2007; Brett et al., 2009). However, the contribution and transfer of bacterial derived C to higher trophic levels is controversial. Some studies indicate that a significant proportion of higher trophic level biomass may derive from terrestrial C sources, potentially mobilized by bacteria (Carpenter et al., 2016; Karlsson et al., 2012; Kelly et al., 2014), while others found the bacterial C transfer to zooplankton and fish to be minimal (Cole et al., 2006). Such issues are compounded in a food web perspective since bacteria lack certain sterols and essential fatty acids such as eicosapentaenoic acid and are thus generally considered poor-quality food for mesozooplankton (Brett and Müller-Navarra, 1997; Martin-Creuzburg et al., 2011). Grazing experiments have shown that Daphnia are unable to survive on bacteria alone (Martin-Creuzburg et al., 2011). Bacteria are instead consumed by microzooplankton, which in turn are consumed by mesozooplankton (Berglund et al., 2007; Lefébure et al., 2013). This adds a trophic link in the food chain, resulting in lower food web efficiency (Berglund et al., 2007; Jansson et al., 2007), as respiratory energy losses occur at each trophic transfer step (McCallister and Giorgio, 2008; Sommer et al., 2002). Consequently, elevated allochthonous matter inputs can alter food web structure and function by shifting the relative availability of light and C, favoring differing trophic transfer pathways.

Zooplankton often consume prey that do not match their nutritional requirements (Meunier et al., 2014; Persson et al., 2010). Thus most micro- and mesozooplankton groups have developed selective feeding strategies for certain prey types, based on taxonomy (Gentsch et al., 2009; Stoecker et al., 1981), prey size (Hansen, 1992; Paffenhöfer, 1988) or nutrient composition (Boersma et al., 2016; Meunier et al., 2016a; Meunier et al., 2012). Although microzooplankton preferentially feed on phytoplankton, elevated terrestrial organic matter input and increased bacterial biomass may result in bacteria becoming a significant (if nutritionally poor) food source for microzooplankton (Bergström et al., 2003; Gast, 1985). Currently, knowledge of light, nutrient and C effects on microzooplankton feeding selectivity is limited, thus investigations of microzooplankton grazing, particularly with climate change scenarios addressed, are imperative.

Our study aims to clarify the mechanisms that influence the partitioning of planktonic basal production (heterotrophic versus autotrophic) in aquatic ecosystems receiving elevated terrestrial organic matter inputs, with a particular focus on the heterotrophic energy transfer to planktonic grazers. We intend to disentangle the effects of light attenuation from the effects of nutrient supply and to determine their ramifications for higher trophic levels. More specifically, we hypothesize that increased terrestrial organic matter input will: (1) decrease light availability, resulting in a lower phytoplankton to bacterial biomass ratio, (2) shift microzooplankton diet from phytoplankton to bacteria, and (3) affect microzooplankton biomass through changes in overall prey availability. To test these hypotheses, we conducted a mesocosm study in the Baltic Sea to identify the independent effects of clear C addition (C fertilization but no change in light availability), reduced irradiance, and dissolved organic matter additions, and we complemented this with dilution experiments to assess microzooplankton grazing activities.

2. Material and methods

2.1. Study system and rationale

The Baltic Sea is the largest brackish water body in the world and is characterized by gradients of salinity and terrestrial organic matter inputs (Deutsch et al., 2012). Climate change is predicted to affect those gradients through increased temperature, wind speeds and elevated precipitation levels, especially in its northern reaches (Andersson et al., 2015; IPCC, 2013; Meier, 2006). Such changes will likely reduce salinity and increase terrestrial organic matter inputs as vast catchments drain into rivers and discharge at the coast (Meier, 2006; Weyhenmeyer et al., 2012). Disentangling the influence of light and riverine subsidies on the planktonic food web will clarify the major drivers forcing biological changes at the base of the food web, and thus the likely impact on higher trophic levels.

2.2. Mesocosm setup

To test our hypotheses, we conducted a seven-week mesocosm experiment in summer 2013. Mesocosms were situated in a sheltered bay (63°33′24.8″N 19°47′54.8″E) of the Bothnian Sea. Twelve bentho-pelagic mesocosms (2 m deep, 1.6 m diameter) were divided into four triplicate repeated treatments. Mesocosms were situated in groups of four and an individual treatment was only represented once in each quad. The mesocosms were deployed by gently pulling the transparent polyethylene bags down and burying a 40 cm high aluminum ring fixed at the bottom of the mesocosm bags into the sediment. Water within the mesocosms remained unamended with the exception of netting and trapping to remove fish, prior to the addition of young of the year perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), and the establishment of treatments. The water column down to the surface of the sediments was oxygenated and a natural pelagic community was maintained, and it was from this water that the dilution experiments were carried out.

2.3. Treatments

The four treatments represented a 2 × 2 factorial design with the factors light (clear/shade) and C (added/not added) being manipulated, resulting in: 1) a control treatment representative of the full light and no C addition, 2) a terrestrial matter addition (TM)

creating shade and C addition by the addition of a soil extract, 3) a Clear-C treatment to which clear C compounds were added leaving the light un-attenuated, and 4) a Shade treatment representative of the shade conditions created by soil addition yet with no C addition. A single inaugural addition was carried out in all treatment mesocosms. The TM treatment was created by the addition of a natural soil extract prepared from soil collected on the banks of the nearby Öre river and extracted as described in Lefébure et al. (2013). Manufacturing soil extract involved mixing the collected soil with Milli-Q water and an ion exchange resin (Amberlite IRC 7481) and then incubating the soil suspension for 48 h at 4 °C, prior to filtering it through a 90 μm mesh. The C, N, P content of the resulting extract was determined using a Shimadzu TOC-5000 carbon analyzer and a Braan and Luebbe TRAACS 800 autoanalyzer. The resulting soil extract addition to the mesocosms was designed to mimick the effects of increased river discharge. The amount of soil extract was calculated to result in a 50% increase of DOC compared to the ambient seawater DOC concentration of this region (Eriksson Hägg et al., 2010; Lefébure et al., 2013), resulting in DOC values being elevated from 8 to 12 mg L^{-1} in our mesocosms (Fig. S1). For the Clear-C treatment a mixture of bioavailable and non-bioavailable colorless C compounds (Table 1 and Supplementary information) were added to the equivalent C concentration of the TM additions. The Shade treatment, created by the addition of a pigment (C77010 Chromatint Brown 2802), simulated the light reducing effects of natural terrestrial runoff, but without the addition of bioavailable C (Supplementary information). This pigment removed a similar spectrum of light as the natural TM treatment to result in similar levels of light attenuation (Fig. S2).

2.4. Abiotic measurements

In order to follow the abiotic conditions over the course of the experiment, colored dissolved organic matter (CDOM) absorption, temperature, dissolved C, N, P, and silicate (Si) were measured right before the establishment of the treatments, two days later, and once a week thereafter. The CDOM absorbance was measured on water sampled at 1 m from the surface and filtered through 0.2 μm polycarbonate filters in the spectral range of 240–600 nm using an Aqualog fluorescence spectrophotometer (Horiba Inc.) and 10 mm quartz cells with fresh Milli-Q water as a blank. The absorption coefficient at 440 nm was calculated following Kirk (2011) and used as a proxy of light attenuation from the treatments. Dissolved C, N, P, and Si were determined following the methods of Grasshoff et al. (1999). Salinity and temperature were measured using a SeaGuard multi-sensors platform (Aanderaa Data Instrument Inc.).

2.5. Dilution experiments

In order to measure microzooplankton specific grazing rates, dilution experiments (Landry and Hassett, 1982; Landry et al., 1993) were conducted at the start (directly prior to treatment establishment) and at the end of the mesocosm study. To conduct the dilution experiments, water from each mesocosm was sieved through a 100 μm mesh to exclude mesozooplankton and subsequently mixed with 0.2 μm filtered mesocosm water to create three dilutions: 87.5, 50, and 0% (undiluted mesocosm water). To prevent nutrient limitation biases during incubation, a nutrient solution was added to the dilution series (as described in Löder et al., 2011). One additional bottle of undiluted water (0%) per mesocosm was incubated without the addition of nutrients, to serve as a control. The incubations were performed in 1.2 L polycarbonate bottles placed in a climate room at 18 °C (in-situ temperature at sampling, Fig. 1), with a 16-8 h light-dark cycle. Incubation was carried out for a 24 h period. Additional incubation bottles were simultaneously prepared and directly sampled to obtain start values. After 24 h of incubation, each experimental incubation bottle was sampled for microzooplankton, phytoplankton, and bacterial abundances. Phytoplankton and microzooplankton samples, 250 mL from the incubation bottles, were fixed with acidic Lugol solution (0.5% final concentration) and stored under cool and dark conditions until further analysis. In order to measure bacterial abundances, 5 mL of water was fixed with glutaraldehyde (0.1% final concentration) and frozen at −80 °C (Marie et al., 2005).

Phytoplankton and microzooplankton abundances were determined to the species level using an inverted microscope following the Utermöhl method (Utermöhl, 1931, 1958). The 87.5% and 50%

Table 1
Composition of the C-rich compounds mixture added to the mesocosms for the Clear C treatment. The concentrations shown are indicative of the mixture ratio of the compounds, with final concentrations of added C being matched to the C concentration of TM treatment.

Carbon compound	Molecule type	Bioavailable	Concentration
α-Cyclodextrin	Polymer	No	0.19 M
D-Cellobiose	Carbohydrate	Yes	0.55 M
D-Xylose	Carbohydrate	Yes	2.1 M
D-Mannitol	Carbohydrate	Yes	1.75 M
Itaconic Acid	Carboxylic acid	No	2.1 M
L-Arginine	Amino acid	No	1.75 M
L-Asparagine	Amino acid	Yes	2.65 M

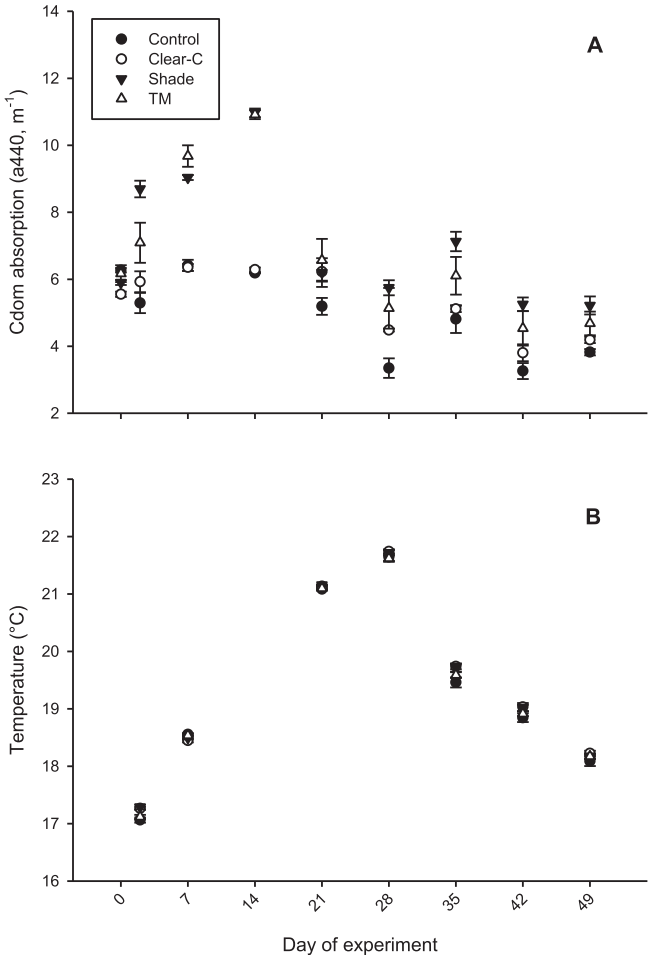

Fig. 1. Mean values of CDOM absorption (A) and temperature (B) in the mesocosms, error bars correspond to one standard error (n = 3).

diluted microcosms were sedimented overnight using a 25 mL sedimentation column. The 0% diluted samples were directly placed in the 2.973 mL counting chamber and settled for at least two hours.

Bacterial samples were quickly thawed in a 30 °C water bath, stained with SYBR Green I (Invitrogen) to a final concentration of 1: 10 000 (Marie et al., 2005) and analyzed on a BD FACSVerse™ flow cytometer (BD Biosciences) equipped with a 488 nm laser (20 mW output) and a 640 nm laser (40 mW output) at a flow rate of 40 μL min^{-1} during 1–3 min. Where necessary, samples were diluted with 0.2 μm filtered seawater. Microspheres of 1 μm (Fluoresbrite plain YG, Polysciences) were added to the samples as internal standard. Forward light scatter (FSC), side light scatter (SSC) and green fluorescence from SYBR Green I (527 nm ± 15) were used to estimate bacteria abundance which was then converted into biomass using a conversion factor of 20 fg C per cell (Lee and Fuhrman, 1987).

2.6. Biomass, growth, and grazing calculations

The biovolume of each phytoplankton species was determined using geometric formulae according to Hillebrand et al. (1999). Cell biovolumes were converted into C biomass according to the equations of Menden-Deuer and Lessard (2000). Ciliate cellular C content was calculated using a conversion factor of 0.19 pgC μm^{-3} (Putt and Stoecker, 1989). Rotifer C was calculated by converting cellular biovolume to wet weight assuming a specific gravity of 1, and was then converted to dry weight using a conversion factor of 0.1, with 50% of dry weight assumed to be carbon (McCauley, 1984; Park and Marshall, 2000). Phytoplankton species were taxonomically grouped in the following categories: chlorophyte, chrysophyte, cyanobacteria, diatom and haptophyte in order to highlight clear trends and responses to the different treatments. Similarly, microzooplankton species biomasses were pooled and are henceforth described as microzooplankton. Phytoplankton growth rates and microzooplankton grazing rates were calculated using linear regressions of apparent phytoplankton growth against the dilution factor (Landry and Hassett, 1982; Landry et al., 1993). Prey selectivity α of the microzooplankton community was calculated for each phytoplankton taxonomic group according to Chesson (1978, 1983). Finally, values of α were used to calculate the electivity index E^* according to Vanderploeg and Scavia (1979a, 1979b) where values of 0 indicate non-selective feeding, values > 1 indicate preferential feeding on a particular prey type, and values < 1 indicate discrimination against a prey type.

2.7. Statistics

Differences in CDOM absorption, temperature, total C, N, P, and Si were analyzed using a repeated-measures ANOVA, with treatments as categorical variables. Phytoplankton, bacteria, and microzooplankton biomasses, as well as the phytoplankton/bacteria ratio were analyzed using a one-way ANOVA followed by a Tukey-HSD posthoc tests to evaluate the effect of the different treatments. Potential differences between treatments in the phytoplankton and microzooplankton community composition were analyzed with an ANOSIM. Microzooplankton electivity index E^* was tested against zero using a two-tailed *t*-test. Significance levels of 0.05 were chosen in our analyses.

3. Results

3.1. Abiotic conditions in the mesocosms

Salinity in the mesocosms remained stable (~2) throughout the study period. Both CDOM and temperature showed temporal variation (repeated measures ANOVA, $p < 0.01$ and $p < 0.01$, respectively). There was no difference in CDOM absorption between any treatments at T0. CDOM absorption was strongly increased during the early phase of the experiment in the Shade and TM treatments and decreased after sampling day 14 (repeated measures ANOVA, Tukey HSD posthoc test, $p < 0.05$), although in both Shade and TM treatments it remained significantly higher than in the Control and Clear-C treatments during the latter stages of the experiment (Fig. 1A). Temperature remained comparable in all mesocosm units (repeated measures ANOVA, $p = 0.75$) and followed a clear seasonal trend, increasing by ~5 °C by the midpoint of the experiment; peaking on sampling day 28 (Fig. 1B). Fish survival was poor, only circa 20% of the fish survived through the whole experiment, and no analysis on the few remaining individuals was possible.

Nutrient conditions did not dwindle during the mesocosm study (Fig. S1). Although a certain level of variation in C concentrations can be observed (Fig. S1A), we did not detect any significant treatment (repeated measures ANOVA, $p = 0.97$) or time effects on C concentrations (repeated measures ANOVA, $p = 0.37$). Similarly, N, P, and Si concentrations were not significantly influenced by treatment (repeated measures ANOVA, $p = 0.39$; $p = 0.89$; $p = 0.42$) but fluctuated over the course of the experiment (repeated measures ANOVA, $p < 0.01$). N and P concentrations respectively increased by 2- and 3-fold during the first two weeks and then decreased, returning to initial levels (Figs. S1B and C). Interestingly, Si concentrations showed a somewhat slower but steady increase from 10 to 100 μg L^{-1} over the experiment duration (Fig. S1D).

3.2. Phytoplankton, bacteria, and microzooplankton biomass

A strong biotic response was observed, with clear differences between the start and end of the mesocosm experiment, indicating that phytoplankton and microzooplankton biomasses increased in the Control (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$; Fig. 2A and D) while bacteria biomass and the ratio bacteria/phytoplankton decreased (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$; Fig. 2B and C). Furthermore, phytoplankton biomass was much lower in the end sample from the Clear-C treatment than in the Control (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$). The Shade treatment had higher end phytoplankton biomass, but was not significantly different from the control (one-way ANOVA, Tukey HSD posthoc test, $p = 0.17$), and TM enrichment had an intermediate influence, reducing phytoplankton biomass by ~35% (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$; Fig. 2A). Bacterial biomass did not increase between the start and end mesocosm sampling events and only the Shade treatment significantly reduced the end bacterial biomass by ~15% (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$; Fig. 2B), with no significant differences between the control and the other treatments being recorded. Interestingly, Clear-C addition strongly increased the bacteria/phytoplankton ratio (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$; Fig. 2C). Changes in bacterial and phytoplankton biomasses were reflected in the total basal biomass (Table 2). Both the clear-C and the TM mesocosms contained lower total basal biomass than the control (one-way ANOVA, Tukey HSD posthoc test, $p < 0.05$), with phytoplankton biomass only contributing to 7% and 32% of the total, respectively (Table 2). Microzooplankton biomass was higher at the end point in all treatments, however the increase was lowest in the Clear-C and Shade treatments (~50% lower than in the Control), whereas the TM treatment was ~2.5 times higher than the Control (one-way ANOVA, Tukey HSD posthoc test, $p < 0.01$; Fig. 2D). Changes in phytoplankton and microzooplankton abundances were however not reflected in the

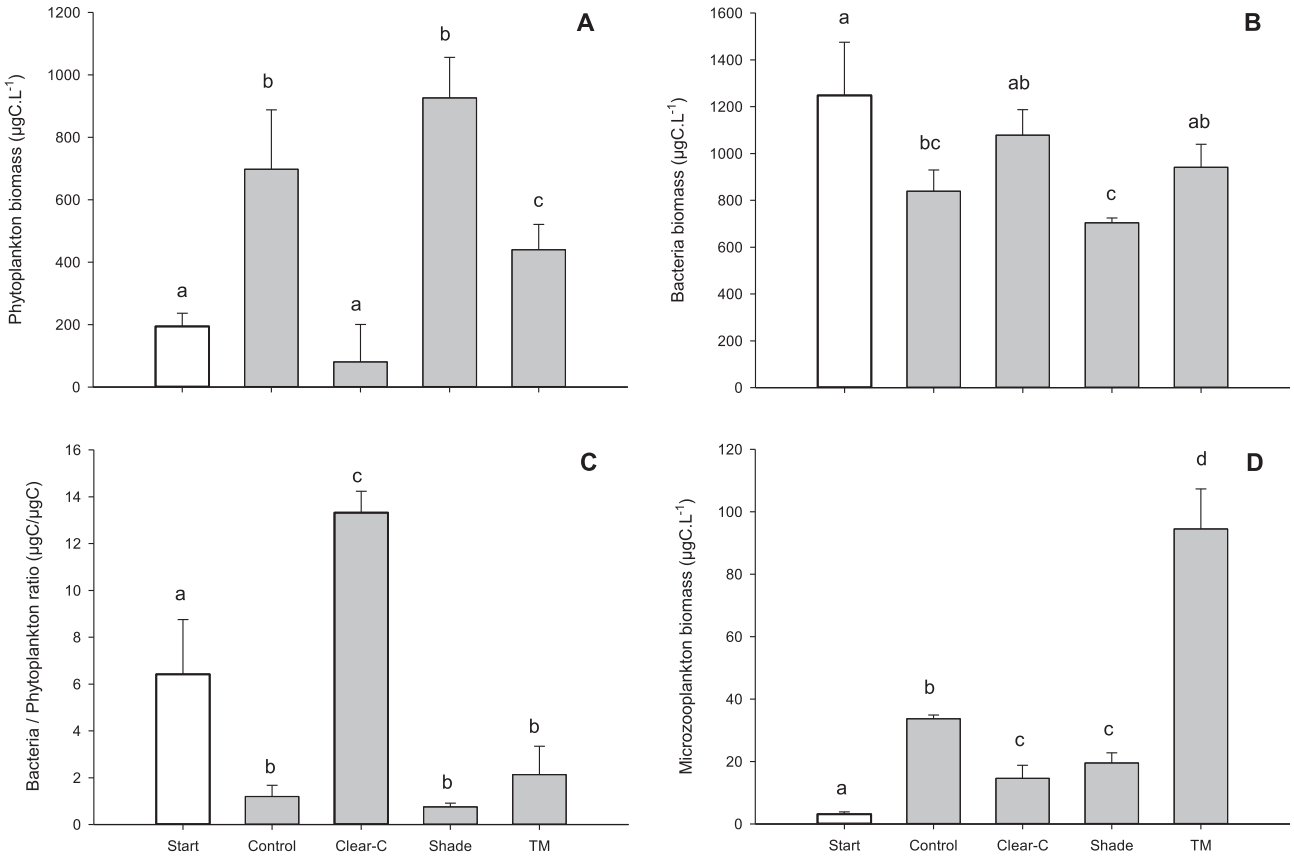

Fig. 2. Mean values of phytoplankton (A) and bacteria (B) biomass as well as phytoplankton/bacteria ratio (C) and microzooplankton biomass (D) at the start of the mesocosm experiment and at the end in the different treatments, error bars correspond to one standard deviation (n = 3). The different treatments represent the initial sampling (start), the control treatment, a clear C compounds addition (Clear-C), a pigment addition (Shade), a terrestrial matter addition (TM). Letters indicate significant differences between treatments ($p < 0.05$).

Table 2
Total basal biomass (i.e. prey available to microzooplankton) and the relative contribution of phytoplankton and bacterial biomass. The different treatments represent the initial sampling (start), the control treatment, a clear C compounds addition (Clear-C), a pigment addition (Shade), a terrestrial matter addition (TM). Letters indicate significant differences between treatments ($p < 0.05$).

Treatment		Total basal biomass (µg C L^{-1})	Relative contribution of phytoplankton (%)	Relative contribution of bacteria (%)
Start		1443.3	13.5	86.5
End	Control	1537.6[a]	45.4[a]	54.6[a]
End	Clear-C	**1159.0**[b]	**7.0**[b]	**93.0**[b]
End	Shade	1631.2[a]	56.8[a]	43.2[a]
End	TM	**1381.9**[c]	**31.9**[c]	**68.1**[c]

community compositions, which were not significantly different between treatments (ANOSIM, $p > 0.05$). The phytoplankton community was essentially composed of chlorophytes and cyanobacteria (60–70%) and the microzooplankton community was dominated by ciliates.

3.3. Microzooplankton grazing

With the exception of the Clear-C treatment, the microzooplankton community had higher carbon-specific grazing rates for phytoplankton than for bacteria (Table 3). Bacteria, chlorophytes, cyanobacteria, and haptophytes were significantly grazed but we identified different selectivity patterns for different prey. The α selectivity index indicates that microzooplankton often preferentially ingested phytoplankton prey with low relative abundances (Table 3). In the Control mesocosms, microzooplankton preferentially fed on chrysophytes whereas they selectively ingested diatoms in the Shade and TM treatments. Moreover, no significant phytoplankton grazing could be measured in the Clear-C treatment (Table 3). Consequently, in almost all treatments microzooplankton had a phytoplankton-dominated diet, while bacteria were avoided (two-tailed *t*-test, $p < 0.01$; Fig. 3). Only in the Clear-C treatment was electivity for prey items not significant.

4. Discussion

We tested the relative influence of light availability and ADOM in shaping planktonic food webs. Although we hypothesized that terrestrial organic matter inputs would decrease light availability, resulting in a lower proportion of phytoplankton to bacteria biomass, our results indicate that light attenuation did not influence the bacteria/phytoplankton biomass ratio. Microzooplankton showed a strong preference for phytoplankton over bacteria as their food source. Only in the Clear-C treatment (i.e. carbon

Table 3
Phytoplankton and bacteria growth rates, microzooplankton grazing rates, and α Chesson's selectivity index (Chesson, 1978, 1983) for the different prey types at the start (between day 0 and day 3) and end of the mesocosm experiment (between both dilution experiments). The different treatments represent the initial sampling (start), the control treatment, a clear C compounds addition (Clear-C), a pigment addition (Shade), a terrestrial matter addition (TM). Numbers in bold indicate significant regression parameter values ($p < 0.05$) and n.a. stands for not available.

	Growth rate (day^{-1})					Microzooplankton grazing rate (day^{-1})					Chesson's α				
	Start	Control	Clear-C	Shade	TM	Start	Control	Clear-C	Shade	TM	Start	Control	Clear-C	Shade	TM
Bacteria	−0.45	0.76	**−0.24**	−0.23	**0.41**	–	–	**0.019**	0.002	**0.002**					
Chlorophyte	**0.43**	**1.67**	−0.38	0.04	0.46	**0.005**	**0.014**	–	–	0.002	0.57	**0.15**	n.a.	n.a.	**0.02**
Chrysophyte	0.36	0.52	−0.33	0.58	−1.16	0.002	0.005	–	–	–	**0.14**	**0.81**	n.a.	n.a.	n.a.
Cyanobacteria	**−0.01**	**0.22**	0.02	**0.80**	**0.15**	**0.005**	**0.001**	–	**0.014**	**0.002**	**0.16**	**0.00**	n.a.	**0.02**	**0.01**
Diatom	0.28	−0.32	−0.32	−0.03	0.47	0.002	–	–	0.002	0.005	**0.11**	n.a.	n.a.	**0.76**	**0.86**
Haptophyte	0.13	**0.51**	−0.21	**0.24**	**0.69**	0.000	**0.007**	0.001	**0.007**	**0.012**	**0.02**	**0.04**	n.a.	0.22	**0.11**
Total phyto	**0.34**	**0.95**	−0.25	**0.98**	**0.35**	**0.005**	**0.010**	–	**0.014**	**0.005**					

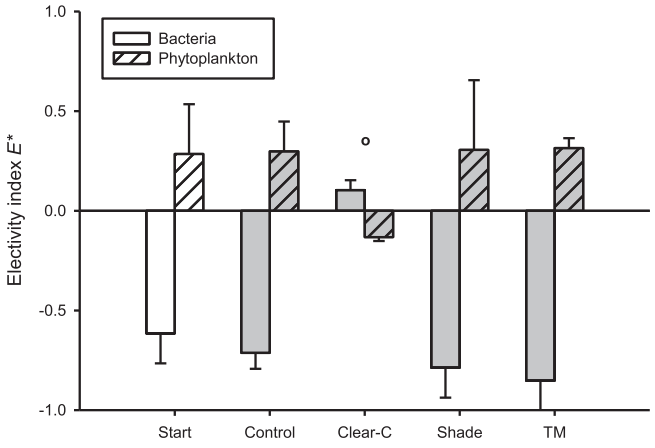

Fig. 3. Electivity index E^* of microzooplankton for phytoplankton and bacteria prey, 'o' marks treatment with insignificant differences to 0 and between both prey groups, error bars correspond to one standard deviation (n = 3). The different treatments represent the initial sampling (start), the control treatment, a clear C compounds addition (Clear-C), a pigment addition (Shade), a terrestrial matter addition (TM).

addition without light disruption), where phytoplankton biomass substantially decreased, did microzooplankton shift their diet towards bacteria. As expected, changes in prey availability had important consequences for microzooplankton biomass, which was lowest in the Clear-C treatment, where lowest total prey availability (biomass of bacteria and phytoplankton) and highest bacteria/phytoplankton ratio were recorded.

Studies in boreal clear-water and humic lakes also report small effects of depleted light conditions on phytoplankton (Jansson et al., 1999; Seekell et al., 2015) and it has been suggested that these negative effects can be partly compensated by a stimulation of basal production due to the terrestrial organic matter inputs and the assimilation of inorganic nutrients (Ask et al., 2009). Our data support this assertion somewhat, as can be seen in total basal (bacterial and phytoplankton) end biomass values that were of similar high levels for Control and Shade treatments, however the dynamics and interactions appear more complex than this alone. Although the light attenuation effect was decreased after 21 days in the experiment (likely natural photo- and bio-degradation processed as well as attachment and settling out) a consistently higher light attenuation effect was recorded in the Shade and TM treatments. Yet, marked differences in the relative contribution of phytoplankton and bacteria to the total basal biomass were recorded at the end of the experiment (Table 2). This decrease in comparative light attenuation effects could explain the weaker effect of light attenuation compared to that of C enrichment observed in our experiment, however, it is also possible that the TM and Shade treatments curtailed the light inhibition effect in such shallow waters, favoring phytoplankton growth.

We observed that Clear-C enrichment (and to a lesser extent TM) decreased total basal biomass, with decreases in phytoplankton biomass and increases in bacteria biomass occurring (Table 2). This suggests that bacteria outcompeted phytoplankton where an alternate, and readily bioavailable C source was accessible. This scenario was particularly acute in the Clear-C treatment and likely explains the stronger decrease in phytoplankton biomass as, unlike in the TM treatment, no concurrent transfer of dissolved organic and inorganic N and P occurred, thus nutrient compensation for the phytoplankton would not have been viable. Nevertheless, these results need to be interpreted with caution. Recent studies indicate that <30% of the DOC entering the Baltic Sea is readily bioavailable (Figueroa et al., 2016; Hoikkala et al., 2015), while in our experiment, despite including both bioavailable and non-available compounds, as much as 60% of the Clear-C additions were in the form of bioavailable compounds (based on Biolog EcoPlates, Biolog, USA). Moreover, even though the C-rich molecules added to the Clear-C treatment were of different types (Table 1), of various molecular weights and ecological relevance (Aluwihare and Repeta, 1999; Groisillier et al., 2015), the selective utilization of these compounds by bacteria, and the potential of these substrates to exert a selective pressure on the bacterial community and its function should be considered (Gómez-Consarnau et al., 2012; Sosa et al., 2015), particularly in the case of those taxa capable of utilizing the bioavailable N-containing amino acids added. Bacteria have high C requirements and often rely on C-rich algal exudates for growth (Baines and Pace, 1991). However, high inputs of allochthonous C can uncouple bacterial reliance on phytoplankton C exudates (Jansson et al., 2007; Tranvik, 1988). Because bacteria have higher uptake efficiency for limiting nutrients such as N and P than phytoplankton (Vadstein, 2000), in systems where allochthonous C inputs are sufficient to alleviate bacteria from their dependence on phytoplankton C exudation, bacteria can outcompete phytoplankton (Blomqvist et al., 2001). It is thus clear that high terrestrial organic matter inputs, if of suitable bioavailability or of large enough discharge rates (Figueroa et al., 2016; Hitchcock et al., 2016), can reduce phytoplankton biomass and favor bacteria, driving planktonic food webs towards heterotrophic bacterial-based energy pathways and heterotrophic energy mobilization (Figueroa et al., 2016; Jansson et al., 2007).

Besides these bottom-up effects, we observed that microzooplankton generally had higher ingestion rates on phytoplankton groups that had lower biomass; suggesting an important top-down control on these taxa. Other mesocosm experiments testing the impact of microzooplankton on phytoplankton communities also found that microzooplankton selective grazing can influence the phytoplankton bloom composition, leading to the dominance of

less-preferred phytoplankton species (Klauschies et al., 2012). In one such mesocosm study, conducted on the North Sea, it was revealed that microzooplankton could on average consume ~120% of the phytoplankton production and that selective grazing by microzooplankton was an important factor in stabilizing a bloom of less-preferred and relatively inedible phytoplankton species (Löder et al., 2011). These results highlight the important role microzooplankton play in structuring and controlling phytoplankton biomass and although we did not detect any changes in the phytoplankton community over the time frame of our experiment it is possible that with longer exposure, or repeated exposure (i.e. seasonal or annual), such changes may be reinforced and even become permanent impacts.

Microzooplankton generally showed strong selectivity for phytoplankton, although under Clear-C enrichment, where the bacteria to phytoplankton ratios was highest, we measured significant microzooplankton grazing on bacteria. The poor food quality of bacteria (Brett and Müller-Navarra, 1997), may in part explain the low final microzooplankton biomass in this treatment. A previous survey of zooplankton production and resource use in ten lakes along a naturally occurring gradient of terrestrial organic matter inputs showed that zooplankton production was negatively related to C concentration (Kelly et al., 2014). However, although the Clear-C treatment deteriorated microzooplankton biomass, our data do not directly support the above conclusion, suggesting there may be a more complex mechanism involved or that the progression and impact of the different treatments on predator-prey cycles and their timing may have differed and may also contribute to the overall trends seen. Despite adding similar C concentrations in our TM and Clear-C treatments (i.e. Clear-C C additions matched to C concentration of the climate change scenario expressed in TM), the microzooplankton biomasses at the end were distinctly different, with Clear-C expressing half the biomass values of the Control, whereas the TM treatment was almost double that of the Control. This would suggest that, as seen in other studies, the addition of terrestrial or allochthonous C may support zooplankton growth and production (Cole et al., 2011; Hitchcock et al., 2016), despite the minimal decrease in overall basal biomass, the lower phytoplankton biomass, and the elevated biomass contribution of bacteria (~70% of basal biomass) in the TM treatment as compared to the Control and Shade treatments (circa 55 and 45% bacterial biomass contribution, respectively). Furthermore, our data suggest that in addition to the amount of allochthonous C subsidy (i.e. the loading of C and the extent of light attenuation) the understanding of another mechanistic tipping point is vital. In the Clear-C treatment, the collapse of microzooplankton biomass corresponded with the dominance of basal biomass by bacteria and the relative depletion of phytoplankton, resulting in a prey pool that was of poor nutritional quality (i.e. bacteria) for microzooplankton, a factor we attribute to the bioavailability of the added C. It is therefore clear that the overall received load of bioavailable C, is a vital factor that influences basal producer balance and thus the efficiency and quality of energy and nutrients transferred to microzooplankton (Findlay and Sinsabaugh, 2004; Taipale et al., 2016).

Overall our results suggest that, at least in shallow coastal areas where the impacts of increased terrestrial organic matter inputs are likely to be most marked, light attenuation does not have such a significant effect, and allochthonous C is the main driver of change, inducing competition between bacteria and phytoplankton. One possible reason for which light attenuation may not have had the expected impact could be that in such shallow waters, TM (soil addition) and Shade actually act in a positive way, decreasing phytoplankton growth inhibition due to excessive light (photo-inhibition, Nevalainen et al., 2015). Furthermore, the region where we carried out this study is strongly exposed to terrestrial organic matter inputs, particularly at the seasonal level (Forsgren and Jansson, 1992; Harvey et al., 2015), and phytoplankton have the ability to adjust their photosynthetic pigment composition to altered light conditions (Moore et al., 2006; Paczkowska et al., 2016). Organisms living in these waters should therefore already be adapted to these conditions and thus drastic changes in trophy or function may not readily take place, at least not over the duration of such experiments. As noted above, the characteristics of the C pool can have a clear influence, both on the C bioavailability and on the extent of light inhibition induced, in controlling the basal producer balance and thus the impact in grazers. While we did not record marked structural changes it is however possible that if tipping points are met then repeated and elongated exposure to such conditions (as may result from regional climate change scenarios) could perceivably catalyze permanent change.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2017.06.008.

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