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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)