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ORIGINAL RESEARCH ARTICLE

Microbial plankton communities in the coastal southeastern Black Sea: biomass, composition and trophic interactions

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Summary We investigated biomass and composition of the pico-, nano- and microplankton communities in a coastal station of the southeastern Black Sea during 2011. We also examined trophic interactions within these communities from size-fractionated dilution experiments in February, June and December. Autotrophic and heterotrophic biomasses showed similar seasonal trends, with a peak in June, but heterotrophs dominated throughout the year. Autotrophic biomass was mainly comprised by nanoflagellates and diatoms in the first half of the year, and by dinoflagellates and *Synechococcus* spp. in the second half. Heterotrophic biomass was mostly dominated by heterotrophic bacteria, followed by nanoflagellates and microzooplankton. Dilution experiments suggest that nano- and microzooplankton were significant consumers of autotrophs and heterotrophic bacteria. More than 100% of bacterial production was consumed by grazers in all experiments, while 46%, 21% and 30% of daily primary production were consumed in February, June and December, respectively. In February, autotrophs were the main carbon source, but in December, it was heterotrophic bacteria. An intermediate situation was observed in June, with similar carbon flows from autotrophs and heterotrophic bacteria. Size-fraction

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dilution experiments suggested that heterotrophic nanoflagellates are an important link between the high heterotrophic bacterial biomass and microzooplankton. In summary, these results indicate that nano- and microzooplankton were responsible for comprising a significant fraction of total microbial plankton biomass, standing stocks, growth and grazing processes. This suggests that in 2011, the microbial food web was an important compartment of the planktonic food web in the coastal southeastern Black Sea.

1. Introduction

Biogenic carbon transfers from autotrophic to heterotrophic organisms through two main pathways: the classical herbivorous food web and the microbial food web (Azam et al., 1983; Legendre and Rassaulzadegan, 1995; Sherr et al., 1986; Sommaruga, 1995). In the classical herbivorous food web, energy is channelled directly from large diatoms to metazoans (Pomeroy, 1974). In the microbial food web energy is channelled to higher trophic levels from bacteria and small phytoplankton (<20 μm) to nano-microzooplankton (Azam et al., 1983; Calbet and Landry, 2004). Therefore, through the microbial food web, heterotrophic nanoflagellates (HNF) and microzooplankton (<200 μm, especially ciliates and heterotrophic dinoflagellates) play significant roles in structuring plankton communities (Calbet, 2008) and in nutrient regeneration (Calbet and Saiz, 2005). They control lower level production and dynamics (Calbet and Landry, 2004) and are a favourite prey for mesozooplankton in a range of aquatic environments, from the poles to upwelling regions to oligotrophic ocean gyres (Atkinson, 1996; Calbet and Saiz, 2005; Stoecker and Capuzzo, 1990). The microbial food web is less efficient due to energy losses in each trophic step and dominant in oligotrophic waters. However, many productive systems have multivorous food webs where both the classical and microbial food webs play important roles in carbon cycling (Legendre and Rassaulzadegan, 1995). Thus, information on the different trophic compartments and their interactions is important for understanding the functioning of the planktonic food web and its representation in ecological models.

The Black Sea ecosystem has significant potential in terms of fishing among the world oceans, but drastic changes in biogeochemical properties occurred during the last four decades (Besiktepe et al., 1999; Daskalov, 2002; Kideys, 2002; Oguz and Gilbert, 2007; Oguz et al., 2012a). Pollution, eutrophication, over-fishing, climatic cooling/warming and introduction of non-native species altered the Black Sea ecosystem in the 1990s (Oguz and Gilbert, 2007). Nutrient concentrations decreased in the 2000s compared with the eutrophication period, which has been regarded as an improvement of the Black Sea ecosystem state (Pakhomova et al., 2014). However, the ecosystem seems not to have recovered to the classical herbivorous food web of the pre-eutrophication period prior to 1970 and is now characterized by a food web dominated by dinoflagellates and other nano-size phytoplankton species with respect to diatoms, and relatively low levels of phytoplankton (Oguz and Velikova, 2010). Despite improvements, the Black Sea is still under serious environmental threats as a result of uncontrolled coastal pollution and high river discharge of several industrialized countries into this semi-enclosed basin. Climatic changes may have also played a role in shifts towards domination of dinoflagellates and nanoflagellates, reduced frequency and magnitude of phytoplankton blooms, and declines in phytoplankton biomass (Daskalov, 2002; Kideys, 2002; Nesterova et al., 2008; Oguz and Gilbert, 2007; Oguz et al., 2012a). Long-term changes of in situ phytoplankton biomass in the interior basin indicate distinct decadal changes that followed closely temperature variations, with higher (lower) biomass occurred during cold (warm) years (Nesterova et al., 2008; Oguz et al., 2006). It has been speculated that warming over the next decades (Collins et al., 2013) might significantly increase carbon flow through the microbial food web (Caron and Hutchins, 2012). However, there is little information on the importance of the microbial food web in the Black Sea, since previous studies mainly analysed the dynamics of classical food web contributors such as diatoms, dinoflagellates and their mesozooplankton predators, in particular, copepods (BSC, 2008). A number of studies have investigated components of the microbial food web (heterotrophic bacteria, pico-autotrophs, small flagellates and microzooplankton), but these have mostly focused on specific compartments or taxonomic subsets during limited periods and in specific regions (e.g. Becquevort et al., 2002; Feyzioglu et al., 2004; Kopuz et al., 2012; Sorokin et al., 1995; Uysal, 2001). To the best of our knowledge, a simultaneous assessment of the whole microbial community has not been done for the Black Sea. A few studies indicate the importance of nano- and microzooplankton as grazers. Bouvier et al. (1998) measured feeding activity of nano- and micrograzers on heterotrophic bacteria and nanoplankton during summer 1995 in the NW Black Sea based on the uptake of fluorescently labelled-prey, and Stelmakh and Georgieva (2014) reported microzooplankton grazing on phytoplankton based on dilution experiments conducted in the Western Black Sea.

The SE Black Sea is an important part of the Black Sea in terms of fishing. A milder climate provides more favourable spawning and overwintering grounds for the anchovy, and the region currently sustains 80% of the total fish catch in the Black Sea (Oguz et al., 2012b). As such lower trophic levels dynamics should be understood as much as possible. However, there are no studies on trophic interactions within a