CARBON FLOW WITHIN PLANKTONIC FOOD WEB

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BLACK SEA MARINE ENVIRONMENT:
THE TURKISH SHELF

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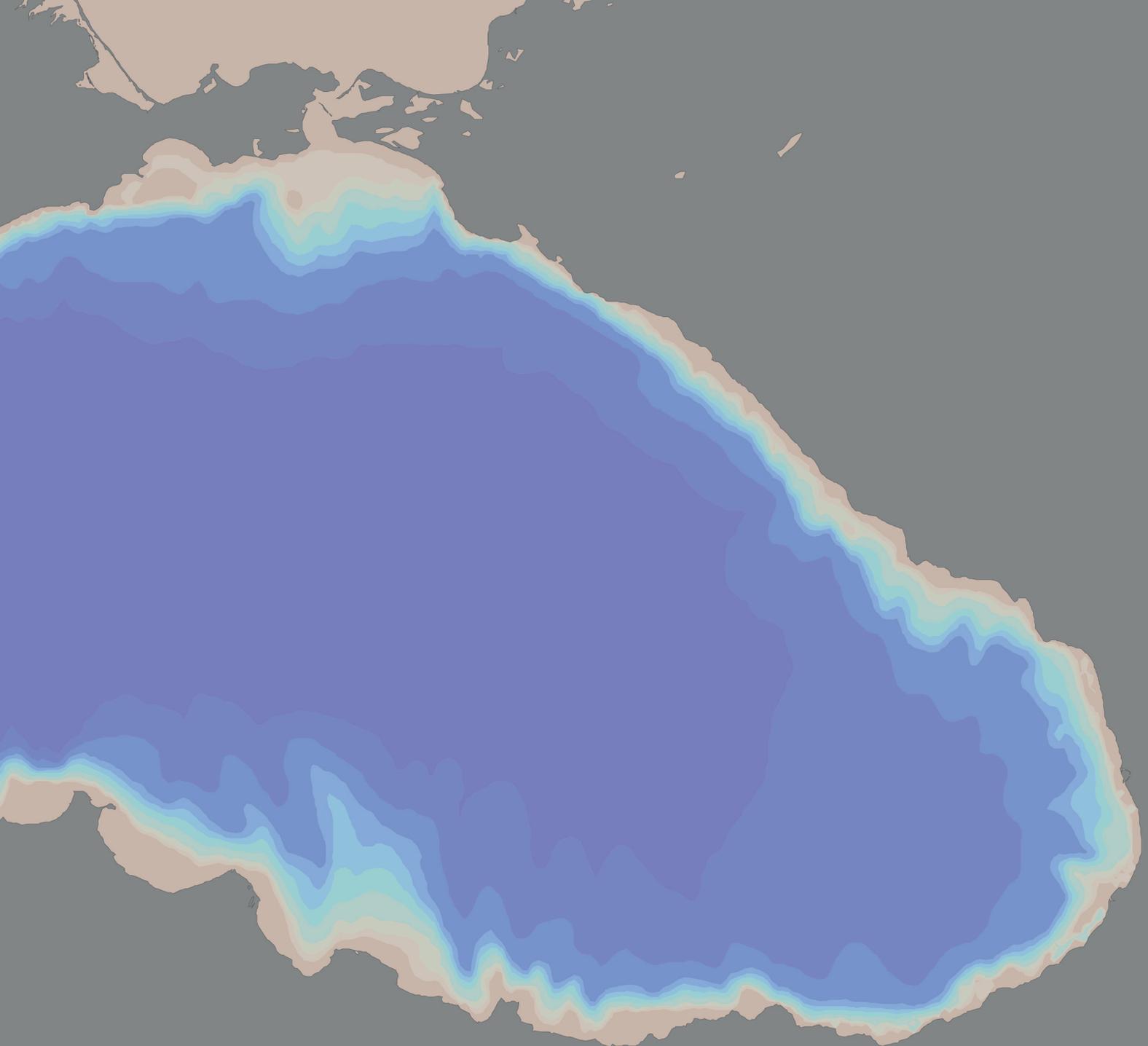
BLACK SEA MARINE ENVIRONMENT:
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BLACK SEA MARINE ENVIRONMENT: THE TURKISH SHELF

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II. BIODIVERSITY

CARBON FLOW WITHIN PLANKTONIC FOOD WEB

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1. Introduction

In aquatic environment, there are two main pathways by which carbon flows from autotrophic to heterotrophic organisms: the classical herbivorous food web and the microbial food web (Azam *et al.* 1983, Sherr *et al.* 1986, Legendre and Rassaulzadegan 1995). In the classical herbivorous food web, the carbon flows directly from large autotrophs to metazoans (Pomeroy 1974). In the microbial food web, the carbon flows from bacteria and small phytoplankton (< 20µm) to nano- microzooplankton and then to higher trophic levels (Azam *et al.* 1983, Calbet and Landry 2004). The importance of the nano- and micrograzers was first described in oligotrophic ecosystems, where autotrophs are dominated by smaller cells. However, since then, it has been recognized that these grazers (heterotrophic nanoflagellates and microzooplankton < 200 µm) also control lower level production and dynamics in productive coastal regions (Calbet and Landry 2004). They are also favourite prey for mesozooplankton in a range of aquatic environments, from the poles to upwelling regions (Stoecker and Capuzzo 1990; Atkinson 1996; Calbet and Saiz 2005). By this way they play significant roles in structuring plankton communities and in nutrient regeneration (Calbet and Saiz 2005, Calbet 2008). Making a distinction between the two historical perspectives, in the herbivorous food web the predators are metazoans, while in the microbial food web the predators are protozoans. An intermediate situation is called the multivorous food web, where both metazoan and protozoan consume both large and small cells (Legendre and Rassoulzadegan 1995). As a result of these studies, the traditional view of a short and efficient herbivorous food web, has been gradually replaced in last decades by a perspective where the year-round workhorses are actually the smaller cells, while larger cells have a more sporadic and seasonal importance.

Drastic changes in biogeochemical properties occurred in the Black Sea ecosystem during the last half century due to pollution, eutrophication, over-fishing, climatic cooling/warming and introduction of non-native species (Besiktepe *et al.* 1999, Kideys 2002, Daskalov 2002, Oguz and Gilbert 2007, Oguz *et al.* 2012). Decreases of nutrient levels during the 1990's were regarded as an improvement of the state of the ecosystem. However, the ecosystem seems not to have return to the classical herbivorous food web of the pre-eutrophication period and is now dominated by dinoflagellates and other nano-size phytoplankton species with respect to diatoms, and relatively low levels of phytoplankton (Oguz and Velikova 2010). In addition, the Black Sea is still under

serious environmental threats in result of being a semi-enclosed basin, with high river discharge of several industrialized countries and uncontrolled coastal pollution. The domination of dinoflagellates and nanoflagellates, reduced frequency and magnitude of phytoplankton blooms, and declines in phytoplankton biomass may have also been related to climatic variability (Kideys 2002, Daskalo 2002, Oguz and Gilbert 2007, Nesterova *et al.* 2008, Oguz *et al.* 2012). For example, in-situ phytoplankton biomass in the interior basin followed closely temperature decadal variations, with higher (lower) biomass occurred during cold (warm) years (Oguz *et al.* 2006, Nesterova *et al.* 2008). Predicted warming over the next decades (Collins *et al.* 2013) might significantly increase carbon flow through the microbial food web (Caron and Hutchins 2012). Monitoring of the status of the marine food web has been considered essential for the implementation of the "food web" descriptive of the Marine Strategy Framework Directive (EU 2008), which aims to achieve a healthy functioning of marine ecosystems and a sustainable use of marine resources.

In this chapter the carbon flow within planktonic food web were reviewed from the available literature in the Black Sea. First the importance of nano-micrograzers as grazers on lower levels is discussed, and then their role as a prey for higher trophic levels is considered.

2. Carbon flow within the microbial food web in the Black Sea

The number of available studies on microbial communities (< 200 um) in the Black Sea are strongly biased toward classical herbivorous food web contributors such as diatoms, dinoflagellates and their mesozooplankton predators, in particular copepods (BSC 2008). A few studies on microbial food web components (heterotrophic bacteria, pico autotrophs, small flagellates, and microzooplankton) are accessible (Bird and Karl 1991, Sorokin *et al.* 1995, Bouvier *et al.* 1998, Uysal 2001, Feyzioglu *et al.* 2004, Morgan *et al.* 2006, Kopuz 2010, Kopuz *et al.* 2012), but for the most part they only contemplate abundances and distribution of specific compartments and do not examine trophic interactions. As a result, little is known about the dynamics of the microbial food web in the Black Sea, in particular the role of nano-and microzooplankton grazing on controlling lower level production. The only available information on the growth and grazing dynamics within microbial food web comes from studies in NW Black Sea (Bouvier *et al.* 1998), in the Western and Northern Black Sea (Stelmakh *et al.* 2009, Stelmakh 2013, Stelmakh and Georgieva 2014) and in the SE Black Sea (Aytan *et al.* 2017). The importance of nano- and micrograzers on heterotrophic bacteria and phytoplankton in the Black Sea will be reviewed in the following subsections.

2.1. Nano- and Microzooplankton grazing on Heterotrophic Bacteria

Heterotrophic bacteria are a crucial component of marine food webs (Pomeroy 1974, Azam *et al.* 1983) and play key role in carbon and nutrient cycling in the ocean

(Azam *et al.* 1994). The flow of carbon from heterotrophic bacteria to upper trophic levels is still a poorly understood aspect of microbial food web dynamics. Abundance and distribution of heterotrophic bacteria were subject to several studies in the Black Sea, but only a few studies are available on bacterial growth and mortality due to nano- and microzooplankton.

Bouvier *et al.* (1999) measured feeding activity of nano- and micrograzers on heterotrophic bacteria during summer 1995 in the NW Black Sea based on the uptake of fluorescently labelled-prey. Predation on heterotrophic bacteria by both nano- and micro-grazer was found, but notably nano-sized mixotrophic ciliates only fed on bacteria. This study proved an active microbial food web. However as noted by the authors the feeding activity might have been underestimated because of the employed methodology. In a recent study (Aytan *et al.* 2017), all compartments of microbial communities (Figure 1) during 2011 in SE Black Sea coastal waters were investigated. They also examined nano- and microzooplankton bacterivory from size-fractionated dilution experiments in February, June and December 2011. Growth and grazing rates of heterotrophic bacteria were calculated based on cell count. Production and grazing losses were computed based on the estimated growth and grazing rates, and initial carbon biomass. In this study, heterotrophic bacteria were the most substantial component of the Hetero-C biomass, with contributions ranging between 19% and 70% (Figure 1b).
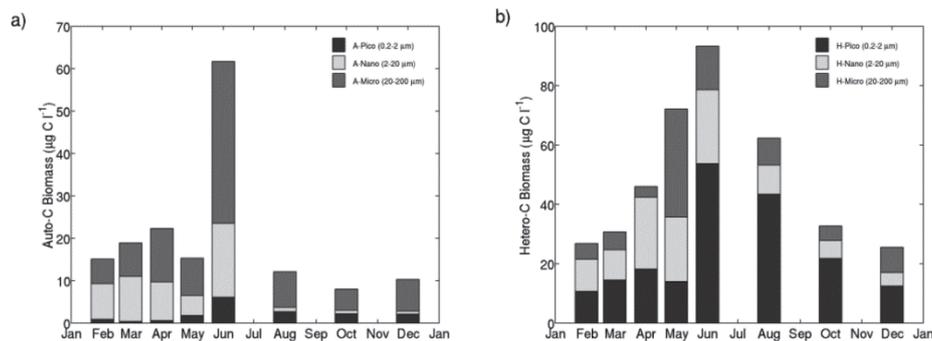
Figure 1. Contribution of size classes to autotrophic (a) and heterotrophic (b) carbon biomass from February to December 2011 at the sampling station (Aytan *et al.* 2017)

In agreement with Bouvier *et al.* (1999), Aytan *et al.* (2017) also found evident grazing of nano- and micrograzers on heterotrophic bacteria. The grazing rates of grazers were always higher than growth rates of heterotrophic bacteria, except on one occasion (< 20 μm size fraction) in December. This clear pattern showed that nano- and microzooplankton heavily grazed on heterotrophic bacteria and removed > 100% of daily

bacterial production (Table 1). The highest daily bacterial production was found in the June experiment together with the highest bacterial biomass.

Table 1. Mean growth and grazing mortality rates of heterotrophic bacteria calculated from the size-fractioned dilution experiments. μ = growth rate, g = grazing mortality rate; r^2 = the correlation coefficient of the linear regression of apparent growth rate against the fraction of unfiltered seawater; BP= bacterial production, G= grazing losses; *ns* = not significant; [*]p < 0.05; [**]p < 0.01 (modified from Aytan *et al.* 2017)

Date	Size Fraction	μ (d^{-1})	g (d^{-1})	g: μ	r^2	BP (μg C l^{-1}d^{-1})	G (μg C l^{-1}d^{-1})
February 2011	< 200 μm	0.34	0.40	1.17	*ns*	*3.7*	*4.3*
	< 20 μm	0.15	0.38	2.53	0.62[*]	1.2	3.1
June 2011	< 200 μm	0.80	1.20	1.50	0.90[**]	37.6	56.5
	< 20 μm	0.77	1.22	1.58	0.95[**]	35.5	56.4
December 2011	< 200 μm	0.63	0.76	1.20	0.96[**]	11.1	13.4
	< 20 μm	0.79	0.49	0.62	*ns*	*18.6*	*11.6*

Despite heavy predation on bacterial production, relatively high standing stocks of heterotrophic bacteria were reported in the region throughout the year (Figure 1b). The high heterotrophic bacteria standing stock was suggested to may have been supported by the high dissolved organic carbon concentrations in the Black Sea (~2 times higher than the ocean; Ducklow *et al.* 2007) and other sources than local phytoplankton production such as river-transported materials, terrestrial runoff, anthropogenic discharges, benthic fluxes, cycles of sediment resuspension and seasonal reemergence of subsurface CDOM accumulations (Lee *et al.* 2001). The author concluded that heterotrophic bacteria are an important carbon source for nano- and micrograzers in the region, especially in the period of low primary production.

2.2. Nano- and Microzooplankton grazing on phytoplankton

Phytoplankton growth and microzooplankton grazing are crucial processes to understand energy flow in the pelagic food web. Phytoplankton are primary producers, and microzooplankton (<20-200μm) are the main consumer of the daily primary production in the sea (Calbet 2008). However, little attention has been given to phytoplankton growth and microzooplankton grazing in the Black Sea.

Seasonal dynamics of microzooplankton grazing were assessed by dilution experiment in Southern Crimea coastal waters during 2006-2007 and 2010 (Stelmahk 2013). Large diatoms were found as favourite prey of microzooplankton and annual removal of primary production in the surface waters was reported as ca. 65%. In May 2013, as a part of Black Sea expedition of the "R/V "Professor Vodyanitsky", removal of

primary production by microzooplankton reported between 4-204% in Western Black Sea coastal waters, 18-72% in Western Black Sea open waters and 12-30% in Eastern Black Sea coastal waters (Table 2) (Stelmak and Georgieva 2014). In the same study, they found that phytoplankton bloom occurred when daily grazing on primary production (g/μ) was less than 75%. Author conclude that microzooplankton play an important trophic function by removing major part of the phytoplankton primary production.

Table 2. Chlorophyll-*a*, microzooplankton grazing rate (g), net phytoplankton growth rate (μ-g), the ratio g/μ (%) over the Black Sea in May 2013 (modified from Stelmak and Georgiva 2014)

Chl *a* (mg/m^3)	g (day^{-1})	μ - g (day^{-1})	g/μ (%)
Western Black Sea, near-shore area			
0.11	0.55	0.65	52
0.12	0.53	0.64	55
1.10	0.53	-0.27	204
0.33	0.13	0.84	13
0.09	0.34	1.00	25
0.11	0.04	0.94	4
0.11	0.32	0.73	30
Western Black Sea, open-sea area			
0.13	0.19	0.84	18
0.13	0.99	0.45	69
0.10	0.50	0.44	53
0.11	0.50	0.63	44
0.10	0.61	0.46	72
Eastern Black Sea, near-shore area			
0.18	0.15	1.12	12
0.14	0.17	1.18	13
0.10	0.20	0.90	18
0.11	0.24	0.56	30
0.10	0.24	0.89	21

In the previously described study of Aytan *et al.* (2017), concomitantly with the bacterivory, nano- and microzooplankton herbivory was also estimated from the size-fractionated dilution experiments (Landry and Hassett 1982) of February, June and December 2011. Growth and grazing rates of phytoplankton were calculated based on the net changes in chlorophyll-*a*. Considering the whole autotrophic community (< 200 μm fraction experiment) the percentage of primary production consumed by nano- and microzooplankton was reported to be as 46%, 21% and 30% in February, June and

December, respectively (Table 3). The relatively low grazing in June was found to be associated with *E. huxleyi* bloom which might deter grazing. This situation was also reported in the Northern Black Sea (Stelmakh 2013, Stelmakh and Georgieva 2014) and other regions (*e.g.* Fileman *et al.* 2002, Strom *et al.* 2003, Fredrickson and Strom 2009). The low grazing in December was suggested to might have been related to nutritional quality of phytoplankton given the low growth rates measured.

Table 3. Mean growth and grazing mortality rates of phytoplankton calculated from the size-fractioned dilution experiments. μ = growth rate, g = grazing mortality rate; r^2 = the correlation coefficient of the linear regression of apparent growth rate against to fraction of unfiltered seawater; P= primary production, G= grazing losses; *ns* = not significant; [*] p < 0.05; [**] p < 0.01 (modified from Aytan *et al.* 2017)

Date	Size Fraction	Initial Chl-*a*	μ (d⁻¹)	g (d⁻¹)	g: μ	r^2	P (μg C l⁻¹d⁻¹)	G (μg C l⁻¹d⁻¹)
February 2011	< 200 μm	0.47	1.67	0.77	0.46	0.67[*]	43.1	20.0
	< 20 μm	0.36	1.14	0.47	0.41	0.82[**]	19.9	8.2
June 2011	< 200 μm	1.52	2.43	0.53	0.21	0.79[*a]	289.7	63.2
	< 20 μm	0.48	1.68	0.11	0.07	*ns*	*50.0*	*3.3*
December 2011	< 200 μm	0.74	0.23	0.07	0.30	*ns*	*3.0*	*0.9*
	< 20 μm	0.29	0.28	0.39	1.44	*ns[a]*	*1.2*	*1.7*

In the same study, in addition to chlorophyll-*a* growth and mortality, the growth and mortality of *Synechococcus* spp. was also estimated based on cell count during February and December 2011. 194 and 44% of daily *Synechococcus* spp. production was removed by nano- and micrograzers in February and December (Table 4). *Synechococcus* spp. can be an important contributor to Auto-C (e.g. Kopuz *et al.* 2012) in the Black Sea. However, carbon flow to grazers was lower during the reported study, because of the low biomass and growth rates of *Synechococcus* spp. Authors stated that the importance of *Synechococcus* spp. to grazers might increase deeper in the water column since maximal biomass has been reported around euphotic depth (~30 m) in the Black Sea especially during thermal stratification (*e.g.* Uysal 2001, Kopuz *et al.* 2012).

Table 4. Mean growth and grazing mortality rates of *Synechococcus* spp. calculated from the size-fractioned dilution experiments. μ = growth rate, g = grazing mortality rate; r^2 = the correlation coefficient of the linear regression of apparent growth rate against to fraction of unfiltered seawater; P= production, G= grazing losses; *ns* = not significant; [*] $p < 0.05$; [**] $p < 0.01$ (modified from Aytan *et al.* 2017).

Date	Size Fraction	μ (d^{-1})	g (d^{-1})	g: μ	r^2	P (µg C l^{-1}d^{-1})	G (µg C l^{-1}d^{-1})
February 2011	< 200 µm	0.35	0.68	1.94	0.90[**]	0.4	0.8
	< 20 µm	0.11	0.72	6.54	0.89[**]	0.1	0.8
December 2011	< 200 µm	0.46	0.19	0.41	*ns*	*1.1*	*0.4*
	< 20 µm	1.27	0.51	0.40	0.56[*]	3.7	1.5

By analysing the full spectrum of prey and predator <200 um, total carbon consumption (bacterivory+herbivory) revealed high-energy flux through the nano- and microzooplankton in the SE Black Sea (Aytan *et al.* 2017). Trophic interactions obtained from the study revealed that in February, an active microbial web with a pronounced importance of autotrophic preys (66%) as a carbon source compared to heterotrophic preys (heterotrophic bacteria and heterotrophic nanoflagellates) (Figure 2). In contrast to February, there was a change in the contribution of different prey to total carbon consumed with an increased importance of heterotrophic prey (53%) compared to autotrophs (47%) in Juna. In December, dilution experiments showed relative importance of HB as a carbon source for nano- and microzooplankton compared to autotrophs (Figure 2).
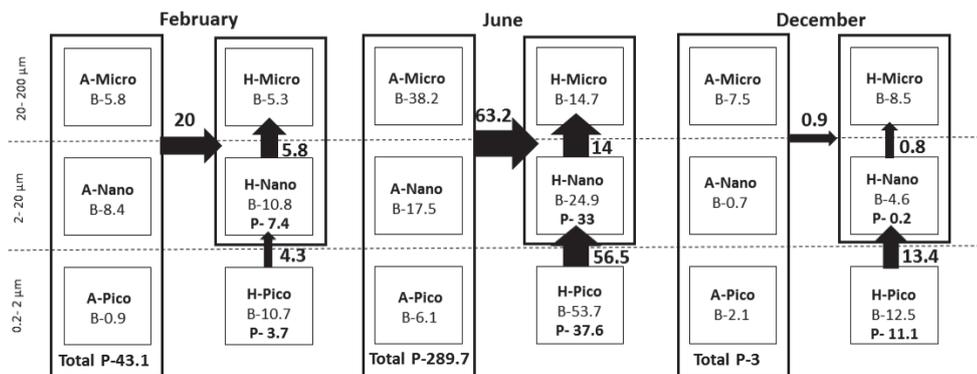

Figure 2. Schematic representation of carbon flow within microbial food web in the SE Black Sea during 2011. Arrows show daily grazing losses (µg C l^{-1} d^{-1}) according to estimation of < 200 µm experiments. A-Pico=Synechococcus, A-Nano=autotrophic nanoflagellates, A-Micro=diatom and autotrophic dinoflagellates, H-Pico=heterotrophic

bacteria, H-Nano=heterotrophic nanoflagellates, H-Micro=Ciliates and heterotrophic dinoflagellates.B= Biomass (μg C l^{-1}), P= Daily production (μg C l^{-1} d^{-1}) (Aytan *et al.* 2017).

Recently, as a part of TUBITAK ÇAYDAG 114Y232 project (entitled "The role of microzooplankton within the planktonic food web of the SE Black Sea"), the dynamics of classical herbivorous food web and microbial food web were assessed in the SE Black Sea between May 2015 and April 2016 in river mouth, and the coastal and open waters of Southeastern Black Sea. Seasonal dilution experiments (Landry and Hassett 1982) were conducted to determine grazing pressure of microzooplankton on phytoplankton size groups. Growth rates and daily primary productions of pico-, nano-and microphytoplankton with mortality rates and daily grazing losses due to microzooplankton grazing were calculated.

For the first time, detailed community assessment of microzoplankton was done. It was found that microzooplankton was represented by a total of 108 species belonging to Protozoa and Metazoa. Microzooplankton abundance ranged from 63 to 2733 cell.l^{-1} dominated by heterotrophic dinoflagellates. Microzooplankton biomass ranged from 0.7 to 28.9 μgC.l^{-1} and dominated by micrometazoans. Abundance and biomass values tended to decrease from river mouth to open waters. Total microplankton abundance was dominated by microphytoplankton, whereas microzooplankton was an important contributor of total microplankton biomass (41-50%). Estimated primary production and grazing losses ranged from 0.2 to 42 μg C l $^{-1}$ d $^{-1}$ and 0.54 to 59.5 μg C l $^{-1}$ d $^{-1}$, respectively. Microzooplankton were main grazers of phytoplankton and responsible for greater than 100 % of daily primary production losses. Microzooplankton mostly consumed micro-size phytoplankton. Primary production and grazing losses due to grazing decreased from the river mouth to the open waters. A significant positive correlation (R^2 = 0.36, p<0.001) between the phytoplankton growth and the microzooplankton grazing rate was found in the study (Figure 3b) and the results strongly agree with the global assessment in the coastal and open ocean regions (Figure 3a) made by Calbet and Landry (2004). The results of TUBITAK ÇAYDAG project 114Y232 suggest that microzooplankton is an important component of plankton and a main grazer of phytoplankton in the Southeastern Black Sea.
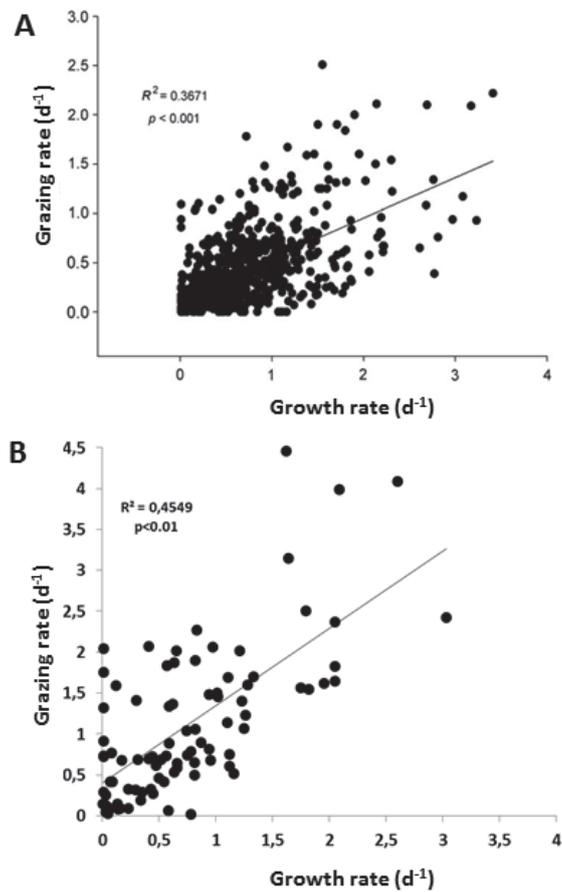
Figure 3. Relation between phytoplankton growth and microzooplankton grazing (A-Global data, Calbet and Landry 2004, B- SE Black Sea, TUBITAK CAYDAG 114Y232

3. Carbon flow from microphytoplankton and microzooplankton to copepods

The transfer of carbon via the microbial food web to higher trophic levels challenges much of the traditional views on marine food webs. As shown above, nano- and microzooplankton can consume more than half of phytoplankton biomass per day and most of the primary production could be circulated by microzooplankton to higher trophic levels instead of sedimentation or advection.

Traditionally, phytoplankton are known to be the main food source for mesozooplankton, in particular copepods (Calbet and Alcaraz 2008). Among mesozooplankton, copepods play a key role in pelagic food web transferring energy from primary producers to planktivorous fish. Copepods, in particular calanoids and cyclopoids are considered as selective feeders (Lampert 1987). Although copepods comprise an important part of total mesozooplankton biomass in the Black Sea, their feeding behaviour is still poorly understood. In the Black Sea, Petipa (1964) reported that dinoflagellates and diatoms were found as dominant food item in the gut content of *Calanus*; Crustacean exoskeletons and small dinoflagellates in the gut of *Calanus* were reported by Arashkevich *et al.* (1997). Besiktepe *et al.* (2005) reported herbivory of female *C. euxinus* ranged from 6% to 11% of their body carbon weight in April and from 15% to 35% in September 1995 by gut pigment content analysis. They indicate that the herbivorous daily ration was sufficient to meet the routine metabolic requirements of female *C. euxinus* in April and September 1995 in the Black Sea. Recently, contrary to traditional view, microzooplankton (< 200µm, protozoa and metazoa) have been recognised as a favourite prey for mesozooplankton (200-2000 µm), in particular copepods in a range of aquatic environments, from upwelling regions to oligotrophic ocean gyres to polars (Calbet 2008). They can consume more than half of phytoplankton biomass per day and most of the primary production is circulated by microzooplankton to higher trophic levels instead of sedimentation or advection (Calbet and Alcaraz 2008).

As a part of previously described TUBITAK CAYDAG 114Y232 project, a total of 51 copepod feeding experiments were conducted between May 2015-April 2016 in the Southeastern Black Sea to assess the contribution of microphytoplankton (diatom and autotrophic dinoflagellates) and microzooplankton (heterotrophic dinoflagellates, ciliates and micrometazoa) to *Calanus euxinus* and *Acartia clausi* diet. Filtration and ingestion rates for each copepod species were calculated. To understand feeding selectivity the "Relative Preference Index" was also calculated. In open waters of the SE Black Sea, filtration rates of *Acartia clausi* ranged between 8-535 (mean 92±181) ml.copepod^{-1}.d^{-1} and 0-485 (mean 148±151) ml.copepod^{-1}.d^{-1} for microphytoplankton and microzooplankton, respectively (Figure 4a). The highest filtration rates of *Acartia clausi* was estimated for heterotrophic dinoflagellates (mean 291±607 ml. copepod^{-1}. d^{-1}). Filtration rates of *Calanus euxinus* ranged between 0-237 (mean 94±88) ml.copepod^{-1}.d^{-1} and 0-247(mean 137±109) ml.copepod^{-1}.d^{-1} for microphytoplankton and microzooplankton, respectively (Figure 4b). The highest filtration rates of *Calanus euxinus* was estimated for micrometazoa (235±171 ml. copepod^{-1}. d^{-1}).
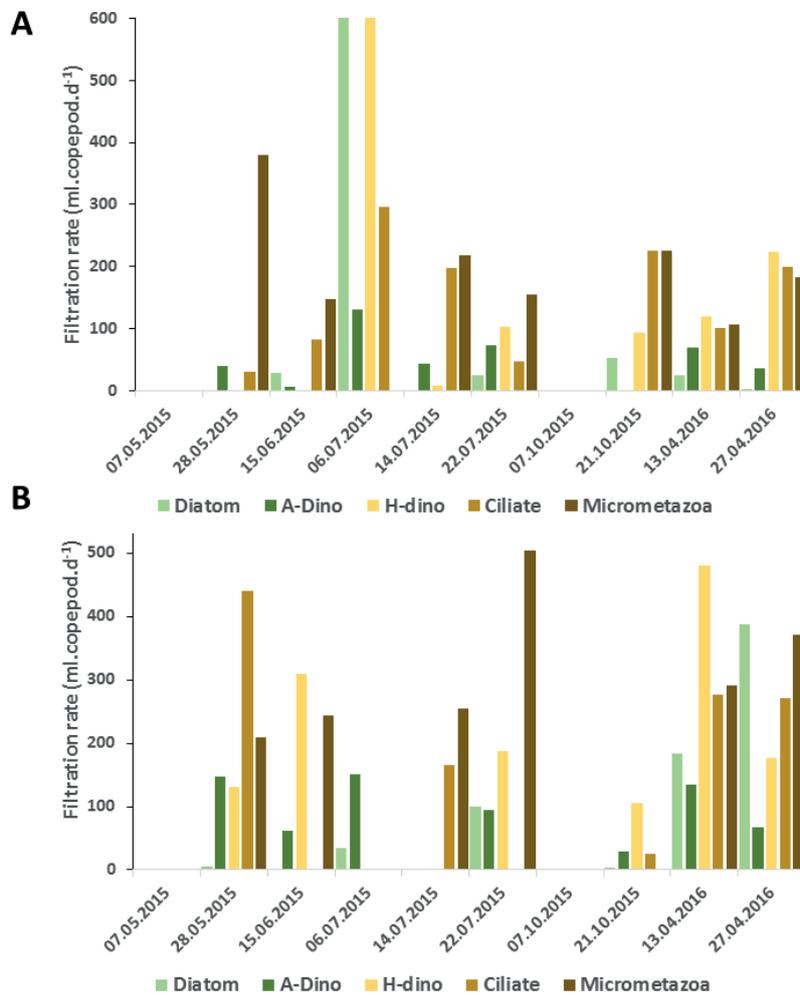
Figure 4. Filtration rates of *Acartia clausi* (A) and *Calanus euxinus* (B) on different prey groups in open waters (20 nm) of SE Black Sea

Results obtained from the study showed that, in open waters, ingestion rate of *Acartia clausi* for microphytoplankton and microzooplankton ranged between 0.003-0.104 (0.06±0.08) µgC. copepod. d^{-1}, and 0-0.301 (0.08±0.1) µg C.copepod.d^{-1} , respectively. Among preys, the highest ingestion rate was estimated for heterotrophic dinoflagellates (0.05±0.12 µg C.copepod.d^{-1}). Overall, averaged contribution of

microphytoplankton and microzooplankton to *Acartia clausi* diet was 46% (10-82%) and 54% (18-90%), respectively (Figure56a). Ingestion rate of *Calanus euxinus* for microphytoplankton and microzooplankton ranged between 0-0.312 (0.081±0.101) µgC. copepod. d^{-1}, and 0-0.224 (0.091±0.087) µg C.copepod.d^{-1}, respectively. Among preys, the highest ingestion rate was estimated for autotrophic dinoflagellates (0.047±0.04 µgC.copepod.d^{-1}) and micrometazoans (0.046±0.04 µgC.copepod.d^{-1}). Overall, averaged contribution of microphytoplankton and microzooplankton to *Calanus euxinus* diet was 42% (0-100%) and 58% (0-100%), respectively (Figure 5b). These results indicate that both calanoid copepods exhibited selective feeding behaviour on microzooplankton. Copepods mostly fed on microphytoplankton during the short-term bloom period. However, microzooplankton was an important carbon source for copepods during critical periods of low food concentration.
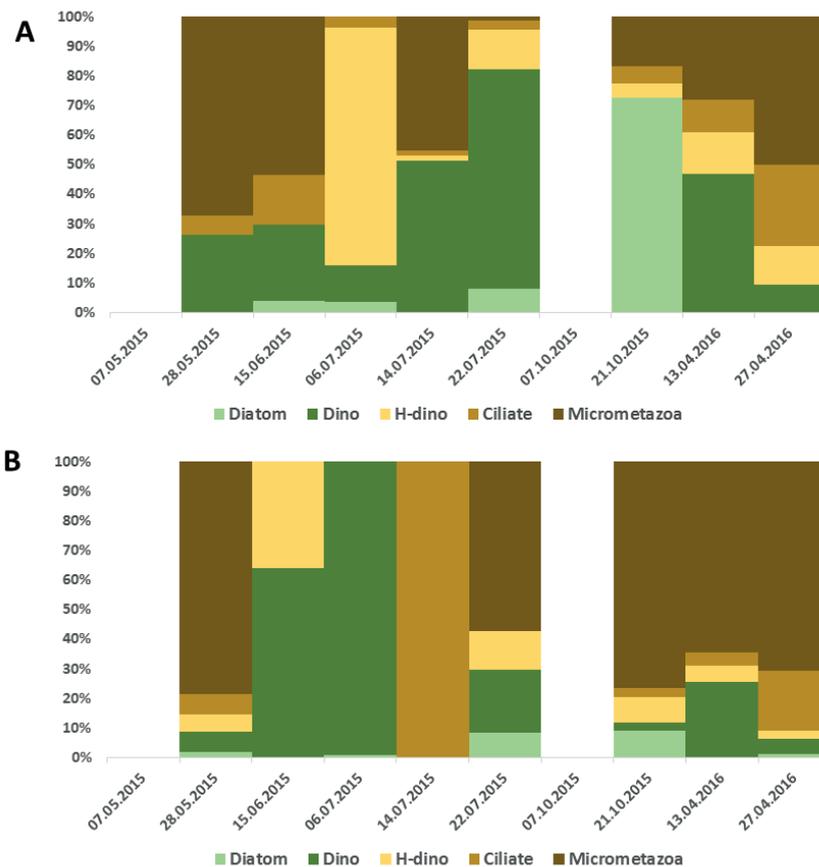
**Figure 5.** Contribution of different prey group to *Acartia clausi* (A) and *Calanus euxinus* (B) diet in open waters (20 nm) of SE Black Sea

4. Conclusion

Reviewed studies in this chapter show the strong grazing impact of nano- and microzooplankton on bacterial and primary production in the Black Sea. It is also shown that microzooplankton is a key group in the energy flow between the primary production and copepods. This suggests an active microbial food web. These results add up to increased evidence indicating that microzooplankton is an important participant of plankton and main grazer of phytoplankton in temperate coastal systems. Nevertheless, the classical food web seems also an important pathway of carbon to higher trophic levels during the phytoplankton seasonal blooms. Therefore, the system seems better described as a multivorous food web since both the microbial and herbivorous food webs appear to play significant roles in carbon flow within pelagic food web. Monitoring studies are necessary to understand the transient nature between these two extreme trophic modes and for realistic approaches in modelling studies these should be considered.

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