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Phytoplankton production and consumption rate in the warm and cold seasons in the coastal ecosystem of Matsu Island

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ABSTRACT

To elucidate the trophic link between classical and microbial food webs in the coastal ecosystem of Matsu Island during the warmer (27.5°C) and colder (16°C) months, we estimated the impact of mesozooplankton and microzooplankton grazing on > 20 μm and < 20 μm phytoplankton groups, respectively. In the warmer months, the > 20 μm fraction of Chl *a* accounted for more than 70% of the total Chl *a*; however, the Chl *a* > 20 μm fraction contributed little to the total phytoplankton biomass, at about 16%, in the colder months. Overall, the < 20 μm fraction represented 26 and 90% of the < 200 μm daily primary production in the warmer and colder months, respectively. Furthermore, the grazing loss of mesozooplankton on microzooplankton was 4.7 mgC m^{-3} d^{-1} in the warmer months; however, no significant loss rate was measured in the colder months. The results showed that large autotrophs (> 20 μm) were available for direct mesozooplankton ingestion, which indicated that they could be considered as an important link in the complex food web structures, particularly during the warmer season.

1. INTRODUCTION

Analyzing the trophic interactions of planktonic food webs is critical for understanding the carbon flux in aquatic ecosystems. An important process in aquatic ecosystem dynamics is the carbon transfer from primary producers to higher trophic levels (Vargas et al. 2007). To date, it has become increasingly clear that the traditional notion of the phytoplankton-zooplankton food chain has been modified by adding the concept of the microbial food web (Azam et al. 1983). In highly productive environments, it has been assumed that the classical food web plays an important role in the carbon and energy flux (Ryther 1969). Furthermore, it is expected that ciliates are most important in the diet of copepods in oligotrophic ecosystems, where the primary production is low, confined to pico-sized cells, and rarely consumed by copepods (Dam et al. 1995; Calbet and Saiz 2005). Similar studies have suggested that the relative importance of a microbial food web increases, with the decreasing trophic status (Vargas et al. 2007). However, there is increasing evidence that the microbial food web is a nearly permanent feature of not only oligotrophic, but also eutrophic, environments (Cuevas et al. 2004; Vargas et al. 2007). Therefore, the data for the comparison of trophic interactions between classical and microbial food webs are still insufficient.

It has been recognized that ciliates appear to be important functional and structural components of planktonic communities, by acting as top predators within microbial food webs (Calbet and Landry 2004). In fact, ciliates have been reported to graze between 82 and 100% of the nanophytoplankton production d^{-1} in some river plume regions (Fahnenstiel et al. 1995; Vargas and Martínez 2009). However, the strength of the trophic control that mesozooplankton may exert on ciliate communities is yet to be explored. Most previous studies have found that the grazing impact of mesozooplankton on the ciliate community appears to be low, with only 2% of the standing stock of ciliates being ingested (Broglio et al. 2004). Overall, the low impact

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indicates that mesozooplankton are unable to control ciliate communities, which suggests the bottom-up control of ciliates (Broglio et al. 2004). However, other studies have found that the feeding rates on ciliates are high, with daily predation pressures of up to 45 and 200% of the ciliate standing stock (Dolan 1991; Fessenden and Cowles 1994). The above variability may due to the different environments where different zooplankton species and microbial communities are found. In recent years, an increasing number of studies have focused on the importance of copepods and ciliates in trophic webs (Levinsen et al. 2000; Broglio et al. 2004; Calbet and Saiz 2005). Thus, the simultaneous estimation on the grazing impact of zooplankton on microbial and classical food webs has seldom been assessed *in situ* (Vargas et al. 2007), and the relative importance of both remain uncertain.

The Matsu archipelago is located near the mouth of the Minjiang River. The coastal regions of Matsu are often turbid and highly productive (Yu and Chen 2012). Regular studies have found that the diluted Minjiang water has a seasonal character, and that it is an unstable environment in the flood season (April to September), with high nutrient (nitrate of up to 80 μM) and Chl *a* concentrations (up to 18 $\mu g\ L^{-1}$) (Tsai et al. 2018). In recent years, the Matsu archipelago has become a famous tourist attraction, with the romantic name of 'Blue Tears'. Noctiluca *scintillans*, with a cell size larger than 200 μm, is the dominant bioluminescent dinoflagellate in the Matsu archipelago. A previous study found diatoms (*Thalassiosira* spp.) in the food vacuoles of N. *scintillans*, which suggests that the diatom population can be suppressed by the grazing pressure of N. *scintillans* (Tsai et al. 2018). However, as for the seasonal changes in Noctiluca *scintillans*, it appears when the seawater temperature is between 16 and 27°C and that it disappears when the temperature rises higher than 27°C after July (Tsai et al. 2018). Therefore, the coastal ecosystem of Matsu is a good site for monitoring the trophic interactions among zooplankton, phytoplankton, and the microbial web during the warmer and colder seasons, respectively. In this marine ecosystem, we hypothesized that phytoplankton will be channeled to higher trophic levels in two ways. One way is by the role of mesozooplankton in the predation on microphytoplankton (> 20 μm) in the grazing food chain, while the other way is by the microbial food chain, which includes components such as pico- and nanophytoplankton (< 20 μm), and stresses the importance of predation by ciliates. These results, combined with those of the dilution and size-fractionation approach, were used to establish a carbon-flow model in this study, and the relative importance of the two food chains was discussed.

2. MATERIALS AND METHODS

2.1 Sampling

Experimental studies of phytoplankton growth and grazing were conducted at the coastal station of Matsu (Fig. 1). One study was performed during the warmer season (21 - 22 August 2017; temperature 27.5°C, salinity 33.5 psu), and the other was performed during the colder season (25 - 26 March 2018; temperature 16°C, salinity 31.1 psu). Seawater was collected from the surface water from 9:00 to 10:00 in the morning (local time) using a plastic bucket, and it was gently siphoned into six clear 20 L polycarbonate (PC) carboys. All samples were brought to the laboratory within 30 minutes. The water temperature was measured immediately after sampling. All carboys were washed with 10% HCl, followed by distilled water and seawater rinses before sampling.

2.2 Grazing Experiments

Using the differential filtration method (Wright and

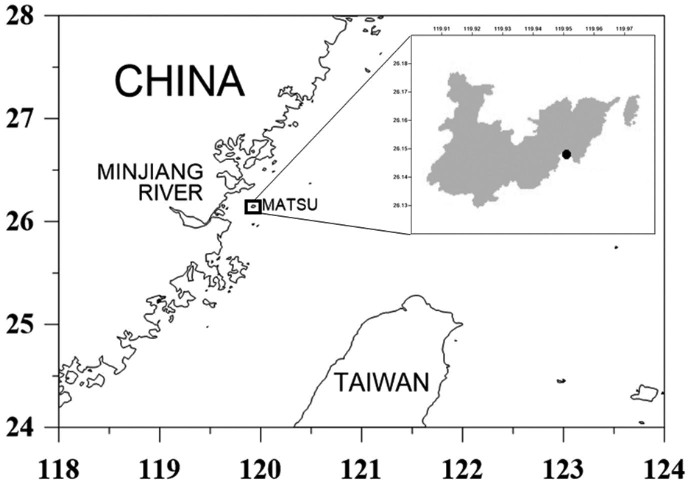

Fig. 1. Map showing the study area and sampling station (●).

Coffin 1984; Tsai et al. 2005, 2008), we estimated the growth and grazing rates of phytoplankton from changes in the chlorophyll *a* concentration. Briefly, we used the 200 and 20 μm nylon meshes to filter the seawater by gravity, in order to remove mesozooplankton, and microzooplankton, respectively. In parallel treatments, another three carboys were filled with unfiltered seawater to determine the total grazing effect on phytoplankton. The treated samples were transferred into polycarbonate carboys, with a volume of 10 L each, and incubated, in triplicate, in a water bath at *in situ* temperatures and a light environment, using running surface water for 24 hours.

Assuming an exponential growth model, the net growth rate of the phytoplankton concentration (ki, d^{-1}) was calculated for each treatment at the start, and at the end, of the experiment (C_{t0} and C_t), according to the formula ki = $\ln(C_t/C_{t0})$. Both before and after incubation, samples were taken from each carboy to determine the chlorophyll concentration and ciliate abundance.

2.3 Data Processing

Here, the model assumed that the phytoplankton would be channeled to higher trophic levels in two ways. Firstly, the microbial food chain energy would be channeled directly from the small phytoplankton (< 20 μm) to the microzooplankton (Fig. 2). In the < 20 μm treatments, the production of < 20 μm phytoplankton (mgC m^{-3} d^{-1}) [ΔChl *a* (< 20 μm)] was estimated according to the following equation:

$$\Delta \text{Chl } a\ (< 20\ \mu\text{m}) = (\text{P1}) \quad (1)$$

where P1 is the size of the < 20 μm phytoplankton production. The chlorophyll concentration was transformed to phytoplankton carbon, using a carbon-to-chlorophyll ratio of 94.4 (Chang et al. 2003).

Secondly, the role of mesozooplankton is that of the major grazer of microphytoplankton (> 20 μm) in the grazing food chain (Fig. 2). Thus, differences in the net increase of the Chl *a* biomass in treatments with (unfiltered) [ΔChl *a* (unfiltered)] and without mesozooplankton (< 200 μm) [ΔChl *a* (< 200 μm)] reflected mortality, due to mesozooplankton or microzooplankton, as follows:

$$\Delta \text{Chl } a\ (< 200\ \mu\text{m}) = (\text{P1} - G_C) + (\text{P2}) \quad (2)$$

$$\Delta \text{Chl } a\ (\text{unfiltered}) = (\text{P1} - G_C) + (\text{P2} - G_Z) \quad (3)$$

where P1 and P2 are the size of the < 20 μm and > 20 ~ 200 μm phytoplankton production and G_C and G_Z represent the microzooplankton and mesozooplankton consumption rates of phytoplankton. In Eq. (2), the value of G_C was estimated by using size-fractionated dilution experiments.

An additional size-fractionated dilution experiment was designed to examine the consumption rate of microzooplankton on the < 20 μm phytoplankton (G_C). Five liters of < 200 μm sub-samples were put through a GF/F filter into a clear carboy to create grazing-free diluents. Then, the < 200 μm sub-samples were siphoned into 20-liter incubation bottles and diluted with grazing-free water (five liters) in 50% of the < 200 μm filtered water. The bottles were incubated for 24 hours under the above incubated conditions.

The apparent growth rate (k, d^{-1}) was calculated from the daily changes in the Chl *a* concentration from the < 200 μm filtered treatment and 50% of the < 200 μm filtered treatment, with the following equations:

$$k\ (< 200\ \mu\text{m}) = \ln(C_{f < 200\ \mu m}/C_{i < 200\ \mu m}) = \mu - g \quad (4)$$

$$k\ (50\%\ \text{of} < 200\ \mu\text{m}) = \ln(C_{f50\%\ of < 200\ \mu m}/C_{i50\%\ of < 200\ \mu m}) = \mu - 0.5\ g \quad (5)$$

where, C_i and C_f represent the concentration of Chl *a* before and after incubation, respectively, and μ and g represent the growth rate of the < 200 μm phytoplankton and the microzooplankton grazing rate on the < 20 μm phytoplankton.

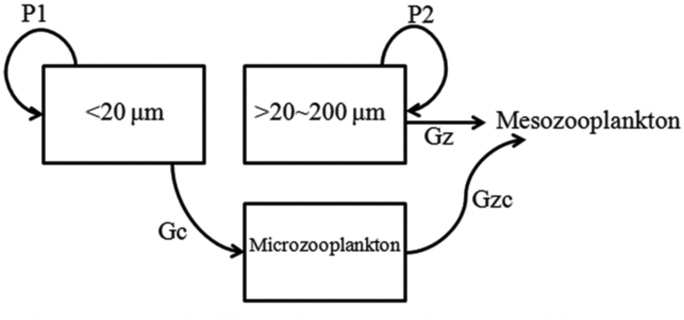

Fig. 2. Model of the trophic pathways of phytoplankton in different sizes. P1 and P2 represent < 20 μm phytoplankton and 20 - 200 μm phytoplankton production; G_C and G_Z represent microzooplankton and mesozooplankton consumption rates of phytoplankton; G_{ZC} represents the mesozooplankton consumption rate of microzooplankton.

The daily microzooplankton consumption rate (G_C) was then determined from the < 20 μm phytoplankton biomass ($B_{< 20\ \mu m}$) and the g value: $G_C = B_{< 20\ \mu m} \times g$.

After calculating the value of P2 from Eq. (2), the mesozooplankton consumption rate of phytoplankton (G_Z) was calculated according to Eq. (3).

2.4 Sample Processing

The Chl *a* was measured, as described by Gong et al. (1995). For the ciliates, 500 mL of surface water was sampled and fixed with neutralized formaldehyde (2% final concentration) (Stoecker et al. 1989) and preserved at 4°C until analysis. To obtain a reliable ciliate abundance count, a 500 mL water sample was concentrated into a 100 mL sub-sample, with a 20 μm mesh size net, after which the sub-samples (100 mL) were settled in an Utermöhl chamber. The entire area of the Utermöhl chamber was examined at magnifications of 200× or 400×, by using an inverted microscope (Nikon-TMD 300). The carbon to volume ratios of 0.148 and 0.19 pg C μm^3 for ciliates and dinoflagellates, respectively, were used (Ohman and Snyder 1991; Gifford and Caron 2000). Statistical analyses were performed by using Statistical for Windows (StatSoft Inc.). The results from all triplicates in the experiments were averaged. The differences of the mean value of the studied parameters between the treatments were analyzed by *ANOVA*. A probability value of < 0.05 was considered to be significant.

3. RESULTS

3.1 Net Growth Rates of Chl *a* and Ciliates

The size-fractionated Chl *a* concentrations of each treatment are shown in Table 1. The initial phytoplankton biomass was 208.5 and 29.3 mgC m^{-3} in August and March, respectively (Table 1). In August, the > 20 μm fraction of Chl *a* accounted for more than 70% of the total Chl *a* in this study (Table 1). However, the Chl *a* > 20 μm size fraction contributed little to the total phytoplankton biomass, namely, only 16% in March (Table 1).

August observations clearly showed that the net growth rate of Chl *a* were significantly lower in the unfiltered treatment (0.29 ± 0.02 d^{-1}) than in the < 200 μm treatments (1.90 ± 0.17 d^{-1}) (*t-test*, $p < 0.05$) (Table 1). Therefore, a mechanism of top-down control could exist between the mesozooplankton and phytoplankton in the warmer season. However, in March, a significant grazing impact was detected in the < 200 μm treatments, evidenced by the net growth rates of the phytoplankton being significantly lower than in the < 20 μm treatments (*t-test*, $p < 0.05$) (Table 1). Furthermore, the size-fractionation experiments showed that the net growth rate estimates of the ciliates averaged 0.11 and 0.36 d^{-1} in the unfiltered and < 200 μm treatments in August, respectively (Table 1). Due to the grazing effects of mesozooplankton on ciliates, the estimated net growth rate of the ciliates was lower in the unfiltered treatments (*t*-test, $p < 0.05$) (Table 1). However, there were no significant differences in the net growth rate of the ciliates between the unfiltered and < 200 μm treatments in March (*t*-test, $p > 0.05$) (Table 1).

We performed dilution experiments to measure the grazing rates of microzooplankton, and found significant differences between the < 200 μm and dilution treatments, during both seasons, for the phytoplankton net growth rate in this study (warm: 1.90 vs. 2.42, cold: 0.96 vs. 1.92) (*t*-test, $p < 0.05$) (Table 1). Based on our calculations, the ciliate grazing rate on phytoplankton was 1.1 and 1.9 d^{-1} in August and March, respectively.

3.2 Food Web Interactions

A proposed trophic level food web for the coastal station of Matsu is established in Fig. 3 with an emphasis on identifying pathways of trophic transfer from microbial to zooplankton consumers. Estimates of the mean daily production of the < 20 μm in size (P1) were 271.6 and 73.4 mgC m^{-3} d^{-1} in August and March, respectively (Fig. 3). The range of the 20 - 200 μm fraction in size of the mean daily production (P2) was 788.6 and 8.1 mgC m^{-3} d^{-1} in August and March, respectively (Fig. 3). Overall, the < 20 μm fraction represented 26 and 90% of the < 200 μm daily production in the warmer and colder seasons, respectively.

To summarize, in the August experiment, the daily grazing loss of microzooplankton (G_C) and mesozooplankton (G_Z) was 60.7 and 928 mgC m^{-3} d^{-1}, respectively (Fig. 3). As a result of the colder season in this study, the daily grazing loss of mesozooplankton (G_Z) was drastically decreased to 2.7 mgC m^{-3} d^{-1}, while the higher grazing loss of microzooplankton (G_C) was 47.2 mgC m^{-3} d^{-1} (Fig. 3). Furthermore, the grazing loss of mesozooplankton on microzooplankton (G_{ZC}) was 4.7 mgC m^{-3} d^{-1} in August; however, no significant loss rate was measured in the March experiment (Fig. 3).

4. DISCUSSION

We performed size-fractionation and dilution experiments in the coastal waters of Matsu and presented valuable data on the temporal variability in different-sized phytoplankton biomasses, on phytoplankton growth and grazing rates, on different-sized phytoplankton production, and on the grazing losses of microzooplankton and mesozooplankton in the warmer and colder seasons. This was the first study to investigate the relative importance of the amount of carbon flux of microbial and classical food webs, and to determine the complexity of food web structures in the coastal waters of Matsu. Large autotrophs (> 20 μm) are available for direct mesozooplankton ingestion in the coastal waters of Matsu, and they could be considered as an important link in the complexity of food web structures, particularly during the warmer season. In the colder season, the microbial food web is an important component of the planktonic food web in this study area.

The present study, although limited by the seasonal variations, revealed that the significant changes between the two months were influenced by different oceanographic processes (i.e., temperature, salinity, and Chl *a*). It is evident from the summarized data that mesozooplankton are the major grazers of phytoplankton during the warmer season (Fig. 3a). Based on our results, the total grazing impact of mesozooplankton could reach up to 118% of > 20 μm phytoplankton production (Fig. 3a). Mesozooplankton generally take advantage of the most common prey available to them during the phytoplankton blooms (Yang et al. 2010). In some studies, zooplankton have been found to graze between 6 and 58% of the primary production off the coast of northern Chile (González et al. 2000), as well as 5 and 40% of the primary production off the coast of Peru (Boyd and Smith 1983). These differences may be due to the varying ecosystem productivity and zooplankton community structures. Furthermore, most mesozooplankton exhibit prey selectivity as a strategy, to maximize their survival (Yang

Table 1. Mean initial biomass of Chl *a*, increased biomass of Chl *a*, phytoplankton net growth rate, and ciliate net growth rate in each treatment during the warmer and colder seasons.

	Treatments	Chl *a* (mgC m^{-3})	Increased of Chl *a* biomass (mgC m^{-3} d^{-1})	Phytoplankton net growth rate (d^{-1})	Ciliate net growth rate (d^{-1})
Warm season (August)	unfiltered water	208.5 ± 2.6	71.5 ± 6.2	0.29 ± 0.02	0.11 ± 0.05
	< 200 μm	175.5 ± 5.3	999.5 ± 15.3	1.90 ± 0.17	0.36 ± 0.07
	< 20 μm	58.4 ± 4.8	271.6 ± 11.6	1.73 ± 0.14	
	< 200 μm (50%) + GF/F (50%)	98.3 ± 3.2	1004.6 ± 18.4	2.42 ± 0.12	
Cold season (March)	unfiltered water	29.3 ± 1.8	46.7 ± 8.2	0.95 ± 0.15	0.26 ± 0.10
	< 200 μm	30.6 ± 5.9	49.4 ± 12.3	0.96 ± 0.07	0.25 ± 0.14
	< 20 μm	24.6 ± 2.1	63.9 ± 9.2	1.38 ± 0.22	
	< 200 μm (50%) + GF/F (50%)	11.8 ± 2.2	69.2 ± 9.5	1.92 ± 0.08	

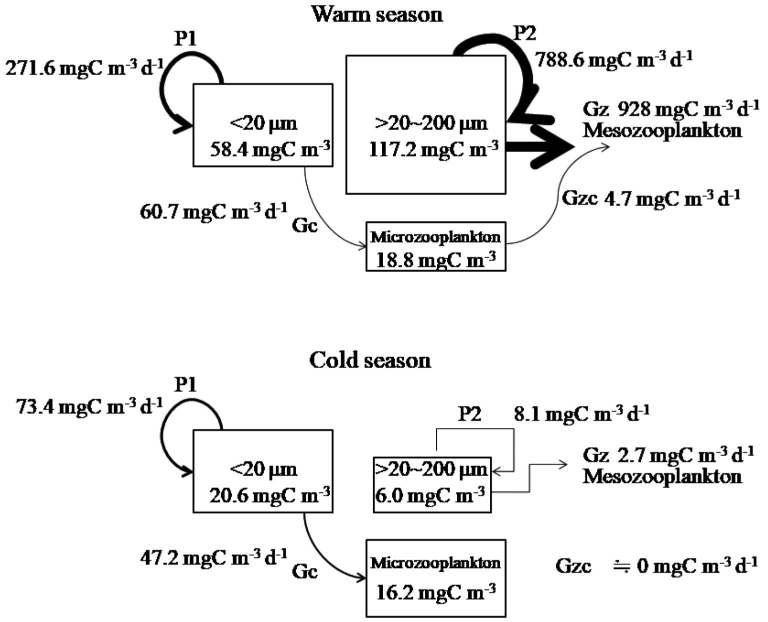

Fig. 3. Schematic carbon flow diagrams depicting variations in the energy transfer of < 20 μm phytoplankton and 20 - 200 μm phytoplankton to microzooplankton grazing (G_C) and mesozooplankton (G_Z), respectively. G_{ZC} represents the mesozooplankton consumption rate on microzooplankton in the warmer (A) and colder (B) seasons. The numbers within the < 20 μm phytoplankton and 20 - 200 μm phytoplankton boxes refer to their biomass. The numbers next to the looped arrows represent the < 20 μm phytoplankton and 20 - 200 μm phytoplankton production rates (mg C m^{-3} d^{-1}). The straight arrows pointing to microzooplankton grazing (G_C) and mesozooplankton (G_Z) show their grazing rates (mg C m^{-3} d^{-1}). The arrow thickness represents the level of values.

et al. 2019). The study of Yang et al. (2019) reported that copepods positively selected > 20 μm of the prey in all incubated experiments. However, compared with previous studies, the estimated potential impact of the mesozooplankton was relatively high in this study (118% of > 20 μm phytoplankton production). The class sizes of phytoplankton production were not estimated in previous studies; thus, the contribution of > 20 μm phytoplankton to the daily grazing impact of mesozooplankton was not calculated correctly. If we consider all of the primary production, this study calculated that about 88% of the total phytoplankton production was consumed by mesozooplankton during the warmer season. Certainly, our comprehension of the trophic interaction of mesozooplankton and phytoplankton suggested that fast phytoplankton growth rates must be balanced by equally fast mortality, caused by zooplankton.

The microzooplabkton-mesozooplankton link is an important pathway for energy flux, and eventually connects to the classic grazing food chain (Calbet and Saiz 2005). The reasons for microzooplankton being consumed by mesozooplankton have been widely discussed in the literature, and it has been stated that ciliates usually fall in the range of the optimal prey size for copepods (Berggreen et al. 1988), whereas some phytoplankton cells are too small (picophytoplankton). The selection of ciliates in the presence of phytoplankton has been studied for some species of copepods, and research has reported that the contribution of ciliates to the copepod carbon ratio is variable, ranging from 0 to 100% of copepod ingestion (Stoecker and Capuzzo 1990; Gifford 1991; Sanders and Wickham 1993; Broglio et al. 2004). The variability of this estimation may result from the differences in the nature of the ecosystems being studied. It was clear from our results that the total grazing impact of mesozooplankton was about 25% of the ciliate standing stock during the warmer season (Fig. 3a), which fell within the range of previous studies (Dolan 1991; Broglio et al. 2004). However, a comparison of the total carbon ingestion rates of phytoplankton and ciliates for mesozooplankton found that ciliates made < 1% of the contribution to the total carbon intake of mesozooplankton in the warmer season (Fig. 3a). We cannot exclude, however, that while formaldehyde's fixation is known to cause the cell shrinkage of ciliates, most studies on the effect of fixatives on ciliates have focused on cell volumes (Menden-Deuer and Lessard 2000; Zinabu and Bott 2000). Thus, the carbon calculation of microzooplankton has been underestimated in this study. Furthermore, the potential problems identified by the dilution experiments were artifacts resulting from changes in the individual grazer activities in undiluted water (Dolan et al. 2000). Thus, the grazer growth in undiluted water is occasionally verified, which may have resulted in the overestimation of the grazing rates of phytoplankton in this study.

Microzooplankton (ciliates and dinoflagellates) appear to be the major grazers on pico-and nano-size prey (Hansen et al. 1994; Vargas et al. 2007). However, we were not able to distinguish between the feeding of dinoflagellates and ciliates in this study, therefore we estimated the potential consumption by the total protozooplankton community with a size of > 20 μm. Our findings demonstrated the potential impact of microzooplankton on the < 20 μm primary production of 22.3 and 64.3% in the warmer and colder seasons, respectively (Fig. 3). A study of the coastal waters in the East China Sea found that microzooplankton grazing has a significant impact on the nanoflagellate community, which accounts for about 15 - 30% of pigmented nanoflagellates and 18 - 60% of heterotrophic nanoflagellate growth during the warmer period (Tsai 2018). Our estimates were within the range that was reported for the East China Sea. Furthermore, some studies have observed higher levels of the grazing impact on nanophytoplankton production. For instance, Fahnenstiel et al. (1995) and Vargas and Martínez (2009) reported that microzooplankton grazing rates on cells < 20 μm average 82 and 100% of the phytoplankton growth rates in the river plume region, respectively. Moreover, the < 20 μm fraction of pigmented nanoflagellates (PNF) grazed heavily on picophytoplankton (*Synechococcus* spp.), thus confirming the role of PNF as an important consumer in the East China Sea (Tsai et al. 2007). Such trophic levels of picophytoplankton to PNF could confound our results and underestimate the value of the grazing of microzooplankton. However, whatever the situation, our consumption rate data constituted reliable values for the estimation of the potential grazing impact of microzooplankton on < 20 μm phytoplankton in this area.

The autotrophic carbon-flow diagrams (Fig. 3) were built by measuring the difference of Chl *a* in different treatments and led us to conclude that the microbial and classical food webs channeled the autotrophic carbon flow in this study. One uncertainty in our data was related to heterotrophy. Generally, heterotrophic nanoflagellates and microsized grazers play an important role in microbial food webs, as they are a major source of mortality for pico- and nanophytoplankton, as well as heterotrophic bacteria (Sanders et al. 1992; Safi and Hall 1999; Tsai et al. 2005, 2008, 2011, 2013). Furthermore, heterotrophic nanoflagellates could be an important prey, due to the transfer of their energy and carbon to microzooplanktons, which, in turn, are the favorite prey of mesozooplankton (Calbet and Saiz 2005). Although the carbon sources of heterotrophic nanoflagellates and bacteria for microzooplankton were not considered in this study, they may contribute significantly to the growth of microzooplankton. Nevertheless, the potential impact of microzooplankton on heterotrophic nanoflagellates and bacteria should be considered in the future.

Our analysis convincingly showed the notable strength of the zooplankton-phytoplankton link, especially during the warmer season, in the coastal waters of Matsu Island. Furthermore, although predation on microzooplankton by mesozooplankton was not detected in the colder months, our findings demonstrate that microzooplankton may control the assemblage of nanophytoplankton and picophytoplankton (< 20 μm) in the colder season, and thus represent an important trophic pathway in the microbial food webs in this coastal ecosystem.

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