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Short Research Note

Impact of microzooplankton and copepods on the growth of phytoplankton in the Yellow Sea and East China Sea

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Abstract

Dilution and copepod addition incubations were conducted in the Yellow Sea (June) and the East China Sea (September) in 2003. Microzooplankton grazing rates were in the range of 0.37–0.83 d^{-1} in most of the experiments (except at Station A3). Correspondingly, 31–50% of the chlorophyll *a* (Chl *a*) stock and 81–179% of the Chl *a* production was grazed by microzooplankton. At the end of 24 h copepod addition incubations, Chl *a* concentrations were higher in the copepod-added bottles than in the control bottles. The Chl *a* growth rate in the bottles showed good linear relationship with added copepod abundance. The presence of copepods could enhance the Chl *a* growth at a rate (Z) of 0.03–0.25 (on average 0.0691) d^{-1} ind^{-1} l. This study, therefore parallels many others, which show that microzooplankton are the main grazers of primary production in the sea, whereas copepods appear to have little direct role in controlling phytoplankton.

Introduction

Our understanding of the role of copepod in the marine planktonic ecosystem is always changing. Before the 1960s, it was a common practice to view the marine planktonic trophic structure as a simple diatom-copepod-fish chain with the copepod being the primary consumer (Beers, 1982; Kleppel, 1993).

With the discovery of small autotrophic cells, the nano- and pico-phytoplanktons were found to be the main producers, with occasional diatom blooms superposed on their productivity (Pomeroy, 1974). With the increasing knowledge of the functional activities of microzooplankton (< 200 μm, such as heterotrophic ciliates, dino-flagellates and flagellates), the planktonic trophic structure was considered to be a web (Azam et al., 1983; Kleppel, 1993). Later, the grazing impact of microzooplankton and copepod on phytoplankton was estimated using the dilution incubation technique (Landry & Hassett, 1982; Calbet & Landry 2004) and the gut pigment method (Mackas & Bohrer, 1976), respectively, in the global oceans. These studies showed that microzooplankton had a much higher grazing impact on phytoplankton than copepods (Burkill et al., 1993; Dam et al., 1993).

Although omnivory in copepods has been known for a long time, they have been considered primarily herbivorous predators. From late the 1980s, more studies have demonstrated the great flexibility in their feeding behavior (Klepppel, 1993). Copepod may consume microzooplankton when phytoplankton is in short supply. Micro-zooplanktons could contribute 0–100% of the total

ingested carbon of copepods (Halvorsen et al., 2001) and act as mediators of energy transfer from primary producers to higher trophic levels such as copepods (Vincent & Hartmann, 2001).

In recent years, copepod was found to enhance phytoplankton growth rather than grazing the phytoplankton to lower levels in natural seawater. In some copepod addition incubations (Calbet & Landry, 1999; Graneli & Turner, 2002; Zeldis et al., 2002; Liu & Dagg 2003), chlorophyll *a* (Chl *a*) concentration was higher in seawaters with copepods than in the control (no copepod was added) after a period of incubation.

However, the enhancement of copepod on phytoplankton growth has not been extensively described. In this paper, we report the copepod enhancement effect on phytoplankton in the Yellow Sea and East China Sea. Microzooplankton grazing pressure on phytoplankton was also studied to compare the impact of copepod and microzooplankton on phytoplankton.

Materials and methods

Dilution incubations (Landry & Hassett, 1982; Burkill et al., 1990) and copepod addition incubations (Calbet & Landry, 1999) were carried out to study microzooplankton grazing and the impact of copepod on the phytoplankton in cruises to the Yellow Sea and the East China Sea. The dates and the stations are listed in Tables 1 and 2. The positions of the stations are shown in Figure 1. During the cruise to the Yellow Sea by R/V Beidou during 24–29 June 2003, both experiments were carried out at Station Y but on different days. During the cruise to the East China Sea by R/V Dongfanghong No. 2 during 4–22 September 2003, dilution incubations and copepod addition incubations were carried out at different stations.

At each station, temperature and salinity were measured using Seabird CTD system. Surface seawater used in the experiments was collected with Niskin water samplers and poured through a 200 μm mesh (to eliminate the mesozooplankton (>200 μm)) into pre-cleaned 25-l polycarbonate carboys. We called this water mesh filtered seawater (MFSW).

The experimental items (25-l polycarbonate carboys, 4 and 1.35-l polycarbonate bottles, glass filter bottles etc.) were soaked in 10% HCl and rinsed with MFSW before use.

To determine the nutrients concentration, a 100 ml sample of the seawater was filtered through pre-cleaned 0.45 μm filters. The filtrates were poisoned by saturated $HgCl_2$ and later, in the laboratory, used to determine the nutrient (including NO_3^-, PO_4^{3-} and dissolved silica) concentrations photometrically (Grasshoff et al., 1999) by an auto-analyzer (Model: Skalar SAN^{plus}) with a precision of <5–10%.

Two 500-ml water samples were filtered onto GF/F filters, which were kept at -20 °C in the dark for the determination of Chl *a* concentration. In the laboratory, the GF/F filters were extracted with 90% acetone at -20 °C in the dark for 24 h. The concentrations were determined using a Turner Designs (Model II) fluorometer that was calibrated with pure Chl *a* from Sigma (Strickland & Parsons, 1972).

Dilution incubation

The dilution incubation protocols by Landry & Hassett (1982) and Burkill et al. (1990) were followed. Some MFSW was filtered through GF/F filters to make Filtered Seawater (FSW). The FSW was assumed to be free of phytoplankton and predator (micro- and mesozooplankton). The FSW for the incubations were also stored in 25-l carboys.

Certain amount of MFSW was poured into four 4-l polycarbonate bottles. The FSW was added to the four bottles to dilute the MFSW with concentrations of 100, 75, 50 and 25% (dilution factor, c), respectively. From each 4-l bottle, 500 ml water was filtered through GF/F filters, which were kept at -20 °C for the determination of initial Chl *a* concentration (P_0). Rest of the water was poured into two 1.35-l polycarbonate bottles. The eight 1.35-l bottles were carefully capped without bubble inside and incubated in a flow-water-incubator on deck for 24 h. Further samples (1000 ml) for the final Chl *a* concentration (P_t) were taken from each 1.35-l bottle after incubation.

Copepod addition incubation

The copepod addition incubation set-up was similar to that of Calbet & Landry (1999). Copepods

were collected by vertically (from bottom or 50 m depth to surface) towing a zooplankton net (mesh size 500 μm). The towed samples were first poured into 500-ml beakers with MFSW. And then, adults of large dominants species such as *Calanus sinicus* (body length 2.6 mm), *Euchaeta concinna* (2.5 mm), *E. subcrassus* (1.9 mm) and *Undinula vulgaris* (2.4 mm) were pipetted and cultured in a 200-ml beaker with MFSW. One species was used in each incubation.

Two MFSW samples of 500 ml were filtered onto GF/F filters for the determination of initial Chl *a* concentration (P_0). MFSW was poured into eight 1.35-l bottles. Active adult copepods were selected, rinsed with MFSW and then added into the 1.35-l bottles with numbers of 0, 5, 10 and 15, with two replicates in one concentration. The bottles were then filled with MFSW, carefully capped without bubbles inside and incubated in a flow-water-incubator on deck for

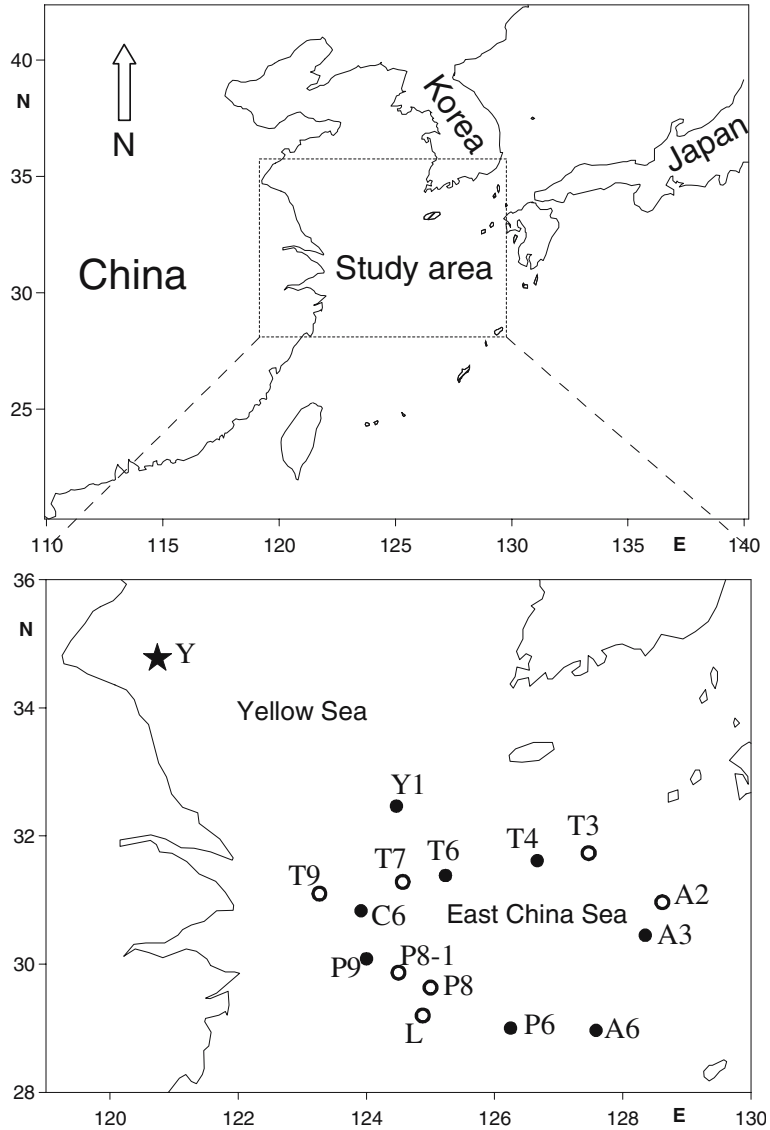

Figure 1. Map showing the study area and the stations where dilution incubations (●), copepod addition incubations (○) and both (★) were carried out.

24 h (48 h at Station L) as in the dilution incubations.

At the end of each experiment, the copepods were checked though no mortality was found in any of the experiments. A water sample of 1000 ml was taken to determine Chl *a* concentration (P_t) from each bottle.

Calculations

In the incubations, the growth rates of phytoplankton were calculated according to the change of Chl *a* concentrations before and after the incubations. If incubated without any zooplankton, the phytoplankton will grow at a rate k (d^{-1}). In both the dilution and copepod addition incubations, we cannot directly determine k because of the grazing of microzooplankton and copepods. Therefore, we call rate k as potential growth rate, while the phytoplankton growth rate in the incubations are called apparent growth rate (u, d^{-1}).

Chl *a* apparent growth rate in the bottles of both dilution and copepod addition incubations were calculated using the equation $u = 1/t \ln (P_t/P_0)$ (Landry & Hassett, 1982), where t was incubation time (d). In the dilution incubations, u in the bottles was the result of microzooplankton grazing (g, d^{-1}) and the potential phytoplankton growth (k, d^{-1}):

$$u = k - (c \times g) \tag{1}$$

Values of k and g were determined from linear regression of u against the dilution factors (c). Chl *a* apparent growth rate in the controls (u_0, d^{-1}) is calculated as

$$u_0 = k - g \tag{2}$$

The microzooplankton grazing pressure on Chl *a* standing stock (P_i) and primary production (P_p) were calculated according to Verity et al. (1993):

$$P_i = 1 - (e^{-gt} \times 100\%) \tag{3}$$

$$P_p = (e^{kt} - e^{(k-g)t})/(e^{kt} - 1) \times 100\% \tag{4}$$

The ratios of g:k were also calculated to represent the microzooplankton grazing pressure on primary production (PP) following Calbet & Landry (2004).

In the copepod addition incubation, u was expressed as

$$u = u_0 + n \times Z \tag{5}$$

where n (ind l^{-1}) is the concentration of copepods added, Z (d^{-1} ind^{-1} l) is the impact on the phytoplankton by one copepod per liter. u_0 is the apparent growth rate in the control bottle (0 copepod was added). Values of Z were determined from linear regression of u against n.

Results

There were totally nine dilution incubations and nine copepod addition incubations. The initial conditions and the results of the experiments are listed in Tables 1 and 2. The initial nutrition concentrations were different in the dilution incubation and copepod addition incubation at Station Y because the two incubations were carried out in different dates.

The dilution experiments (Table 1, Figure 2) showed that the potential Chl *a* growth rate was 0.29–0.86 d^{-1}. Microzooplankton grazing rate was in the range of 0.37–0.83 d^{-1} in most of the experiments (except Station A3). Correspondingly, 31–50% of the Chl *a* stock and 81–179% of the Chl *a* production was grazed per day by microzooplankton. At Station A3, microzooplankton grazed at a low rate of 0.08 d^{-1}, only 8 and 16% of the Chl *a* stock and production was grazed per day, respectively (Table 1).

Eight out of the nine copepods addition incubations were carried out for 1 day, except that the incubation at Station L lasted for 2 days (Table 2). After incubation, Chl *a* concentrations were higher in the copepod-added bottles than in the control bottles. The Chl *a* growth rates in the bottles showed good linear relationship with concentrations of added copepods (Figure 3). The estimated Z value according to Equation (5) ranged from 0.03 to

Table 1. Initial conditions and results of the dilution incubation experiments

Station	Depth (m)	Date	T (°C)	S	Chl a (μg l^{-1})	Nitrate (μM)	Phosphate (μM)	Silicate (μM)	k (d^{-1})	g (d^{-1})	R^2	P_i (%)	P_p (%)	PP (%)
Y	20	27 Jun	18.2	31.56	0.54	1.63	0.02	1.52	0.32	0.66	0.82	48	176	206
Y1	48	6 Sep	29.38	28.25	0.91	0.70	0.10	5.26	0.75	0.83	0.85	56	107	111
C6	54	8 Sep	29.59	31.66	0.78	1.31	0.10	1.36	0.48	0.37	0.80	31	81	77
P9	55	13 Sep	28.46	32.14	1.20	1.69	0.08	2.05	0.33	0.70	0.96	50	179	212
A6	1055	14 Sep	27.96	34.35	0.25	0.33	0.12	1.72	0.86	0.66	0.92	48	84	77
T4	100	16 sep	23.04	32.56	4.41	2.98	0.12	10.65	0.64	0.68	0.89	49	104	106
P6	119	18 Sep	28.38	33.75	0.20	0.41	0.09	3.55	Bad regress					
A3	785	23 Sep	26.98	33.72	0.22	0.14	0.06	2.55	0.68	0.08	0.52	8	16	12
T6	50	24 Sep	25.18	31.82	1.13	0.11	0.09	2.78	0.29	0.54	0.85	42	166	186

Date: beginning date (Jun: June; Sep: September); T: surface temperature; S: surface salinity; Chl a: initial Chl a concentration; k: potential Chl a growth rate; g: microzooplankton grazing rate; P_i: microzooplankton grazing pressure on Chl a standing stock; P_p: microzooplankton grazing pressure on Chl a primary production; PP: the microzooplankton grazing pressure on primary production calculated as ratios of g:k following Calbet & Landry (2004).

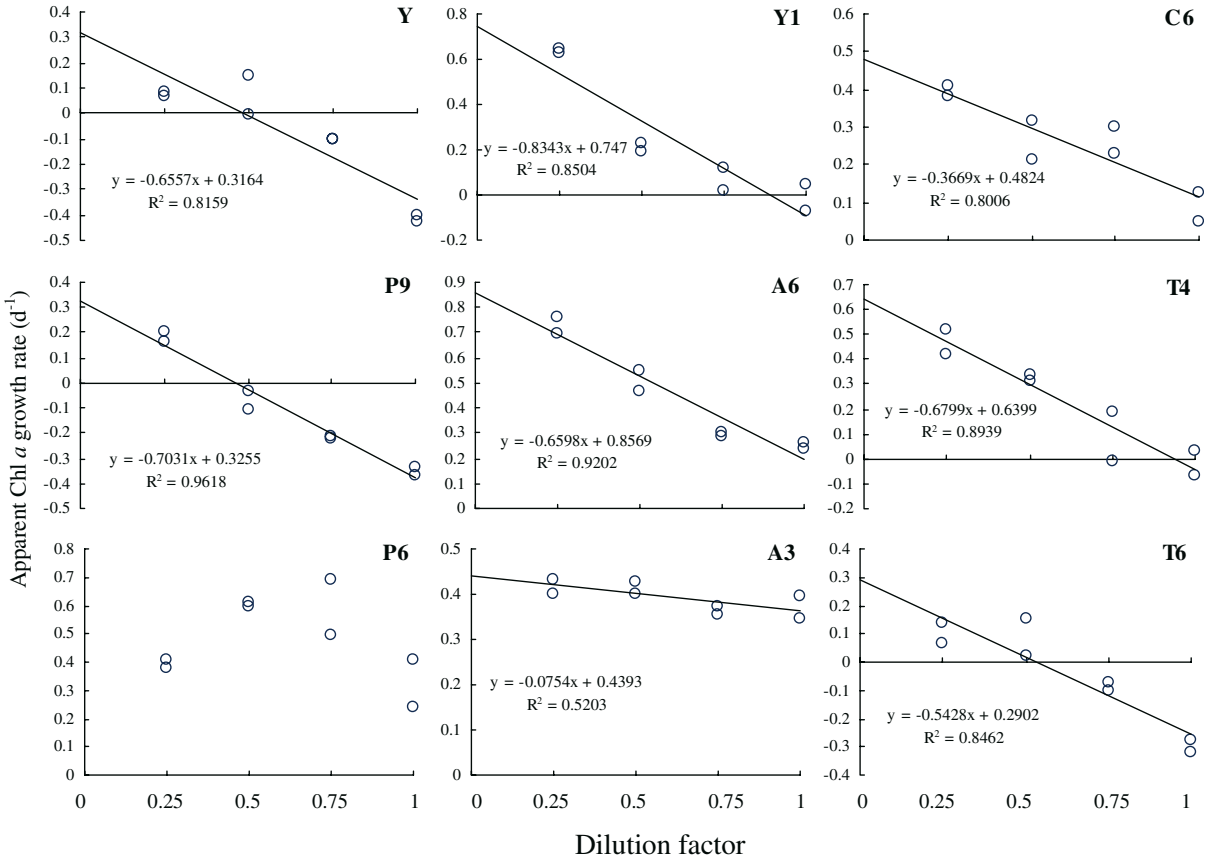

Figure 2. The regressions between the apparent Chl a growth rates (u) and the dilution factors (c) in the dilution experiments.

Table 2. Initial conditions and results of the copepod addition incubations

Station	Depth (m)	Date	T (°C)	S	Chl *a*	Nitrate (μM)	Phosphate (μM)	Silicate (μM)	Copepod	DW	Ex N	Ex P	u_0 (d^{-1})	Z	R^2
Y	20	28 Jun	18.2	31.56	0.65	2.10	0.03	5.79	*C. sinicus*	1.2	0.28	0.02	−0.29	0.07	0.90
P8	86	13 Sep	29.23	32.41	0.89	0.51	0.08	2.37	*E. concinna*	1.15	0.47	0.03	0.09	0.06	0.90
A2	760	15 Sep	28.83	33.75	0.15	0.72	0.12	2.94	*E. concinna*	1.15	0.46	0.03	0.91	0.03	0.83
P8-1	65	17 Sep	29.21	32.64	0.43	0.51	0.08	2.37	*E. subcrassus*	0.87	0.38	0.02	−0.11	0.14	0.96
L	83	19 sep	28.62	33.67	0.21	/	/	/	*E. subcrassus*	0.87	0.37	0.02	−0.07	0.25	0.88
A2	760	23 Sep	27.33	33.38	0.18	0.47	0.09	3.07	*U. vulgaris*	1.11	0.42	0.02	0.44	0.07	0.74
T3	130	24 Sep	27.25	34.01	0.32	0.08	0.13	2.55	*E. concinna*	1.15	0.43	0.02	0.15	0.06	0.79
T7	58	25 Sep	26.60	32.89	1.40	0.11	0.09	2.78	*E. concinna*	1.15	0.41	0.02	−0.69	0.07	0.82
T9	58	25 Sep	26.10	32.50	0.95	0.07	0.09	3.56	*E. concinna*	1.15	0.40	0.02	−0.38	0.05	0.85

Date, T, S and Chl *a* are as in Table 1. DW: Maximum dry weight (mg l^{-1}) in the copepod added bottles; Ex N: estimated maximum N excretion (μM d^{-1}) in the copepod added bottles using Equation (8); Ex P: Maximum P excretion (μM d^{-1}) in the copepod added bottles using Equation (9); u_0: the regressed Chl *a* apparent growth rate without copepod according to Equation (5); Z: the impact of copepod on the phytoplankton (d^{-1} ind^{-1} l); /: not determined.

0.25 d^{-1} ind^{-1} l. The Z value at Station P8–1 (0.14 d^{-1} ind^{-1} l) and L (0.25 d^{-1} ind^{-1} l) with the copepod *E. subcrassus* were much higher than at other stations ($\leq$ 0.07 d^{-1} ind^{-1} l). The average Z of the eight 1-day incubations (the one at Station L was excluded) was 0.0691 d^{-1} ind^{-1} l (SD = 0.0324).

Discussion

The dilution incubations

The nutrient concentrations were low in the dilution incubations (Table 1). According to Paasche & Erga (1988), phytoplankton will become nutrient limited when N and P concentration was lower than 1.0 and 0.1 μM, respectively. However, no signs of nutrient limitation were found in our dilution incubations (Figure 2). In the design of the dilution incubation method, nutrients should be added to the bottles to prevent them from becoming depleted in the less dilute treatment (Landry & Hassett, 1982), especially when nutrients concentrations were as low as in this study. The estimated k will be overestimated when no nutrient is added in the dilutions series.

We did not add nutrients in our incubations because results of dilution incubations with nutrient addition cannot be considered to be *in situ* growth rate of phytoplankton. For example, McManus & Ederington-Cantrell (1992) compared two parallel dilution series with and without nutrient addition. Their results showed that the microzooplankton grazing rates (g) were similar in the two series, while phytoplankton potential growth rates (k) with nutrient addition were four fold higher than that of the series without nutrient addition.

Dilution experiments have been carried out in many sites around the world (Dolan et al., 2000; Calbet & Landry, 2004). The results of k and g in this study (k: 0.29–0.86 d^{-1}; g: 0.37–0.83 d^{-1}) were within the ranges of the previous data (k: 0–3.5 d^{-1}; g: 0–2.5 d^{-1}; Calbet & Landry, 2004). However, the k value was comparatively low possibly due to the low nutrient concentration. This might explain that in five of the nine dilution incubations, microzooplankton grazing rate was larger than the phytoplankton potential growth rate. That made the microzooplankton grazing pressure (both P_p and PP) on the primary production (Table 1) higher than the average 60% in the coastal areas (Calbet & Landry, 2004).

The situation that the microzooplankton grazing rate was higher than phytoplankton potential growth rate could not be a stable condition. Otherwise, phytoplankton would be grazed down to a lower level rather than keep relatively constant.

Apparent Chl a growth in copepod addition incubations

Some copepod addition incubations with contradictory results had been reported. Gifford et al. (1995) and Vincent & Hartmann (2001) reported

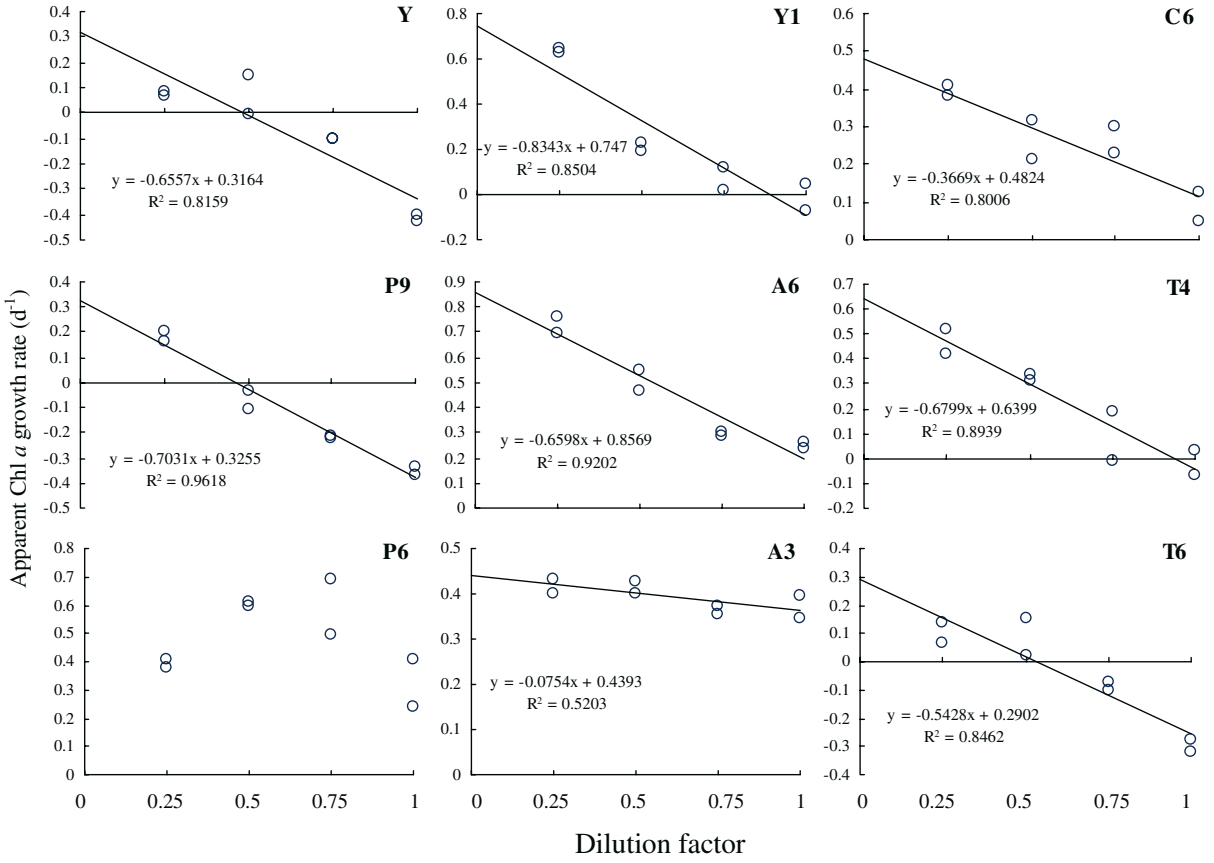

Figure 3. The results of the copepod addition incubations. The data were regressed according to Equation (5).

copepods grazing impact on the Chl *a* according to the decrease of Chl *a* concentration in the copepods added bottles and the control.

However, some authors found that total, or some fraction of Chl *a* will be higher in the copepods added incubations than in control. Experiments in the subtropical North Pacific (Calbet & Landry, 1999) showed that the growth rates of both <2 and >2 μm Chl *a* are positive with increasing mesozooplankton biomass added. However, the >2 μm Chl *a* fraction responded more dramatically. Irigoien et al. (2000) found that abundance of small phytoplankton groups (pelagophytes, green algae and cyanobacteria) increased in the copepod *Calanus helgolandicus* incubation bottles compared to the controls. But the larger cells such as dinoflagellates, diatoms, haptophytes and cryptophytes were grazed down. In the study of Graneli & Turner (2002) using the mesocosm experiment, it was found that Chl *a* concentrations in the mesocosm with 10× natural mesozooplankton abundance were significantly higher than in control mesocosm at the late period of 7-day incubation. In the 24 h copepod addition incubations of Zeldis et al. (2002) and references therein, some results of copepod clearance rates of phytoplankton were negative. Liu & Dagg (2003) found that phytoplankton in the <5 μm and 5–20 μm size category increased with increasing copepods concentration at most of the stations in their study in the Mississippi river plume.

Our results, along with Calbet & Landry (1999) and Graneli & Turner (2002), suggested that the copepods addition would enhance the growth of total Chl *a*. However, we should keep it in mind that different species or size fractions of phytoplankton may behave differently during the incubation.

Impacts of copepod additions

The addition of copepods in the bottles may have three impacts. Firstly, the copepods will graze (g_1)

on the phytoplankton. Secondly, omnivory feeding of copepods on microzooplanton might result in the decrease of microzoopankton grazing activity (g_2), which is proportional to microzooplankton concentration as in the assumptions of the dilution incubation experiments. Thirdly, the excretion of nutrient would increase the potential growth rate by k_1. We assume that g_1, g_2 and k_1 are proportional to the concentration (n) of copepod added. Then

$$\begin{aligned} u &= (k - nk_1) - (g - ng_2) - ng_1 \\ &= (k - g) + n(g_2 - g_1 + k_1) \end{aligned} \tag{6}$$

Comparing Equations (5) and (6), we get

$$u_0 = k - g, \qquad Z = g_2 - g_1 + k_1 \tag{7}$$

In the conception of Carpenter et al. (1985), trophic cascade happened among strictly defined trophic levels: piscivore, planktivore, herbivore and phytoplankton. Because the two herbivores: copepods and microzooplanktons, have trophic interaction (Perez et al., 1997), the copepod-microzooplankton-phytoplankon interaction is more complicated than trophic cascade depicted by Carpenter et al. (1985).

The possible change of nutrients due to copepod excretion in the incubation bottles might change the potential growth rate of phytoplankton. In order to compensate for differential effects of copepod excretion, both Liu & Dagg (2003) and Calbet & Landry (1999) added nutrients in the copepod addition incubations. However, no nutrient was added in the incubations of Zeldis et al. (2002). Nejstgaard et al. (2001) pointed out that the effects of copepod nutrient regeneration are complex and, after analysis, concluded that the main factor causing negative uncorrected copepod grazing rates was not nutrient limitation.

In our experiments, we could estimate the amounts of nutrients excreted by the added copepods according to their dry weight (DW) and temperature (T) using Equation (1) of Ikeda (1985):

$$\mathrm{N} = \mathrm{e}^{(-2.89+0.7616\times\ln(\mathrm{DW})+0.0511\times T)} \tag{8}$$

$$P = \mathrm{e}^{(-4.3489+0.7983\times\ln(\mathrm{DW})+0.0285\times T)} \tag{9}$$

We have determined the DW of *C. sinicus* to be 110 μg copepod^{-1} (Zhang & Wang, 2000). If we simply assume that the body weight is proportional to body length in the copepods, the maximum DW of *E. concinna*, *E. subcrassus* and *U. vulgaris* were estimated to be 106, 60 and 102 μg copepod^{-1}, respectively. Therefore, the DW added in the bottles with maximum concentrations of *C. sinicus*, *E.concinna*, *E. subcrassus* and *U. vulgaris* were 1.20, 1.15, 0.87 and 1.11 mg l^{-1}, respectively. The maximum excretions of N and P by copepods in the bottles with maximum added copepod concentrations were estimated to be 0.28–0.47 and 0.02–0.03 μM d^{-1} (Table 2). These were quite large values compared to the initial nutrient concentrations. The excreted nutrients might help enhance the growth rate of phytoplankton significantly in our experiments, especially in the bottles with more copepods.

Although copepods did graze on phytoplankton, the decrease of Chl *a* concentration due to copepod grazing was minor compared to the increase caused by the two effects stated above. Thus in our study the overall role of copepods in the marine pelagic system is to enhance phytoplankton growth rather than to graze the phytoplankton down to a lower level.

We used a linear regression in the Equation (5). However, the Z value might become saturated when n increased to some point. This trend was more prominent, for example, in the copepod addition incubations at Station P8, L, A2 (2) and T3 (Figure 3).

The enhancement of the four species to the phytoplankton growth was different. *C. sinicus*, *E. concinna* and *U. vulgaris* had close Z values. However, the Z value of *E. subcrassus* was much higher. Therefore, the role of copepods in the pelagic food web was species specific. Although omnivory in copepods has been known for a long time, less information exists on the quantification of omnivory (Verity & Paffenhofer, 1996; Halvorsen et al., 2001). There was no report on the feeding preferences (degree of omnivory) of the copepods

used in our experiments. The higher Z values of *E. subcrassus* might indicate that this species is more omnivory than others.

Conclusion

The dilution incubation experiments showed that microzooplankton exert heavy grazing pressure in the Yellow Sea and East China Sea. The presence of copepods could enhance the apparent growth rate of Chl *a* at a rate (Z) of 0.03–0.25 d^{-1} ind^{-1} l. Therefore, microzooplanktons were the main grazers of primary production, whereas copepods appeared to have little direct role in controlling phytoplankton.

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References

Azam, F., T. Fenchel, J. G. Field, J. S. Gray, L. A. Meyer-Reil & F. Thingstad, 1983. The ecological role of water column microbes in the sea. Marine Ecology Progress Series 10: 257–263.

Beers, J. R., 1982. An introduction and historical overview. Annales de l'Institut Oceanographique 58: 5–11.

Burkill, P. H., E. Head, G. Fransz, M. Lenz & M. Landry, 1990. Grazing by microzooplankton. In SCOR/JGOFS Report No.6, Core measurement protozoa. Reports of the Core Measurement Working Groups : 31–37.

Burkill, P. H., E. S. Edwards, A. W. G. John & M. A. Sleigh, 1993. Microzooplankton and their herbivorous activity in the northeastern Atlantic Ocean. Deep-Sea Research 40: 479–493.

Calbet, A. & M. R. Landry, 1999. Mesozooplankton influences on the microbial food web: direct and indirect trophic interactions in the oligotrophic open ocean. Limnology and Oceanography 44: 1370–1380.

Calbet, A. & M. R. Landry, 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnology and Oceanography 49: 51–57.

Carpenter, S. R., J. F. Kitchell & J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

Dam, H., C. A. Miller & S. H. Jonasdottir, 1993. The trophic role of mesozooplankton at 47 °N, 20 °W during the North Atlantic Bloom Experiment. Deep-Sea Research 40: 197–212.

Dolan, J. R., C. L. Gallegos & A. Moigis, 2000. Dilution effects on microzooplankton in dilution grazing experiments. Marine Ecology Progress Series 200: 127–139.

Gifford, D. J., L. M. Fessenden, P. R. Garrahan & E. Martin, 1995. Grazing by microzooplankton and mesozooplankton in the high-latitude North Atlantic Ocean: spring versus summer dynamics. Journal of Geophysics Research 100: 6665–6675.

Graneli, E. & J. T. Turner, 2002. Top-down regulation in ctenophore–copepod–ciliate–diatom–phytoflagellate communities in coastal waters: a mesocosm study. Marine Ecology Progress Series 239: 57–68.

Grasshoff, K., K. Kremling & M. Ehrhardt, 1999. Methods of Seawater Analysis (3rd ed.). WILEY-VCH, Weinheim 600 pp.

Halvorsen, E., A. G. Hirst, S. D. Batten, K. S. Tande & R. S. Lampitt, 2001. Diet and community grazing by copepods in an upwelled filament off the NW coast of Spain. Progress in Oceanography 51: 399–421.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Marine Biology 85: 1–11.

Irigoien, X., R. N. Head, R. P. Harris, D. Cummings & D. Harbour, 2000. Feeding selectivity and egg production of *Calanus helgolandicus* in the English Channel. Limnology and Oceanography 45: 44–54.

Kleppel, G. S., 1993. On the diets of calanoid copepods. Marine Ecology Progress Series 99: 183–195.

Landry, M. R. & R. P. Hassett, 1982. Estimating the grazing impact of marine microzooplankton. Marine Biology 67: 283–288.

Liu, H. & M. Dagg, 2003. Interaction between nutrients, phytoplankton growth, and micro- and mesozooplankton grazing in the plume of the Mississippi River. Marine Ecology Progress Series 258: 31–42.

Mackas, D. & R. Bohrer, 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. Journal of Experimental Marine Biology and Ecology 25: 77–85.

McManus, G. B. & M. C. Ederington-Cantrell, 1992. Phytoplankton pigments and growth rates, and microzooplankton grazing in a large temperate estuary. Marine Ecology Progress Series 87: 77–85.

Nejstgaard, J. C., L. Naustvoll & A. Sazhin, 2001. Correcting for underestimation of microzooplankton grazing in bottle incubation experiments with mesozooplankton. Marine Ecology Progress Series 221: 59–75.

Paasche, E. & S. R. Erga, 1988. Phosphorus and nitrogen limitation of phytoplankton in the inner Oslofjord (Norway). Sarsia 73: 229–243.

Perez, M. T., J. R. Dolan & E. Fukai, 1997. Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods. Marine Ecology Progress Series 155: 89–101.

Pomeroy, L. R., 1974. The ocean's food web, a changing paradigm. BioScience 24: 499–504.

Strickland, J. D. H. & T. R. Parsons, 1972. A practical handbook of seawater analysis. Journal of the Fishery Research Board of Canada 167: 1–310.

Verity, P. G. & G. A. Paffenhofer, 1996. On assessment of prey ingestion by copepods. Journal of Plankton Research 18: 1767–1779.

Verity, P. G., D. K. Stoecker, M. E. Sieracki & J. R. Nelson, 1993. Grazing, growth and mortality of microzooplankton during the 1989 North Atlantic spring bloom at 47°N, 18°W. Deep-Sea Research 40: 1793–1814.

Vincent, D. & H. J. Hartmann, 2001. Contribution of ciliated microprotozoans and dinoflagellates to the diet of three copepod species in the Bay of Biscay. Hydrobiologia 443: 193–204.

Zeldis, J., M. R. James, J. Grieve & L. Richards, 2002. Omnivory by copepods in the New Zealand subtropical frontal zone. Journal of Plankton Research 24: 9–23.

Zhang W., R. Wang, 2000. Effect of temperature on metabolic rates of *Calanus sinicus*. Marine Science 24: 42–44. (in Chinese with English abstract).