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# Response of copepod grazing and reproduction to different taxa of spring bloom phytoplankton in the Southern Yellow Sea

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ABSTRACT

The responses of copepod grazing and reproduction to the spring phytoplankton bloom were studied in the temperate shelf water of the Southern Yellow Sea in March–April, 2009. Two different algal blooms were found during the cruises. A diatom-dominated bloom at Station Z11, and a dinoflagellate-dominated bloom at Station Z4. The gut pigment contents indicated that different sized copepods exhibited different responses to different-species phytoplankton blooms. Large copepods (LC: body size larger than 1000 μm) and medium copepods (MC: body size ranging from 500 to 1000 μm), grazed actively on diatom blooms, but inactively on dinoflagellate blooms, although the chlorophyll-*a* concentrations of dinoflagellate blooms were twice as high as than those of the diatom blooms. For small copepods (SC: body size smaller than 500 μm), however, there was no significant difference in gut pigment contents between the two different algal blooms. Among the three size groups, LCs were the major grazers on the diatom bloom, while SCs were major grazers on the dinoflagellate bloom. Grazing impacts of copepod assemblages on phytoplankton blooms were low, only being equivalent to 1% $day^{-1}$, or less, of the chlorophyll-*a* standing stock. The egg production rates of a large copepod, *Calanus sinicus*, were on average, 11.3 egg $ind.^{-1}$ $day^{-1}$, which was among the higher levels recorded in the study area, especially at the two stations where phytoplankton was blooming (21.8 and 14.9 egg $ind.^{-1}$ $day^{-1}$ at Stations Z11 and Z4, respectively). However, *C. sinicus* could only obtain sufficient food to support this high reproduction from the diatom bloom, but could not if relying only on the apparently unpalatable dinoflagellate bloom. Our analysis of copepod grazing and reproduction suggests that, although the spring blooms do enhance the reproduction of copepods, the taxa changed during spring blooms from large diatoms to small dinoflagellates would change the pathway of primary production. This would restructure secondary-producers (e.g. copepods) community structure, and have important ramifications through various marine trophic levels in the Southern Yellow Sea.



## 1. Introduction

Zooplankton plays a key role in the marine food web. As the main pathway to transfer primary production to higher trophic levels, its feeding efficiency will control phytoplankton productivity and biomass (top-down control), and also determine its own productivity, which ultimately influences fishery resources (bottom-up control).

The spring phytoplankton bloom is one of the most important biological production processes in temperate shelf seas (Voipio, 1981; Legendre, 1990). Usually these blooms are triggered directly by increasing light and nutrient availabilities (Sommer, 1996) and indirectly by temperature, via the effects of thermal stratification, and/or cloud cover (Sverdrup, 1953; Wiltshire and Manly, 2004). Enhancing primary production provides abundant food resources to zooplankton for the development of their populations, channeling primary production to fish (reviewed by Legendre, 1990). The responses of zooplankton to the spring phytoplankton bloom have an important role in regulating the energy flux in shelf ecosystems.

Copepods are generally the major herbivorous zooplankton in marine ecosystems. Although copepod feeding increases with increasing food, such as during the phytoplankton bloom periods, it has been demonstrated that copepod grazing rates are affected by food size (e.g. Frost, 1972), motility (Atkinson, 1995), nutritional quality (Prince et al., 2006), and food toxin content (Colin and Dam, 2005). Copepods can capture, handle, and ingest large particles more efficiently than small ones, within their adaptive size range (Frost, 1977). They may feed preferentially on motile over non-motile prey (Jonsson and Tiselius, 1990), or they may

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feed on some prey species or strains more than on others, despite similarities in size and motility (Teegarden, 1999). Also they are capable of rejecting toxin-containing prey, based on mechanical or chemical cues (Teegarden, 1999; Schultz and Kiørboe, 2009).

Climate changes and human impacts are altering the rate and distribution of primary production in the world's oceans (Brown et al., 2009). It is a common prediction that the timing of the phytoplankton spring bloom will advance under a warmer climate (Weyhenmeyer et al., 1999; Walther et al., 2002; Weyhenmeyer, 2001; Edwards et al., 2002). These changes will affect zooplankton recruitment which is coupled with spring blooms, and further restructure the entire ecosystems (Beaugrand et al., 2008). More significantly than climate warming, nutrient enrichment in eutrophicated coastal ecosystems induces a shift in the composition of phytoplankton, often characterized by the development of unpalatable or toxic phytoplankton species (Anderson et al., 2002). It is important to elucidate the feeding responses of zooplankton to such food environments and their consequences on the ecosystems.

The Yellow Sea is a semi-closed shelf sea in the Northwest Pacific. Spring phytoplankton blooms are usually observed in April. During this period, diatoms and dinoflagellates dominate phytoplankton biomass in the initial phase of the bloom. A post-bloom phase occurs when the nutrient pool is exhausted and is characterized by dinoflagellates, nanoflagellates, and autotrophic ciliates. Most copepods start their population recruitment following the spring blooms and have their biomass peaks in May–June. Increasing evidence indicates that the marine system of the Yellow Sea has markedly changed during last decades, impacted by natural and anthropogenic factors (such as increase of temperature, eutrophication, dinoflagellate increase and zooplankton fluctuation) (Yoo and Kim, 2004 and references cited therein). Understanding the relationships among these changes will help determine how ecosystems might change in the future.

In this paper, we report the response of copepod grazing and reproduction to spring blooms dominated by different taxa in the Southern Yellow Sea. This provides a field case to examine the ecological consequences of changes on the taxa of primary producers on the pelagic food web.

## 2. Materials and methods

A cruise was carried out in the Southern Yellow Sea in March–April, 2009. Two different algal blooms were found during the cruise. One was a diatom-dominated bloom at Station Z11, another was a dinoflagellate-dominated bloom at Station Z4 (Fig. 1). When the blooms were found, the vessel was anchored at the bloom station for 3–4 days to study the responses of zooplankton to the blooms. Temperature and salinity were recorded with a CTD (Sea Bird Electronics, SBE-19) at 1-h intervals. Seawater samples (500 ml) for the measurement of chlorophyll-*a* were collected at 3-h intervals from depths of 0, 10, 20, 30, 50 m and at the bottom, and filtered through GF/F glass-fiber filters. The filters were then extracted in 90% aqueous acetone for 24 h at 0 °C and the extracts were measured in a *Turner Designs Trilogy* fluorometer.

### 2.1. Zooplankton sampling

Zooplankton samples were collected by a net with mouth area of 0.5 $m^2$ and mesh size of 200 μm towed vertically from the bottom to the surface. A flowmeter was mounted in the center of the mouth of the net to measure the volume of water filtered. Samples were preserved in a 5% formalin-seawater solution. In the laboratory, the entire contents of each sample were sieved through 1000, 500 and 200 μm mesh to divide into three size fractions. 100% of the large fraction, 50–100% of the medium fraction and 10–50% of the small fraction were examined under a dissecting microscope, and the copepods were counted. We took day/night pairs of samples for mesozooplankton abundance at all stations. Mean values of the two samples taken at each station were used to calculate mesozooplankton abundance. Samples for gut pigment analysis and gut evacuation experiments were captured using the same net but with a sealed cod-end.

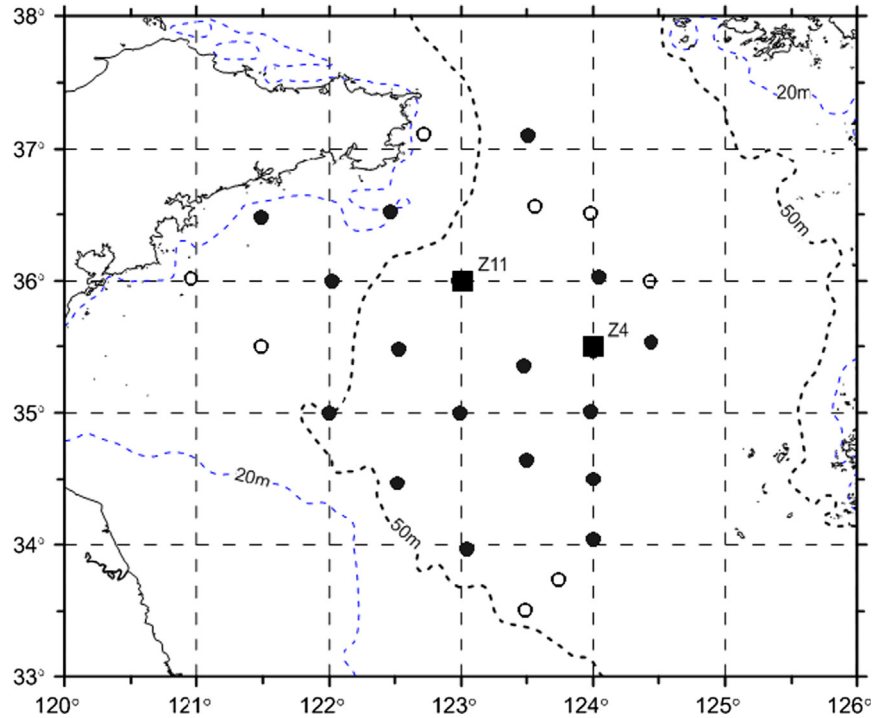


**Fig. 1.** Map of the sampling stations. ■ indicates the stations with herbivorous grazing measurements. • indicates the stations with egg production measurements. Contour lines indicate isobaths (m).

### 2.2. Feeding activity determination

Gut pigment was chosen as the index to analyze zooplankton feeding activities. Immediately after sampling, the cod-end contents were poured into soda/seawater solution (1:5, v/v) to anaesthetize the animals, sieved through 1000, 500 and 200 μm mesh, then gently rinsed with filtered seawater to wash away coarse phytoplankton cells. The resultant fractions were sorted under dim light and about 20 animals of the large fraction, 40 of the medium fraction and 80–100 of the small fraction were individually picked and placed in a 10 ml glass centrifuge tube to which 2–3 ml of 90% acetone solution were added. This operation took about 5–10 min. The tube was capped and stored in the dark at −30 °C. After completing all the sampling for each station, the contents of each tube were homogenized in a glass grinder, transferred back to the centrifuge tube, diluted to 10 ml with 90% acetone solution and extracted in the dark at -30 °C for 24 h. The tubes were then centrifuged for 10 min and the fluorescence of the suspension from each tube was measured before and after acidification with 10% HCl, using a *Turner Designs Trilogy* fluorometer. Absolute values for chlorophyll-*a* and phaeopigments were calculated according to Wang and Conover (1986). The sum was used as the index of gut pigment content (GPC). An empirical equation of $C=50$ chl was used to convert chlorophyll-*a* into phytoplankton carbon. At each station, samples were collected at 3-h intervals for more than a complete daily cycle to investigate feeding variations of the zooplankton following the bloom development.

Ingestion rates ($I$) were calculated by the expression:

$$I = \mathrm{GPC} \times \mathrm{GER}$$

where GPC is the average value of the survey period and GER is the gut evacuation rate. The gut evacuation rate (GER) was calculated according to Uye and Yamamoto's (1995) empirical model for *C. sinicus* as below:

$$\mathrm{GER} = 0.0222 + +0.00278T$$

where $T$ is the average water temperature of the whole water column.

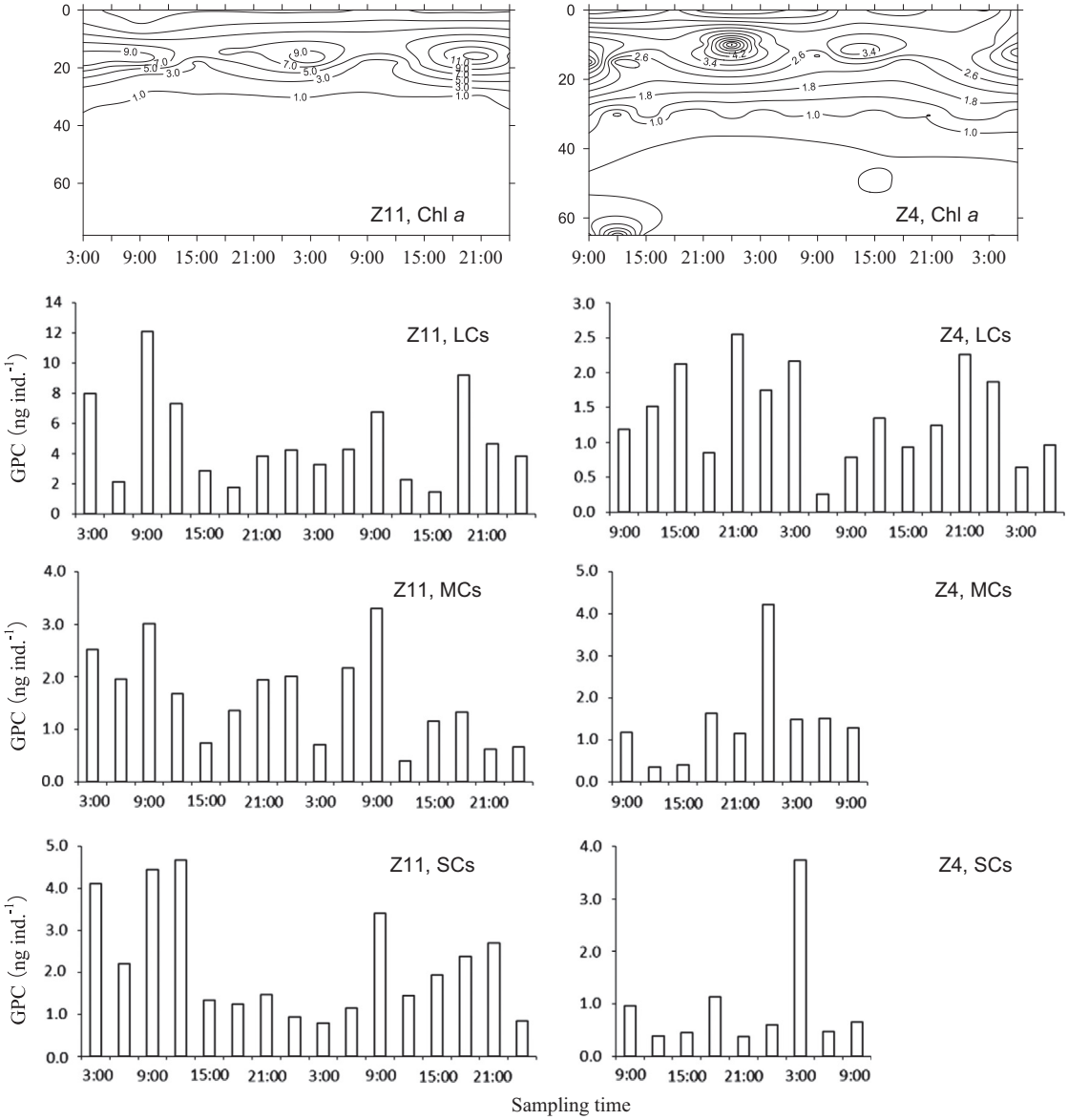


**Fig. 2.** Variation of GPC (ng ind.$^{-1}$) of copepods and chl-*a* concentration (mg m$^{-3}$) at Stations Z11 and Z4.

### 2.3. Egg production of Calanus sinicus

For egg production rate (EPR) measurements, additional vertical hauls were taken with the same net to catch live females. After capture, 25–50 healthy females of *C. sinicus* were immediately pipetted into plastic bottles (with false bottoms of 220 μm mesh size to avoid cannibalism; five females per bottle). We added 70 μm-filtered in-situ seawater as the culture water. Eggs were collected and counted after 24 h in the bottle culture.

## 3. Results

### 3.1. Hydrographic conditions and phytoplankton blooms

During the study period, the water temperature was 7.3–11.9 °C at Station Z4 and 7.2–9.5 °C at Station Z11. But the vertical patterns of water temperature were different between the two stations. At Station Z4, the weak thermocline started to form above 20 m depth, following the surface water temperature increase. However, at Station Z11, the effects of the Yellow Sea warm current were such that the surface waters were characterized by low temperature and the deep waters were characterized by high temperature.

Furthermore, both causative species and bloom sizes were different between the two stations (Fig. 2). At Station Z4, the phytoplankton bloom was mainly constituted by dinoflagellates (*Heterocapsa lanceolata*, cell size: approximately 15 μm), which contributed 94% of the total phytoplankton cells above 30 m depth and more than 99% of the phytoplankton cells at maximum chlorophyll-*a* level (MCL). The chlorophyll-*a* concentrations of MCL were 5.33 mg $m^{-3}$ on average (1.03–14.60 mg $m^{-3}$). At Station Z11, the phytoplankton bloom was mainly constituted by chain diatoms (*Detonula pumila*, *Guinardia delicatula*, *Thalassiosira pacifica*), which contributed to more than 90% of total phytoplankton cells, on average. The chlorophyll-*a* concentrations of MCL were 3.35 mg $m^{-3}$, on average (ranged between 1.84 and 6.39 mg $m^{-3}$) (Table 1).

### 3.2. Copepod composition

Copepods were the most abundant zooplankton found during the cruise (Table 2), contributing up to 71.4% of total zooplankton at Station Z4 and 65.4% at Station Z11. Their concentrations in the different size fractions and the identities of constituent species are shown in Table 2. Some species occurred in more than one size group because different developmental stages were present. The species compositions were similar between the two stations. The most abundant species of the Large copepods (LCs) were *C. sinicus.*

**Table 1**
Densities (cell. $ml^{-1}$) and percentage of dominant phytoplankton species at blooming stations.

| Species | Z11 | | Z4 | |
|---|---|---|---|---|
| | Abundance | % | Abundance | % |
| Diatoms | | | | |
| *Detonula pumila* | 14.7 | 35.6 | 1.5 | 0.5 |
| *Skeletonema dohrnii* | – | – | 10.1 | 4.0 |
| *Guinardia delicatula* | 9.5 | 23.1 | – | – |
| *Thalassiosira pacifica* | 2.3 | 6.4 | – | – |
| Other diatoms | 8.0 | 19.1 | 1.3 | 0.4 |
| Dinoflagellates | | | | |
| *Heterocapsa lanceolata* | – | – | 472.2 | 94.1 |
| *Prorocentrum minimum* | 2.5 | 6.9 | – | – |
| Other dinoflagellates | 0.3 | 0.8 | 0.9 | 0.2 |
| Others | 3.8 | 8.1 | 2.2 | 0.6 |

**Table 2**
Abundance (ind. $m^{-3}$) of potentially herbivorous copepods and dominant species at blooming stations.

| Station | LCs | Species | MCs | Species | SCs | Species |
|---|---|---|---|---|---|---|
| Z4 | 29.6 | *C. sinicus* | 5.4 | *C. sinicus* | 46.9 | *O. similisi*<br>*P. parvus* |
| | | | | *C. abdominalis* | | *A. bifilosa* |
| Z11 | 25.5 | *C. sinicus* | 8.1 | *C. sinicus* | 26.2 | *O. similisi*<br>*P. parvus* |
| | | | | *C. abdominalis* | | *A. bifilosa* |

*Centropages abdominalis* and copepodites of *C. sinicus* represented >90% of the medium copepods (MCs). The small copepods (SCs) were mainly composed of *Oithona similis*, *Paracalanus parvus*, and *Acartia bifilosa*. The abundances of SCs were highest among the three groups, which represented 57% of the total at Station Z4 and 43% at Station Z11. The MCs were fewest and only accounted for 7% at Z4 and 14% at Z11.

### 3.3. Feeding activities

Although phytoplankton blooms occurred at both stations, different sized copepods had different gut pigment contents (Fig. 2). At Station Z11, where a diatom bloom occurred, the GPCs of copepods increased with increasing body size. These were $4.39 \pm 2.30$ ng $ind.^{-1}$, $2.67 \pm 2.77$ ng $ind.^{-1}$ and $1.60 \pm 0.88$ ng $ind.^{-1}$ for LCs, MCs and SCs, respectively. At Station Z4, where a dinoflagellate bloom occurred, the GPCs for LCs and MCs were lower than those at Station Z11 (Mann–Whitney *U*-test, $p < 0.01$), decreasing to $0.73 \pm 0.38$ ng $ind.^{-1}$ and $0.49 \pm 0.53$ ng $ind.^{-1}$, respectively. However, for SCs, there was no significant difference in GPCs between the two stations (Mann–Whitney *U*-test, $p > 0.05$). During the survey period, no diel cycle of GPCs of copepods was observed at either station. Also, there was no significant correlation between GPCs and ambient chlorophyll levels (mean chlorophyll-*a* concentrations of the whole water column and/or maximum chlorophyll-*a* concentrations) at either station.

Individual pigment-specific ingestion rates by copepods were higher at Station Z11 than those at Station Z4, especially for LCs and MCs (Table 3). Daily grazing rates by copepod assemblages were calculated from the data on gut pigment contents and evacuation rate constants, and then converted to the ratios for the population in the water column from bottom to surface by using population density (Table 4). At the diatom bloom Station (Z11), the LCs were the major grazers among the three size groups, contributing 64% of the total copepod grazing. At the dinoflagellate bloom station (Z4), however, the SCs became the major grazers (74% contribution). The MCs were the lowest contributors at both stations, due to their low abundances. The grazing impact of copepods on phytoplankton was low, being equivalent to only 1.3% and $< 0.1\%$ $day^{-1}$ of the chlorophyll-*a* standing stock at Stations Z11 and Z4, respectively.

### 3.4. Egg production of C. sinicus

Positive egg production of *C. sinicus* was observed at all stations. The mean egg production rates (EPR) at each station ranged between 1.2 and 28.3 eggs $female^{-1}$ $day^{-1}$. At the two stations where the phytoplankton was blooming, the EPRs were 21.8 (9–77) and 14.9 (11–47) eggs $female^{-1}$ $day^{-1}$ at Stations Z11 and Z4, respectively. There was a significant ($P < 0.01$) positive correlation between EPRs and the ambient chlorophyll-*a* concentrations (Table 5).

**Table 3**
Estimates of mean gut pigment contents, gut evacuation rate constant and ingestion rate. The fractional loss of pigment during passage through the gut was 0.33 (Dam and Peterson, 1988).

| Station | Size groups | GPC (ng ind.$^{-1}$) | $K$ (min$^{-1}$) | Ingestion rate | |
|---|---|---|---|---|---|
| | | | | ng pigment ind.$^{-1}$ day$^{-1}$ | μg C ind.$^{-1}$ day$^{-1}$ |
| Z11 | LCs | 4.39 | 0.0462 | 442.4 | 22.1 |
| | MCs | 2.67 | | 269.1 | 13.5 |
| | SCs | 1.60 | | 161.2 | 8.1 |
| Z4 | LCs | 0.73 | 0.0424 | 67.6 | 3.4 |
| | MCs | 0.49 | | 45.4 | 2.3 |
| | SCs | 1.47 | | 136.1 | 6.8 |

**Table 4**
Daily grazing rates of copepod assemblages, fractional contributions to the total copepod grazing, and grazing impacts on phytoplankton.

| Station | Size groups | assemblage grazing (μg chl-*a* m$^{-2}$) | Fractional contribution (%) | Phytoplankton biomass (mg chl-*a* m$^{-2}$) | Grazing pressure (% biomass day$^{-1}$) |
|---|---|---|---|---|---|
| Z11 | LC | 801.0 | 64 | 96.0 | 0.8 |
| | MC | 155.0 | 12 | | 0.2 |
| | SC | 300.4 | 24 | | 0.3 |
| | Total | 1256.4 | | | 1.3 |
| Z4 | LC | 164.0 | 23 | 156.6 | 0.1 |
| | MC | 20.0 | 3 | | < 0.1 |
| | SC | 523.8 | 74 | | 0.3 |
| | Total | 707.8 | | | 0.4 |

**Table 5**
*Calanus sinicus* Pearson's product moment correlation between EPRs and Chl-*a* concentrations.

| | Chl-*a*—average | Chl-*a*—maximum |
|---|---|---|
| *EPR* | | |
| Pearson correlation | 0.527** | 0.407* |
| Sig. (2-tailed) | 0.001 | 0.012 |
| *n* | 37 | 37 |

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

## 4. Discussion

Many authors have reported enhanced copepod ingestion in parallel with blooming phytoplankton (Atkinson, 1995; Bautista and Harris, 1992; Barquero et al., 1998). Compared with the previous results of copepod feeding in the Yellow Sea (Li et al., 2002, 2007), higher GPCs of copepods in this study also indicated that higher phytoplankton concentration enhanced copepod feeding. However, copepod ingestion rates did not always increase with increasing food concentration. The LCs and MCs, which were mainly composed of *C. sinicus* and *C. abdominalis*, showed lower gut pigment contents at Station Z4 than those at Station Z11, though the concentrations of chlorophyll-*a* at Station Z4 were twice as higher. This substantiated the importance of food quality on copepod feeding.

It is well known that copepods can feed selectively (see reviews in Huntley, 1988; Harris, 1996). Food particle size is considered to be one of the factors in selection by copepods (Frost, 1977; Poulet, 1973; Hansen et al., 1994). In our case, it can explain the differences in GPCs of LCs and MCs between the two stations. At Station Z11, the dominant blooming phytoplankton were large diatoms (*D. pumila*, *G. delicatula*, *T. pacifica*), whose cell sizes are mostly larger than 20 μm (Sun, personal communication). The results of chlorophyll-*a* size fractions also indicated that micro-phytoplankton contributed nearly 50% of the total chlorophyll-*a*. At Station Z4, however, dinoflagellates dominated the phytoplankton bloom and nano-phytoplankton were the largest fraction and contributed to more than half of total chlorophyll-*a*. Li et al. (2007) reported that *C. sinicus*, the dominant species of LCs and MCs in this study (Table 2), prefer grazing on particles larger than 20 μm. Therefore, LCs and MCs grazed more effectively at Station Z11.

More importantly than food particle size, the species composition was different between the two blooming stations. LCs and MCs grazed actively on diatom blooms (*D. pumila*, *G. delicatula*, *T. pacifica*). This is in agreement with some spring bloom studies, showing selection for diatoms when they are abundant (Meyer-Harms et al.1999; Teegarden et al. 2001). However, the dinoflagellate bloom (*Heterocapsa* spp.) in this study seemed to be an inadequate food to copepods even though most dinoflagellates have a higher volume-specific organic content than diatoms under the same growth conditions (e.g., Hitchcock, 1982) and are recognized as being important in the diet of copepods (Price et al., 1983; Gill and Harris, 1987; Kleppel et al., 1991; Kleppel, 1993). *Calanus*-genus copepods can have both a passive and an active feeding mode (Landry, 1981). They can discriminate between different particle types, even of a similar size, and show preferences between different types of food (Huntley, et al., 1983). Huntley et al. (1986) also suggested that copepods such as *C. pacificus* might use chemical cues associated with the prey item to actively reject unsuitable or toxic prey. While feeding on both toxic and nontoxic dinoflagellates along with a mixture of several diatom species, *C. finmarchicus* selectively preyed upon various diatom species, and mainly avoided the toxic dinoflagellates (Teegarden et al., 2001). We do not know whether the *Heterocapsa* spp. at Station Z4 were toxic or not. However, some *Heterocapsa* spp., such as *Heterocapsa circularisquama*, are specifically harmful to grazers under dense bloom conditions (Kamiyama and Arima, 1997). The relatively lower GPCs suggested that this dinoflagellate bloom provided undesirable food to LCs and MCs at least.

Unlike the LCs and MCs, SCs continued grazing actively at both stations. Small copepods have also been shown to select phytoplankton cells based on size (Paffenhöfer et al., 1982; Price et al., 1983; Tackx et al., 1989). However, they are capable of feeding at higher rates on nanoflagellates than on larger prey (Vargas and Gonzalez, 2004) and are more selective during periods of high food concentration (RollwagenBollens and Penry, 2003). *Acartia hongi* and *P. parvus* showed higher clearance rates on smaller phytoplankton ( < 20 μm) (Lee et al., 2012). *O. similis* is an ambush feeding copepod that detects its prey remotely from the hydromechanical signals generated by the swimming of prey organisms (Svensen and Kiørboe, 2000). The prey size has less influence on its feeding preference (Nishibe et al., 2010). Hence, smaller, motile dinoflagellates may have higher detectability by *O. similis* compared with immobile diatoms.

In this study, grazing impact of copepod assemblages on phytoplankton was small, only removing daily 4.4% and 0.2% of the chlorophyll-*a* standing stock at Station Z11 and Z4, respectively. This is consistent with previous studies, which found that copepod grazing is not the major control to the spring blooms (Bautista and Harris, 1992; Harris et al., 1998; Morales et al., 1991; Li et al., 2003). In another words, copepods transfer fewer primary products to the higher trophic levels than thought previously, although it is universally acknowledged that spring blooms are the most productive period in the temperate shelf seas (Voipio, 1981; Cushing, 1990; Legendre, 1990).

The grazing impact of copepod community on phytoplankton is affected by many factors, including the estimation of ingestion rate using the gut fluorescence technique, and the estimation of copepod abundances.

The gut fluorescence technique has some potential sources of error resulting from (1) diel feeding periodicities, (2) pigment degradation, and (3) calculation of gut evacuation rate. Gut pigment contents obtained in our study were based on more than one day–night cycle sampling, which avoided the errors from the feeding rhythms. We have not performed experiments to estimate pigment destruction degree, which could underestimate the actual ingestion. Pigment destruction does occur in copepod during gut passage and that the degree of pigment destruction varies greatly (Head and Harris, 1992; Li et al., 2003; McLeroy-Etheridge and McManus, 1999; Wang and Conover, 1986), but the pigment destruction rates are generally low ($<20\%$) in the chlorophyll range that most animals will experience in nature (Harris,1996). An average value of $\sim 30\%$ has been estimated (Dam and Peterson, 1988, Lopez et al. 1988). Finally, considering *C. sinicus* accounted for most of LCs and MCs in this study, we employed the GRE-temperature equation of Uye and Yamamoto (1995), which was also obtained from *C. sinicus*, to calculate the GER of all copepods. So, extrapolation of this GER to rates of SCs are possibly influenced by specific differences.

Although some copepodites and small copepods might have passed through the 200 μm mesh filter and thus number of SCs was underestimated, our results are within the reported range of values for copepod abundance of the same season in the study areas (Anon 1977; Huo et al., 2011). According to historical data, zooplankton biomass in the Yellow Sea declines to the lowest level in January, starts to increase in March–April and reaches its annual maximum in June. Therefore, during the study period, the copepod populations had just started to increase and needed time to numerically respond to the presence of phytoplankton food. Even though relatively high individual ingestion rates were observed, the community grazing only accounted for small percentage of phytoplankton standing stock. However, microzooplankton (ciliates and heterotrophic dinoflagellates), which can contribute considerably to the diets of mesozooplankters (Kleppel, 1993), have more rapid production per unit weight than mesozooplankton (Mueller and Geller, 1993; Montagnes and Lessard, 1999). This enables an instantaneous response to increasing food availability during the phytoplankton spring bloom (Johansson et al., 2004; Zhang et al., 2006). The pathway through microzooplankton therefore enables additional transfer of primary products to copepods, and further on to higher trophic levels.

Among the three size groups, LCs were the major grazers (64%) during the diatom bloom, whereas SCs contributed most to copepod assemblage grazing (74%) during the dinoflagellate bloom. This accounts for the sharp decrease in the ingestion rates of LCs in the dinoflagellate bloom. In this case, the species shifts in the phytoplankton bloom could cause a change in the path of carbon flow between the primary producers and the mesozooplankton, as different quality food is available for different animals.

The magnitudes of egg production of *C. sinicus* found in this study (1.2 and 28.3eggs female$^{-1}$ day$^{-1}$, on average, 11.3 eggs female$^{-1}$ day$^{-1}$) were comparable to the high fecundities reported in the literature (Uye and Murase, 1997; Zhang et al., 2005; Huo et al., 2008; Wang et al., 2009), and were more than 10 times higher than what had been observed one month earlier in the same area (Ning et al., 2013). This indicates that the population in the active reproduction phase and that spring blooms initiate the annual population development. The positive correlation between the EPRs and the ambient chlorophyll-*a* concentrations further suggests the essential role of external food to *C. sinicus* reproduction (Wang et al., 2009).

To estimate the attribution of phytoplankton to *C. sinicus* reproduction, EPR was converted into carbon weight by multiplying egg number by 0.20 μg C per egg (Uye, 1988). The gross growth efficiency (GGE) was estimated by GGE = EPR/ingestion rate × 100. GGE at the diatom bloom station (Z11) was about 20%, which is lower than the average value (0.33) for copepods (Peterson 1988; Båmstedt et al., 1999). The low GGE suggests that *C. sinicus* obtained sufficient food from phytoplankton to support their high reproduction. At the dinoflagellate bloom station (Z4), however, the calculated GGE was extremely high, 88%, which indicates herbivorous feeding alone could not provide the necessary carbon to sustain the observed demands for reproduction. The disparity between ingestion and egg production has been reported by a number of other studies (Harris et al., 2000; Zhang et al., 2006; Koski, 2007; Huo et al., 2008), and attributed to non-phytoplankton food items (Ohman and Runge, 1994; Irigoien et al., 1998; Richardson et al., 1999), feeding history (Båmstedt et al., 1999; Irigoien et al., 2000) and internal reserves (Harrison, 1990; Niehoff and Hirche, 1996; Mayor et al., 2006). For *C. sinicus*, non-phytoplankton food items (mainly microzooplankton) may be important under some circumstances (Li et al., 2004; Zhang et al., 2006; Huo et al., 2008). The reproduction of *C. sinicus* can be sustained for 3–5 days under starvation, and it recovers spawning after a few days of food addition (Wang, 2009). However, the energy for reproduction is derived mainly from the recent diet, rather than from inner lipid storage (Wang et al., 2009). The most likely explanation for the discrepancy between herbivorous ingestion and egg production rates in this study seems to be that part of the eggs were produced based on previous feeding, with a possible small contribution from other food items. The higher egg production would be unsustainable if *C. sinicus* only relied on the unpalatable dinoflagellate bloom.

In conclusion, we found that copepods displayed different responses to different-species spring blooms. Diatom blooms provided good food resource for copepods and herbivorous diets were sufficient to support their high reproduction. Dinoflagellate blooms (dominated by *Heterocapsa* spp.) seemed undesirable to LCs and MCs, and herbivorous diets could not meet their reproduction demands. In such a case, the species changes in spring blooms from large diatoms to small dinoflagellates would influence the pathway of primary production. This would restructure the community structure of secondary producers (e.g. copepods) and would have important ramifications for various marine trophic levels.

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