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The impact of giant jellyfish *Nemopilema nomurai* blooms on plankton communities in a temperate marginal sea

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ABSTRACT

This study focused on the bloom-developing process of the giant jellyfish, *Nemopilema nomurai*, on phytoplankton and microzooplankton communities. Two repeated field observations on the jellyfish bloom were conducted in June 2012 and 2014 in the southern Yellow Sea where blooms of *N. nomurai* were frequently observed. We demonstrated that the bloom was made up of two stages, namely the developing stage and the mature stage. Total chlorophyll *a* increased and the concentrations of inorganic nutrients decreased during the developing stage, while both concentrations maintained stable and at low levels during the mature stage. Our analysis revealed that phosphate excreted by growing *N. nomurai* promoted the growth of phytoplankton at the developing stage. At the mature stage, size compositions of microzooplankton were altered and tended to be smaller via a top-down process, while phytoplankton compositions, affected mainly through a bottom-up process, shifted to be less diatoms and cryptophytes but more dinoflagellates.

1. Introduction

Increasing jellyfish blooms have been reported frequently worldwide in recent decades, and have caused serious ecological and environmental disasters, such as declining fishery production, poisoning swimmers and blocking cooling water intakes in coastal power plants (Mills, 2001; Purcell et al., 2007; Richardson et al., 2009; Dong et al., 2010; Purcell, 2012; Lucas et al., 2014). Mesocosm incubations have shown that bloom-forming jellyfish influences marine phytoplankton via both top-down (grazing) and bottom-up effects as they prey on zooplankton and excrete inorganic nutrients (Pitt et al., 2007; West et al., 2009). The top-down effect can not only change the mesozooplankton, but also alter the microzooplankton composition and affect the phytoplankton biomass and community structure (West et al., 2009; Kamiyama, 2011). Generally, the jellyfish community can be classified into zooxanthellate and non-zooxanthellate jellyfish. The bottom-up effect is mainly contributed by non-zooxanthellate jellyfish, i.e., inorganic nutrients excreted by non-zooxanthellate jellyfish can stimulate phytoplankton growth and change community compositions if those nutrients are limited in that system (Pitt et al., 2009; West et al., 2009). Recent field observations have also found that the biomass of phytoplankton was correlated closely with that of jellyfish during blooms of the large jellyfish *Chrysaora plocamia* in the northern Humboldt Upwelling System (Quiñones et al., 2018). However, studies on the effects of jellyfish blooming processes in situ on the phytoplankton assemblages are quite rare. Quantifying such effects is important for our understanding of how jellyfish blooms may affect the ecosystem function via changing of the structure of aquatic food webs, which are governed by phytoplankton biomass and composition.

The Yellow Sea is a highly dynamic, temperate marginal sea in the northwestern Pacific Ocean. Mounting evidences have indicated that massive blooms of the giant, non-zooxanthellate jellyfish *Nemopilema nomurai* occurred frequently in the Yellow Sea (Yang et al., 2004; Dong et al., 2010; Zhang et al., 2012; Sun et al., 2015). Biomass of *N. nomurai* was low during April, but increased with the increase of temperature in summer, reached the peak in September, and then decreased with the

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decrease of temperature in winter (Zhang et al., 2012; Sun et al., 2015). Yang et al. (2004) observed that the biomass of *N. nomurai* in the southern Yellow Sea was much higher during their observations than the early 1990s. In a high N:P ratio marine ecosystem, as in the Yellow Sea, studies have shown that phytoplankton biomass and community structures are usually determined by the availability of phosphorus (Wang et al., 2003; Liu et al., 2015). Therefore, the lower N:P ratio of jellyfish excreta could largely affect phytoplankton growth in this ecosystem (West et al., 2009). The jellyfish blooms are likely to affect phytoplankton communities through bottom-up and top-down controls. However, although jellyfish blooms have become a threat to the Yellow Sea (Yang et al., 2004; Jiang et al., 2008), there has been no report focused on the effect of jellyfish blooms on the phytoplankton assemblages in this ecosystem.

Here, we conducted four cruises in the southern Yellow Sea in June of 2012 and 2014, during blooms of *Nemopilema nomurai* were observed. By investigating environmental variables, the biomass of *N. nomurai*, biomasses and compositions of phytoplankton and microzooplankton, growth rate of phytoplankton, and grazing rate of microzooplankton on phytoplankton, we tested the following hypotheses:

(1) Increase in biomass, *Nemopilema nomurai* should excrete large amounts of phosphate, thereby promoting the growth of phytoplankton via a bottom-up process.
(2) Bloom of *Nemopilema nomurai* should alter the composition of microzooplankton via a top-down process.
(3) Bloom of *Nemopilema nomurai* should alter the composition of phytoplankton via both top-down and bottom-up processes.

2. Methods

2.1. Sampling

Four cruises, each with two transects (Transects K and I), were conducted in the southern Yellow Sea during 7–15 and 22–29 June 2012 and 6–13 and 20–27 June 2014 (Fig. 1). Hydrographic measurements and water samples were taken at each station using a Seabird SBE-911 plus CTD with a 12-bottle Niskin Rosette sampler. Water samples were taken at 3–5 depths ranging from 24 to 50 m. Bottom trawl surveys for jellyfish collection and calculation of jellyfish biomass ($t\,m^{-2}$) were described in detail in Zhang et al. (2012) and Sun et al. (2015). In brief, a bottom trawl net was deployed at each station with a towing speed at about 3 kt and a duration of 0.3–1 h. The bottom trawl net was 83.2 m in length, 167.2 m in circumference, about 7 m in height, about 22 m in width, and 10 cm in mesh size.

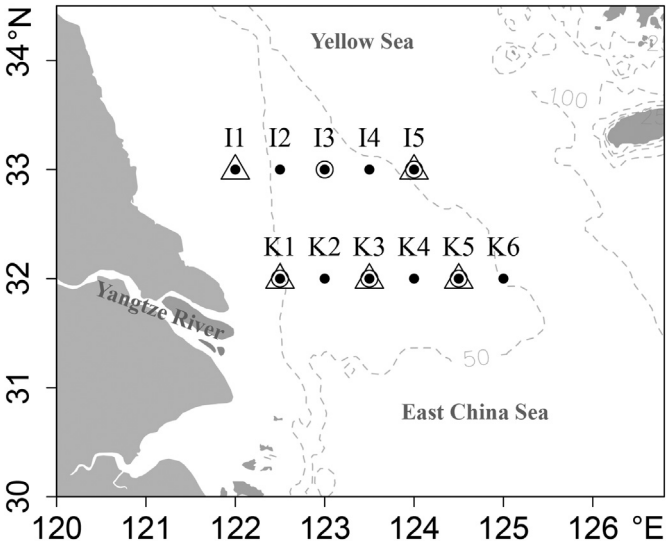

Fig. 1. Sampling stations in the southern Yellow Sea during June 2012 and 2014. Circle (○) and triangle (△) represent dilution experiment stations during 7–15 June 2012 and 22–29 June 2012, respectively.

2.2. Inorganic nutrients

Water samples for inorganic nutrient analysis were taken with a Niskin water sampler and were filtered immediately through acid-cleaned 0.45 μm pore size acetate cellulose filters. The filtrates were treated with 50 μL saturated $HgCl_2$ solution and were kept frozen until analysis. Nutrients were measured within 3–6 months after collection using the autoanalyzer QUATTRO. The detection limits for nitrate, phosphate and silicate were 0.02 μM, 0.01 μM and 0.04 μM, respectively.

2.3. Phytoplankton biomass and community composition

Collection of seawater samples for phytoplankton pigment measurement and the determination using high performance liquid chromatography (HPLC) have been reported in detail previously (Huang et al., 2010; Liu et al., 2012; Liu et al., 2015; Liu et al., 2016; Xiao et al., 2018b). Diagnostic pigments were used to estimate contributions of nine phytoplankton groups to total chlorophyll *a* (TChl *a*: chlorophyll *a* plus divinyl chlorophyll *a*) using the CHEMTAX program (Mackey et al., 1996; Xiao et al., 2018b). The nine phytoplankton groups were dinoflagellates, diatoms, prymnesiophytes, chrysophytes, chlorophytes, cryptophytes, prochlorophytes, cyanobacteria, and prasinophytes. These samples were grouped by depths of 2–10 m, 10–30 m, and > 30 m. Successive runs were performed for each group to gain convergence between input and output ratios (Latasa, 2007).

2.4. Microzooplankton abundance and group composition

Microzooplankton samples of 0.5–1 L were collected by a sampling tube from the surface water at each station and fixed in 4% buffered Lugol's solution. Fixed samples were then stored in dark areas until laboratory analysis. After 24 h of precipitation, the samples were concentrated to 10 mL with a silicon tube, and each subsample of 0.1 mL for the microzooplankton were enumerated and photographed using a Leica DMIRB microscope. If the counted organisms were lower than 200 in cell number, another subsample of 0.1 mL was added for measurements until > 200 organisms were counted. Volumes of ciliates, heterotrophic dinoflagellates (HDFs, *Gyrodinium* only), and copepod nauplii were estimated based on their geometric shapes (sphere, spheroid, columnar, and cone) (James and Hall, 1995). Individual organism's biomass was estimated based on the carbon conversion coefficient (Verity and Lagdon, 1984; Putt and Stoecker, 1989; Menden-Deuer and Lessard, 2000).

2.5. Phytoplankton growth rate and microzooplankton grazing rate

Dilution experiments were performed during the two cruises in 2012 (Fig. 1) to measure phytoplankton growth rate (μ) and microzooplankton grazing rates (m) (Landry and Hassett, 1982; Landry et al., 2008). Surface seawater sample of 10 L was collected and filtered through a 0.2 μm filter capsule to 1.2 L clear polycarbonate bottle. Two sets of samples were taken, one with 100% unfiltered sea water and one with 30% of the filtered water and 70% of unfiltered sea water. This experiment was duplicated.

All the above bottles were tightly capped and incubated for 24 h in a deck incubator cooled by running surface seawater at ambient light levels and samplings were taken at the beginning and the end of incubation. Chl *a* was analyzed by concentrating 0.1–0.5 L seawater onto 25 mm Whatman GF/F filters before and after incubation. All containers in the dilution experiments were rinsed with 10% HCl followed by Milli-Q water. The above experimental design followed the two-

treatment dilution approach of Landry et al. (2008). The natural logarithm of the ratio of the Chl *a* concentrations after and before incubation was regressed with the proportion of unfiltered water (1 and 0.7 in these experiments) in the culture container. The slope of the regression line is equal to -m, and the intercept is equal to μ.

2.6. Data analyses

In order to illuminate the effects of *Nemopilema nomurai* on inorganic nutrient concentrations and phytoplankton, concentrations of all inorganic nutrient metrics and each phytoplankton group and TChl *a* were integrated from the sea surface to near the bottom. The principal component analysis (PCA) was used to elucidate the relationships between the biomass of *N. nomurai*, the integrated concentrations of nitrate, phosphate, and TChl *a*, and the sea surface temperature and salinity. The PCA was carried out using the R package 'vegan' (Borcard et al., 2011). Kruskal-Wallis test was used to contrast the overall difference in all parameters between the developing stage and the mature stage of jellyfish bloom (Hollander and Wolfe, 1973). All analyses in this study were done using the R version 3.4.4 (R Development Core Team, 2018).

3. Results

In the jellyfish bloom season of the Yellow Sea, the two transects K and I showed similar patchiness characteristics in terms of both hydrological and inorganic nutrient parameters during our investigations. Take transect K for an example, affected by the Changjiang River Plume, surface water was less saline and warmer as compared with the deep water of the same station (Fig. 2a–h). However, high concentrations of inorganic nutrients, especially phosphate, showed patchiness distributions and did not always appear in the surface less saline waters (Fig. 2i–p). The high concentration of TChl *a* also displayed a patchiness distribution and did not match well with either the intrusion of river plume or the high concentrations of inorganic nutrients (Fig. 2q–t).

At the same time, wide variations in jellyfish biomass, inorganic nutrient and TChl *a* concentrations were noted. The integrated jellyfish biomass ranged from 0 to over 80 t km^{-2}, the integrated phosphate was 2–60 μmol m^{-2}, the integrated nitrate was 76–3296 μmol m^{-2} and the integrated TChl *a* was 12–268 mg m^{-2}. The integrated nutrient and the integrated TChl *a* concentrations significantly fluctuated when the biomass of *N. nomurai* was lower than 10 t km^{-2}, but curiously enough their concentrations stayed at extremely low levels as the jellyfish biomass exceeded 10 t km^{-2} (Fig. 3). The indication is that the former was in the developing stage of jellyfish bloom and the latter in the mature stage. In the developing stage, both integrated concentrations of inorganic nutrients and integrated TChl *a* varied substantially and decreased to low values during the mature stage, except for two extremely high values of the integrated phosphate at the 10 m depth of stations K_4 and K_5 in late June 2012 (Fig. 3).

In the developing stage of jellyfish, the PCA revealed that TChl *a* was positively correlated with jellyfish biomass and negatively correlated with inorganic nutrient concentrations. Among the two nutrient metrics, TChl *a* was more closely correlated with phosphate than with nitrate. Both temperature and salinity had very weak relationships with TChl *a* (Fig. 4).

3.1. Phytoplankton community

Diatoms, dinoflagellates, cryptophytes, and prasinophytes were the top four dominant groups of phytoplankton in our study area. They contributed 90.5 ± 5.9% and 84.6 ± 3.4% to total phytoplankton in the developing stage and the mature stage of the jellyfish bloom, respectively (Fig. 5a). Comparing the developing stage and the mature stage of jellyfish bloom, significant decreases were noted for diatoms and cryptophytes in both absolute and relative biomass during the mature stage (Fig. 5b–e). For dinoflagellates, the biomass was nonsignificantly different between both stages of jellyfish bloom (Fig. 5f), while its relative biomass significantly increased from 10.7 ± 11.7% to 16.5 ± 10.9% (Fig. 5g). Prasinophytes decreased nonsignificantly from 4.36 ± 2.67 mg m^{-2} in the developing stage to 3.78 ± 3.12 mg m^{-2} in the mature stage, but its relative biomass remained almost the same in both stages.

3.2. Microzooplankton

Microzooplankton biomass and abundance were nonsignificantly different between the developing stage and the mature stage of the jellyfish bloom, while both decreased from 15.6 ± 14.2 μgC L^{-1} and (11.8 ± 13.7) × 10^3 cells L^{-1} in the developing stage to 10.6 ± 6.4 μgC L^{-1} and (2.5 ± 0.8) × 10^3 cells L^{-1} in the mature stage, respectively (Fig. 6a). The mean decrease was 32% in biomass and 79% in abundance. Ciliates, HDFs and nauplii were the three major microzooplankton groups present in our study area. Comparing the three major microzooplankton groups, ciliates, HDFs, and copepod nauplii, in the mature stage with those in the developing stage of jellyfish bloom, decreases of 42%, 17%, and 10% in biomass and 79%, 81%, and 51% in abundance were recorded, respectively. The most dominant group was ciliates, which contributed 83.6 ± 13.3% to the total abundance and 67.3 ± 18.0% to the total biomass of microzooplankton. The ciliates, with a biovolume higher than 10^4 μm^3, had significantly higher frequency of occurrence in the developing stage than in the mature stage of jellyfish bloom (Fig. 6b). The indication is that ciliates, and even microzooplankton, were significantly smaller in size following the jellyfish bloom development process.

3.3. Phytoplankton growth rate and microzooplankton grazing rate

The phytoplankton growth rate and microzooplankton grazing rate were measured in some stations of the study area. The data of stations with jellyfish bloom were too less to draw statistical inferences. Phytoplankton growth rates showed potential decreases from 0.43 to 1.36 d^{-1} in the developing stage to 0.10 d^{-1} and 0.72 d^{-1} in mature stage of jellyfish bloom in two stations (Fig. 6c), and microzooplankton grazing rates also decreased potentially from 0.31 to 0.83 d^{-1} in the developing stage to 0.11 d^{-1} and 0.47 d^{-1} in mature stage of jellyfish bloom in two stations (Fig. 6d).

4. Discussion

4.1. The succession of jellyfish bloom

Many previous studies reported the mechanism and the influence of jellyfish bloom on marine ecosystems (Pitt et al., 2007; Purcell et al., 2007; Pitt et al., 2009; West et al., 2009; Dong et al., 2010; Purcell, 2012; Condon et al., 2013). However, reports on the development process of jellyfish bloom, especially its impact of dissolved organic matter excreted by jellyfish on phytoplankton and of grazing pressure on the compositions of phytoplankton and microzooplankton, are rare. In the continuous field observations of jellyfish blooms in the Yellow Sea in June 2012 and 2014, we demonstrated that the jellyfish bloom was made up of two stages, namely the developing stage and the mature stage. The concentration of inorganic nutrients and TChl *a* varied widely with the increasing jellyfish biomass during the developing stage and both stayed at a stable low level in spite of the growing jellyfish biomass in the mature stage. In the developing stage, the PCA revealed that TChl *a* was positively correlated with the jellyfish biomass and negatively correlated with inorganic nutrients, whereas the relationships between TChl *a* and hydrological parameters, temperature and salinity, were much weaker (Fig. 4). The result supports our suggestion that the phytoplankton biomass increased through bottom-up processes as excreted inorganic nutrients increased following the

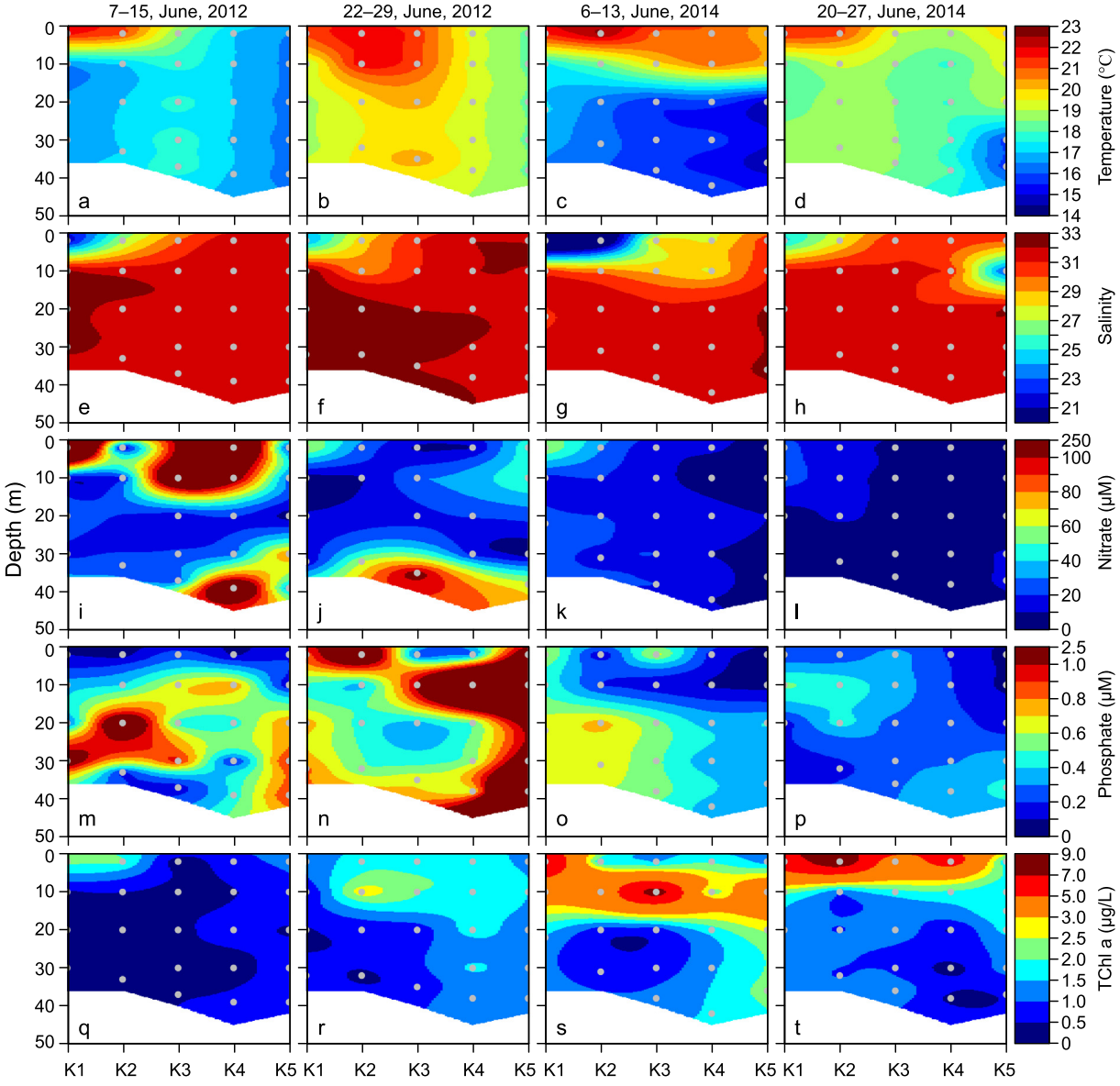

Fig. 2. Vertical distributions of environmental parameters along the transect K. (a–d) Temperature, (e–h) salinity, (i–l) nitrate, (m–p) phosphate and (q–t) total chlorophyll *a* (TChl *a*). From left to right are cruises during 7–15 and 22–29 June 2012 and 6–13 and 20–27 June 2014, respectively.

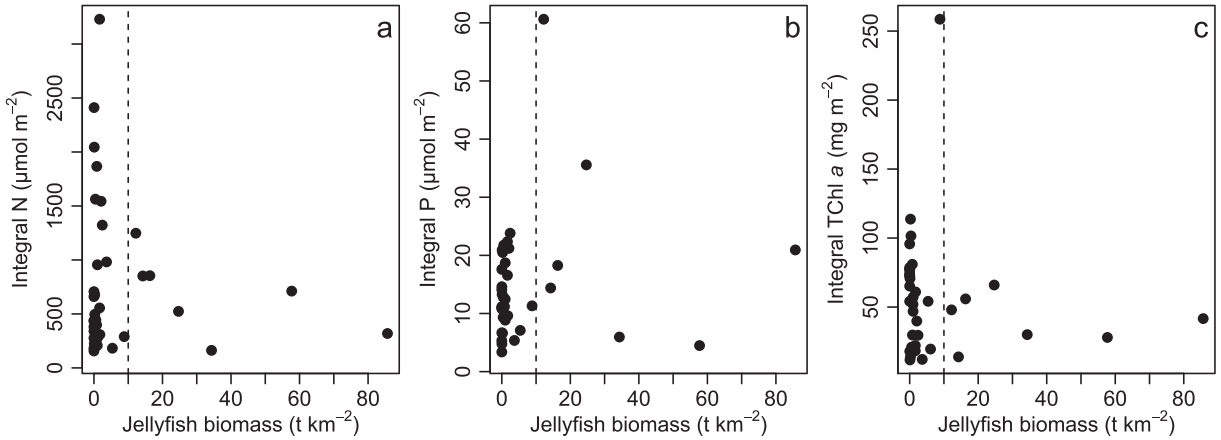

Fig. 3. Depth-integrated environmental parameters as functions of jellyfish biomass. (a) Nitrate (N), (b) phosphate (P), and (c) total chlorophyll *a* (TChl *a*). The vertical dash line represents the threshold between the developing stage and the mature stage of jellyfish bloom.

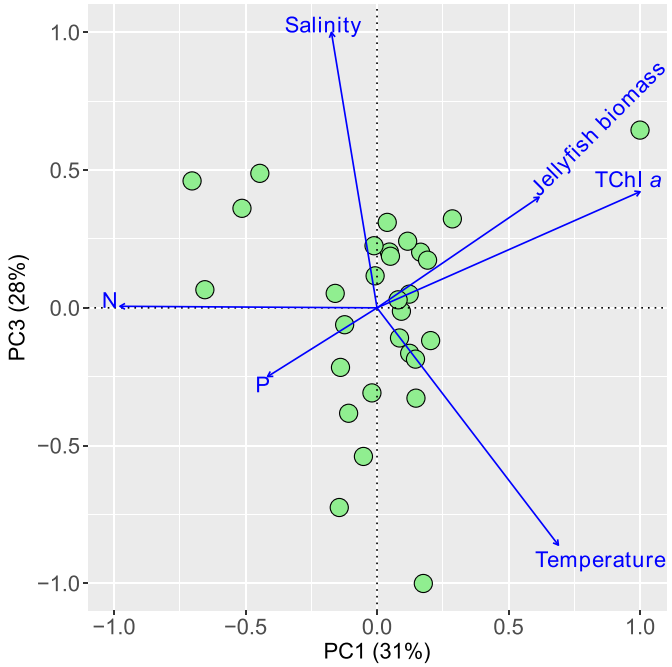

Fig. 4. Principal component analysis (PCA) based on samples with the jellyfish biomass lower than 10 t km^{-2}. N, P, and TChl *a* are depth-integrated nitrate, phosphate, and total chlorophyll *a*, respectively. Temperature and Salinity are sea surface temperature and salinity, respectively.

growing of jellyfish population. However the requirement of phytoplankton exceeded the excreted inorganic nutrients of jellyfish, therefore the inorganic nutrient decreased following the bloom development of jellyfish, i.e., all nutrients released by jellyfish were immediately consumed and used to build up phytoplankton biomass so that we cannot measure them in the water column.

As a non-zooxanthellate jellyfish, *Nemopilema nomurai* excreted into the water column the dissolved organic matter (Pitt et al., 2009; West et al., 2009), which were quickly metabolized by bacterioplankton (Condon et al., 2011; Tinta et al., 2012; Blanchet et al., 2015; Sweetman et al., 2016). Rates of excretion ranged from 77 to 2639 μM NH_4^+ g^{-1}C d^{-1} for pelagic cnidarians (Schneider, 1990), and phosphorus excretion turns over more rapidly than nitrogen (Shimauchi and Uye, 2007). These excreted inorganic nutrients could be high enough to support the phytoplankton growth, but were insufficient to remain and accumulate in the water column during our study period.

Previous reports have demonstrated the biomass of *N. nomurai* during the peak of jellyfish bloom was in the same order of magnitude of biomass that we found in the mature stage (Sun et al., 2015). When the jellyfish bloom transformed from the developing stage to the mature stage, the concentrations of TChl *a* and inorganic nutrients showed a stable and extremely low level following the increase of jellyfish biomass. This could infer that the supply of inorganic nutrients from jellyfish were not sufficient for supporting the growth demand of phytoplankton, or the production of phytoplankton was consumed by their predators, such as mesozooplankton, or there was no bloom of phytoplankton. Both the phytoplankton growth rate and the microzooplankton grazing rate on phytoplankton are higher in the developing stage than in the mature stage of jellyfish bloom (Fig. 6c), indicating the limited inorganic nutrients and low food availability during the mature stage.

Among the two nutrient metrics, phosphate and nitrate, phosphate was more closely related to jellyfish biomass and TChl *a* than nitrate (Fig. 4). This result reflects that phosphate excreted from jellyfish could affect phytoplankton more than nitrate, as was evidenced by the fact that the N:P ratio of jellyfish excreta is much lower than the Redfield ratio (16:1). The N:P ratio of jellyfish excreta ranges from 6.9 to 11.4 for *Aurelia aurita* (Shimauchi and Uye, 2007) and 8.7 for *Pelagia noctiluca* (Pitt et al., 2005). West et al. (2009) also demonstrated that phosphate excreted by non-zooxanthellate jellyfish (*Catostylus mosaicus*) was responsible for a 10-fold increase in primary production in a phosphate-limited coastal saline lake in Australia. Shimauchi and Uye (2007) reported that inorganic phosphorus from the jellyfish accounted for 21.6% of phytoplankton uptake rates while inorganic nitrogen from the jellyfish accounted for only 10.0% of uptake rates by phytoplankton in the Inland Sea of Japan. Therefore, jellyfish improved the availability of phosphorus relative to nitrogen. In another aspect, the phosphate is usually the limiting nutrient for phytoplankton growth in marine ecosystem of the Yellow Sea (Wang et al., 2003), the phosphate-rich jellyfish excreta could play an important role in making up the shortage of phosphate for the growth of phytoplankton in the Yellow Sea. Our findings, therefore, demonstrate the first hypothesis that phosphate excreted by the increasing *N. nomurai* promotes the growth of phytoplankton.

It has been demonstrated that living non-zooxanthellate jellyfish excretes dissolved organic matter into the water column, which could be quickly decomposed by bacterioplankton and provided a small but significant portion of inorganic nutrients for phytoplankton growth, whereas decaying jellyfish could result in much more release of inorganic and organic nutrients via decomposition (Pitt et al., 2009; West et al., 2009; Condon et al., 2011). Our result that inorganic nutrients decreased to basically low values in the mature stage of jellyfish bloom (Fig. 3) therefore suggest that the jellyfish during our observations could be mostly living. It has been found that jellyfish blooms are able to last until October in the Yellow Sea (Zhang et al., 2012; Sun et al., 2015), which also supports that jellyfish decomposition might not have frequently occurred during our observations. Exceptions were noted at stations K_4 and K_5 during late June 2012, where extreme high phosphate concentrations might be a hint of jellyfish decomposition (Fig. 2). For living jellyfish, previous studies have shown that their excreting rates of inorganic nutrients are positively related to the availability of prey (Kremer, 1982; Pitt et al., 2009).

4.2. The change of plankton composition during the development process of jellyfish bloom

By comparing the mature stage with the developing stage, we found that jellyfish bloom, transforming from developing stage to mature stage, was associated with decreasing biomass and abundance of microzooplankton (Fig. 6a), and so did for each of the three detected groups, ciliates, HDFs, and copepod nauplii. However, nauplii were only a very small part of the microzooplankton community and showed a very small decrease (10%). A previous study supported the result of the present study and indicated that the jellyfish feeding pressure on the copepod nauplii biomass increased to 694%–3055% due to a *N. nomurai* bloom in the southern Yellow Sea (Wang and Xu, 2013). Nauplii is a good food source to *N. nomurai*, while it could not meet the necessity of jellyfish. We found that most of the decreased biomass was contributed by the dominant ciliates, an indication that ciliates might be a good prey for the giant jellyfish, especially the large ciliates (larger than 10^4 μm^3). This result agrees with that of a previous study (Wang and Xu, 2013). Our result therefore further suggests that the giant jellyfish might feed on ciliates of larger sizes, and thus support the second hypothesis that bloom of *N. nomurai* should alter the composition of microzooplankton via top-down control.

We found that the composition of phytoplankton communities was affected by the development process of jellyfish bloom. Among the dominant groups, significant decreases in biomass were noted in diatoms and cryptophytes, whereas the biomass of dinoflagellates increased nonsignificantly (Fig. 5). The result is that the phytoplankton community has shifted toward relatively more dinoflagellates. The decreases of diatoms and cryptophytes might result from the declines in

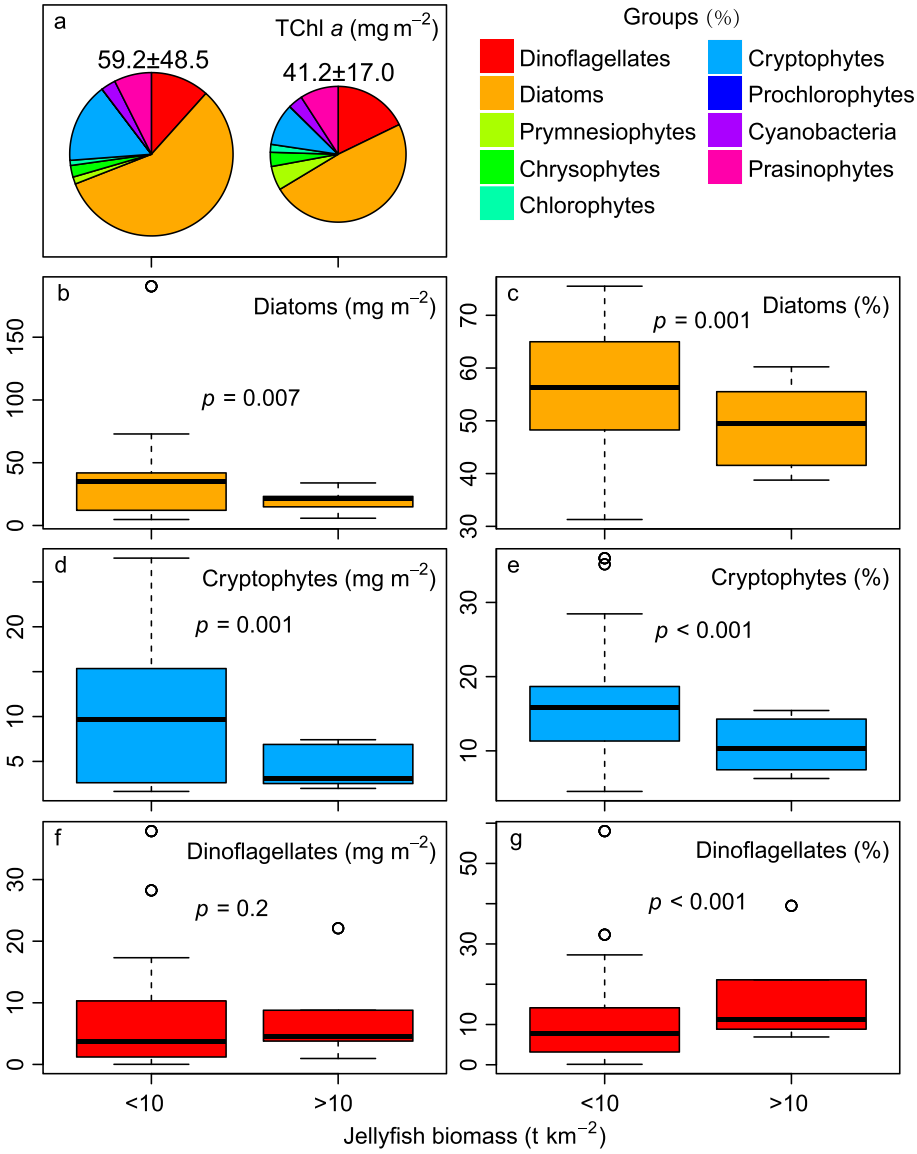

Fig. 5. Comparisons of phytoplankton groups between conditions with the jellyfish biomass less or > 10 t km^{-2}. (a) Total chlorophyll *a* (TChl *a*) and phytoplankton compositions, (b) biomass of diatoms, (c) relative biomass of diatoms, (d) biomass of cryptophytes, (e) relative biomass of cryptophytes, (f) biomass of dinoflagellates, and (g) relative biomass of dinoflagellates. The boxes in (b-g) define the hinge (25–75% quartile, and the line is 1.5 times the hinge). Points outside this interval are represented as dots. The black horizontal line inside each box is the median.

inorganic nutrient concentrations (Liu et al., 2016; Xiao et al., 2018a; Xiao et al., 2018b). The stability of dinoflagellates might be attributed to the fact that a large proportion of this group has the ability of mixotrophic growth (Smayda and Reynolds, 2003; Xiao et al., 2018a) and could utilize dissolved organic phosphorus (DOP) that excreted by jellyfish (Pitt et al., 2009). Our third hypothesis states that bloom of *N. nomurai* should alter the composition of phytoplankton via both top-down and bottom-up processes. However, our findings suggest that it is very likely that the bottom-up process controlled the alteration of phytoplankton communities.

5. Conclusions

This study, for the first time, reported the bloom process of *Nemopilema nomurai* with field observations, demonstrating that this development process had an important influence on the phytoplankton biomass and on the compositions of phytoplankton and microzooplankton via the bottom-up control and top-down control, respectively. A previous review proposed a conceptual model of the contributions of non-zooxanthellate jellyfish to the nutrient cycle during the growth of jellyfish blooms (Pitt et al., 2009). Taken together, our results revealed two scenarios that link jellyfish, microzooplankton, and phytoplankton in the marine ecosystem. In the first scenario during the developing stage of jellyfish bloom, the growth of jellyfish excreted a significant portion of inorganic nutrients with low N:P ratio and promoted the growth of the phytoplankton. The most apparent beneficiaries of this scenario were diatoms and cryptophytes that prefer high concentrations of inorganic nutrients. In the second scenario during the mature stage of jellyfish bloom, the excretion of inorganic nutrients should be increased when jellyfish growth sustained in this stage. While the increase in phytoplankton growth could be entirely consumed, this low phytoplankton state of equilibrium will be maintained. Thus diatoms and cryptophytes significantly reduced, whereas the importance of dinoflagellates significantly increased in the mature stage, which may result from many mixotrophic species of dinoflagellates that could grow with DOP.

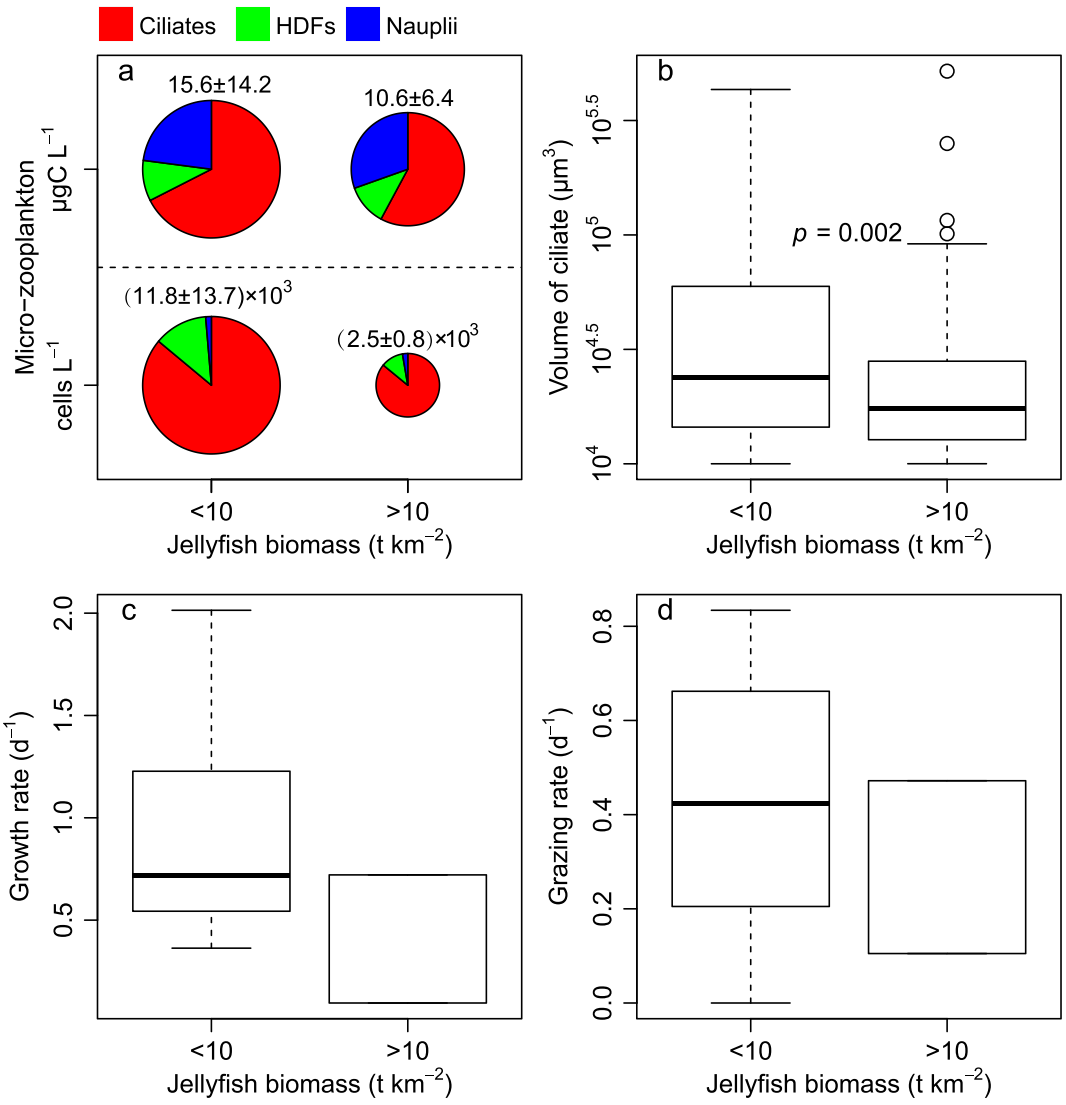

Fig. 6. Comparisons of (a) microzooplankton total amount and compositions, (b) ciliates of larger sizes, (c) phytoplankton growth rate, and (d) microzooplankton grazing rate between conditions with the jellyfish biomass less or > 10 t km^{-2}. Pies above and below the dash line in (a) are based on biomass and abundance, respectively. The boxes in (b–d) define the hinge (25–75% quartile, and the line is 1.5 times the hinge). Points outside this interval are represented as dots. The black horizontal line inside each box is the median. No medians are shown in the right boxes of (c) and (d) as there are only two values.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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