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Zooplankton Population and Community Structure Changes in Response to a Harmful Algal Bloom Caused by *Prorocentrum donghaiense* in the East China Sea

Anglu Shen [1], Wenwen Chen [1], Yongjiu Xu [2,*] and Kin-Chung Ho [1,3,*]

[1] College of Marine Ecology and Environment, Shanghai Ocean University, Shanghai 201306, China; alshen@shou.edu.cn (A.S.); chenww1016@163.com (W.C.)
[2] School of Fishery, Zhejiang Ocean University, Zhoushan 316022, China
[3] Department of Geography, The University of Hong Kong, Hong Kong
[*] Correspondence: xuyongjiu@zjou.edu.cn (Y.X.); kcho2@hku.hk (K.-C.H.)

Abstract: Blooms of the dinoflagellate *Prorocentrum donghaiense* have had adverse impacts on marine ecosystems. However, ecological details, particularly the impacts and processes of the *P. donghaiense* bloom on the zooplankton community structure are poorly known. We investigated the changes of zooplankton communities in situ within the whole process of a *P. donghaiense* bloom in the coastal waters in southern Zhejiang Province, China, in May 2016. Results showed that ecological changes during the blooms of *P. donghaiense* could be divided into three major phases, namely the growth, maintenance, and dissipation phases with regard to the cell abundance of *P. donghaiense* by bottle sampling of plankton. A total of 42 species of zooplankton were identified. The average abundance and species number of zooplankton in the growth phase were significantly higher than those in the maintenance and dissipation phases. It is shown that the top-two highest proportions of zooplankton in the growth phase were small jellyfishes and copepods, while small jellyfishes and chaetognaths, and copepoda larvae and chaetognaths were the top-two highest in the maintenance and dissipation phases respectively. However, the values of biodiversity index have no statistically significant differences between the three phases. The present results suggested that *P. donghaiense* bloom produced significant negative impacts on the abundance and species composition of zooplankton with particular reference to copepods.

Keywords: *Prorocentrum donghaiense*; zooplankton; small jellyfishes; chaetognaths; copepods; ecological succession in HAB

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1. Introduction

Zooplankton is an important component of marine food webs, as predator (e.g., phytoplankton) or prey (e.g., fish larvae or fish). It plays key roles in the succession process of the marine ecosystem [1–3]. Zooplankton feeds on phytoplankton. When the abnormal proliferation of phytoplankton develops into algal bloom, the zooplankton community will also be changed due to the biological features of harmful algal blooms (HABs), mainly because of ecotoxicity, nutritional insufficiency, and autecology [4,5]. A number of studies have focused on the effects of HAB-causative species on the survivorship, swimming behavior, feeding, and fecundity of zooplankton in the laboratory [5–11]. However, the effects of HABs on the zooplankton community and succession in the field are rarely documented. Chai et al. [12] stated that the outbreak of HABs significantly reduces the resource-use efficiency in a coastal zooplankton community by comparing the data of the blooming period and the nonblooming period. Yet, no follow-up research has been found. More details were reported by Lin et al. [13] that the zooplankton community changed from copepod-and-small-jellyfish-dominated to small -jellyfish-dominated during a HAB caused by *Prorocentrum donghaiense* in the East China Sea (ECS). Zhou et al. [14]

also reported the effects of a natural dinoflagellate (*Alexandrium catenella*) bloom process in a salt pond on the microbial community structure and succession via the metagenomic approach. However, these investigations were neither in situ of a bloom in open sea nor sampled on a big scale and continuous process in the field, i.e., they were only sampled at intervals on a weekly or monthly basis in nonregular locations. In this regard, it is difficult to understand the whole ecological picture—particularly the completed process of changes of zooplankton during algal blooms in the open sea, taking into account the suddenness and randomness of bloom occurrences. Therefore, it is necessary to conduct in-depth research with fixed locations and more intensive sampling time (on a daily or hourly basis) to observe the complete ecological picture of HAB [15,16].

The Yangtze River estuary and the coast of Zhejiang Province constitute one of the best-known, high-frequency areas of HAB in China [17,18]. In this district, diatoms (e.g., *Skeletonema costatum*) are often the most dominant group, which will form blooms in early spring. Dinoflagellate blooms (e.g., caused by *P. donghaiense* and *Karenia mikimotoi*) usually occur during the period from late spring to early summer [19]. In the past 20 years, large-scale blooms of *P. donghaiense* have occurred annually in the coast of ECS by field investigation and remote sensing [20–22]. Although *P. donghaiense* is considered to be a nontoxic bloom-forming species that does not release known phytotoxins [23], some zooplankton species (for examples *Moina mongolica*, *Brachionus plicatilis*, and *Calanus sinicus*) presented significantly decreased survival or fecundity when fed with high concentrations of *P. donghaiense* [5,24]. Furthermore, Lin et al. [13] found that the abundance of copepods was significantly reduced but small jellyfish and chaetognaths had no significant variation in the nonbloom areas, peak-bloom areas, and decaying bloom areas during a *P. donghaiense* bloom in the coast of Fujian Province, China. In addition, the whole process of HAB can be divided into initiation, growth, maintenance, and dissipation phases according to the different cell abundances [25]. Previous study showed that there were significant changes in the phytoplankton community structure in the different phases during a *P. donghaiense* bloom on the coast of the ECS [16]. It is noted that while numerous papers have reported on the consequence of algal population changes, there are relatively few papers that have reported on and discussed the changes of the zooplankton population and relevant community structure changes correspondent to different phases of algal blooms. Particularly, information on the zooplankton that occurs during the blooms of *P. donghaiense*, which is a common causative organism of HAB in the ECS, is of importance to control and management of HAB in East China, as well as in other parts of the world. Therefore, we intend to provide significant scientific information for understanding the completed ecological process of HAB with the following hypothesis to be tested: that the zooplankton population and dominant species in the affected ecological community would be significantly affected by HAB during different phases of the event. A bloom of *P. Donghaiense*, which is common causative microalgae in the ECS, is investigated in depth.

During the study, an HAB incident happened in the coastal waters of Zhejiang Province, China. In May 2016, a *P. donghaiense* bloom resulted in severe depletion of oxygen and coloration in the sea surface. Together with other experts of HAB, our team was assigned to study the variations of zooplankton species focusing on their abundance correspondent to the growth, maintenance, and dissipation phases during the occurrence of relevant the HAB. We aimed to clarify the relationships among the abundance of *P. donghaiense* and changes of main zooplankton group/species. We also want to study the biodiversity indices to evaluate the community structure change with respect to ecological succession. It is widely known that copepods are important food resources for fish; we therefore also want to find out and discuss in depth about the impacts of relevant HAB on variations of copepods in the ECS so that it further impacts on fishery resources being verified. It is expected that relevant research results will help to elucidate the effects of dinoflagellate blooms on the zooplankton community, ecological succession, and the impacts on the marine food chain in general and specifically in the ECS.

2. Materials and Methods

2.1. Study Locations

The study area was located in the waters near Dongtou and Nanji Islands in the southern coast of Zhejiang Province (Figure 1). Details on the location of the sampling sites are presented in Supplemental Table S1. The sample IDs including sampling dates, and sites numbers are shown in Figures 2–4 such as (5.9-1) to (5.9-3). We collected a total of 112 samples for phytoplankton and zooplankton in this investigation, which took place from 9 to 20 May 2016.

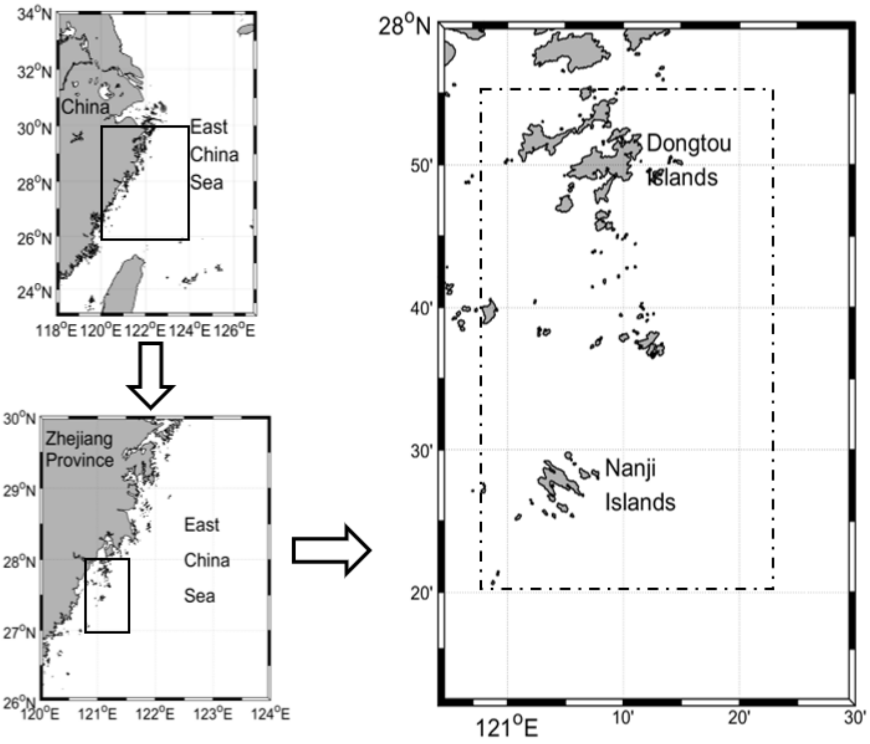

Figure 1. Map of sampling locations in the East China Sea (remarks: the area of the dashed frame in the right figure is the ship observation area, which is located on the southern coast of Zhejiang province).

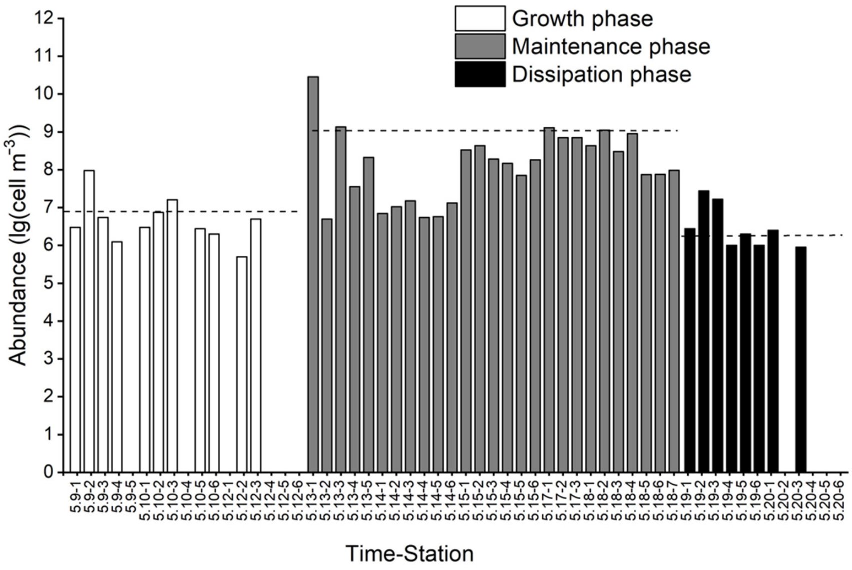

Figure 2. The abundance of *P. donghaiense* at each sampling station in different phases of the *P. donghaiense* bloom (remarks: the dash represents average value).

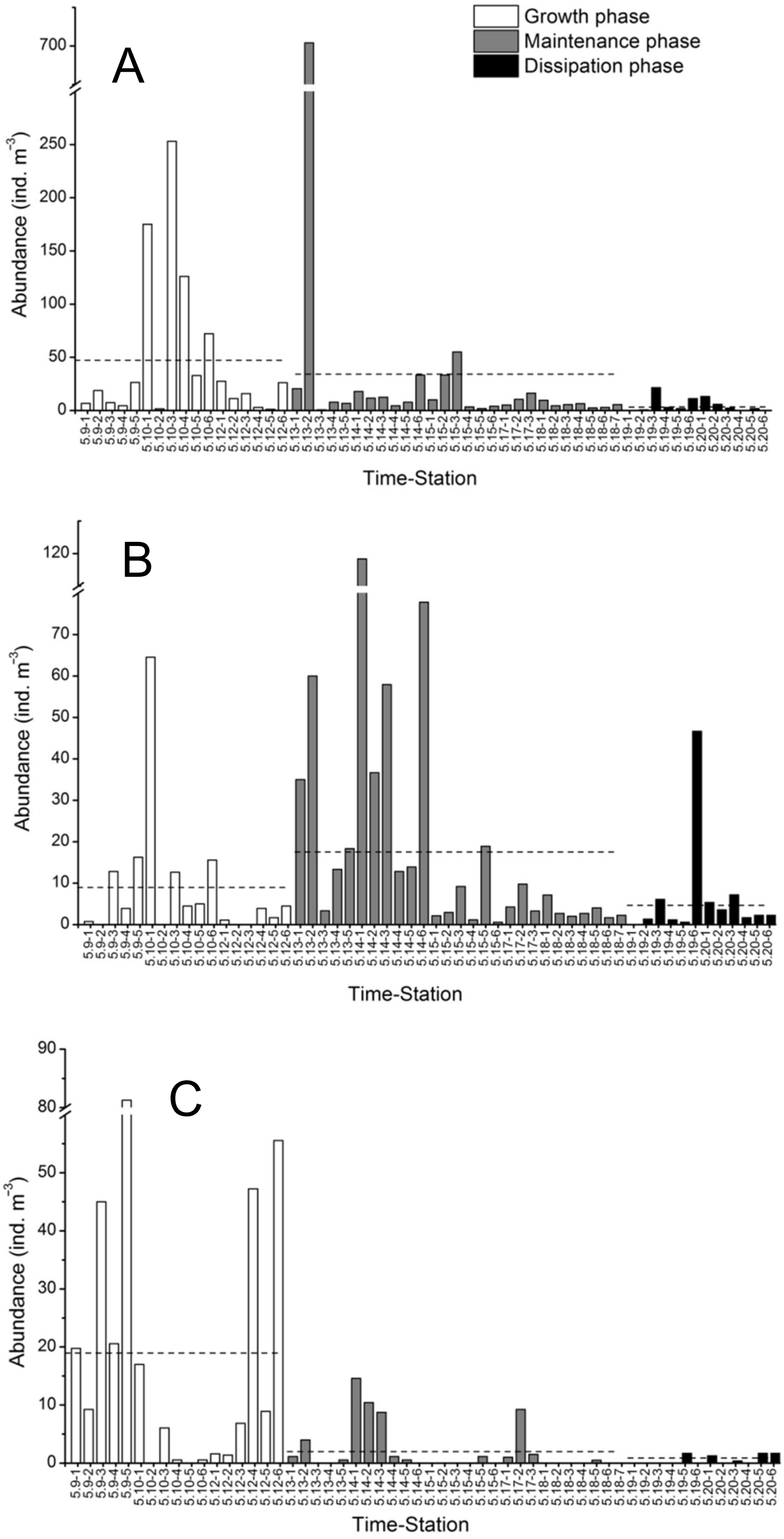

Figure 3. The abundance of small jellyfishes *M. atlantica* (**A**), chaetognaths *Z. nagae* (**B**), and copepods *C. sinicus* (**C**) at each sampling station in different phases of the *P. donghaiense* bloom (the dash represents average value).

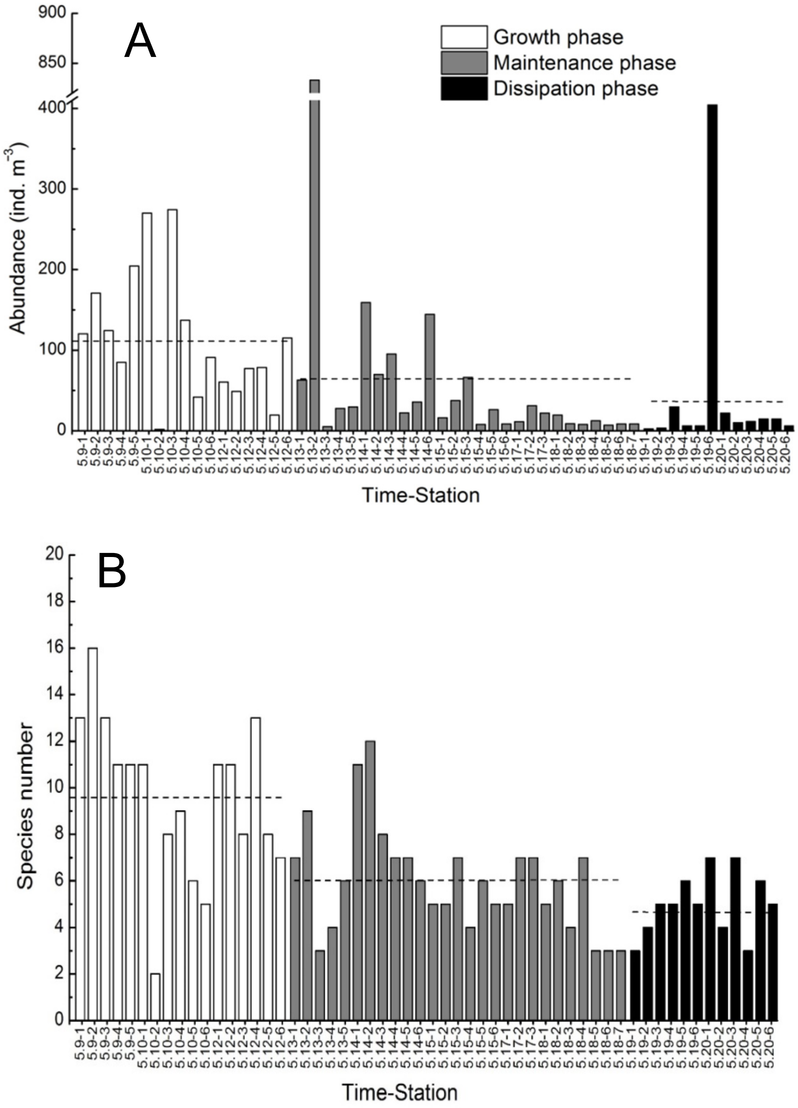

Figure 4. The abundance of zooplankton (**A**) and diversity changes (**B**) at each sampling station in the different phases of the *P. donghaiense* bloom (the dash represents average value).

2.2. Sample Collections and Analysis

During the study, 1000 mL of seawater samples were collected from 0.5 m below the surface every day at each site. They were fixed with Lugol's iodine solution to a final concentration of 1.5% for phytoplankton analysis. Taxonomic study and phytoplankton counts were conducted under an optical microscope (BX43, Olympus, Japan), which aimed to clarify diversity, abundance, and population changes. Phytoplankton identification followed taxonomic guidebooks, including but not limited to Jin et al. [26], Yamaji [27], and Yang and Dong [28].

Zooplankton were collected by vertical tow plankton net type-I (50 cm diameter, 145 cm length, 505 µm mesh size) from 1 m above the bottom layer to the surface. Those concentrated samples were fixed with 4% formalin solution. Zooplankton samples were identified and counted under a stereomicroscope (SZX10, Olympus, Tokyo, Japan). The abundance of zooplankton is calculated by the ratio of the number of zooplankton to the amount of water filtered by the plankton net. Identifications were made to the lowest possible taxon using the taxonomic literature cited in Chen and Zhang [29] for copepods, Xiao [30] for chaetognaths, and Shu and Han [31] and Yamaji [27] for small jellyfishes and tunicates, respectively.

In addition, the dominance index (Y) suggested by Xu and Chen [32], the Simpson index (C) (Sun and Liu [33]), the Shannon index (H') (Shannon and Weaver [34]), and the Pielou evenness index (J') (Pielou [35]) were applied to denote the different levels of diversity of the zooplankton community. The indices Y, C, H', and J' were calculated according to the following formulae:

$$Y = \frac{n_i}{N} \times f_i$$

$$C = \sum_{i=1}^{S} \frac{{n_i}^2}{N^2}$$

$$H' = -\sum_{i=1}^{S} \frac{n_i}{N} \log_2 \frac{n_i}{N}$$

$$J' = \frac{H'}{H'_{Max}} = \frac{H'}{\log_2 S}$$

where N is the abundance of zooplankton, n_i is the abundance of the ith species, f_i is the frequency of the ith species occurring in the samples, S is the total number of zooplankton species, and H'_{Max} is the maximum possible value of $H' = \log_2 S$. The occurrence rate (OR) of each group/species was also calculated according to Tseng et al. [36].

2.3. Statistical Analyses

The IBM SPSS-Statistics package version-22.0 (IBM SPSS Software, Chicago, IL, USA) was applied for all statistical analyses. Results were considered statistically significant only when $p < 0.05$. The raw data were checked for normality and homogeneity of variance using Shapiro—Wilk's and Levene's tests, respectively. If the data-set violated the assumption of normal distribution or homogeneity of variances, it was transformed with log(X + 1). One-way analysis of variance (ANOVA), alongside with Tukeys post-hoc multiple comparison test, was applied to test the differences of plankton abundance (mean ± S.E.) and other indices in the different phases of *P. donghaiense* bloom. In addition, if the assumption of normal distribution or homogeneity of variances was not fulfilled, even after the transformation, a nonparametric test (Kruskal–Wallis Test) would be applied. Additionally, the zooplankton community structures were analyzed using the PRIMER v6 (Plymouth Routines in Multivariate Ecological Research) package, the nonmetric multidimensional scaling (MDS) ordination was used to summarize species distribution, using the Bray Curtis similarity from the data of species abundance (log(X + 1)-transformed). Finally, Spearman rank correlation coefficients were used to identify correlations between the environmental factors (including *P. donghaiense* abundance) and zooplankton abundance (the total zooplankton abundance and main dominant species).

3. Results

3.1. Changes in P. donghaiense Abundance and the Environmental Variables of Seawater during the Algal Bloom Process

From 9 May to 20 May 2016, an HAB caused by *P. donghaiense* was reported in the southern coast of Zhejiang Province. During our research sampling, a total of 37 species of phytoplankton were identified. *P. donghaiense* was found to be the most dominant species of phytoplankton ($Y = 0.819$, OR = 82.46%) in water samples. The total abundance of *P. donghaiense* ranged from 9.00×10^5 to 2.87×10^{10} cells·m^{-3} (Figure 2), with an average abundance of 6.59×10^8 cells·m^{-3} (see Supplemental Table S2). According to previous research results (Shen et al. [16]), the average abundance of *P. donghaiense* in the growth (0.79×10^7 cells·m^{-3}) and dissipation phases (0.45×10^7 cells·m^{-3}) were significantly (Kruskal–Wallis, $p < 0.05$) lower than those in the maintenance phase (1.38×10^9 cells·m^{-3}), therefore, the process of current *P. donghaiense* bloom could be divided into three phases namely the growth phase (9–12 May), maintenance phase (13–18 May), and dissipation phase (19–20 May) on the basis of algal cell abundance (Figure 2).

During the investigation period, the variation range of physical parameters is small (Supplemental Table S3), the average values of depth of sample, temperature, pH, salinity, and dissolved oxygen were 15 m, 20.3 °C, 8.23, 27.8, and 9.64 mg$\cdot$L^{-1}, respectively—see the detailed data in Supplemental Table S3. However, the variation range of chemical parameters is large (Supplemental Table S3), the values of dissolved inorganic phosphorus in each station ranged from 0.03 to 2.97 μM, with an average of 0.56 μM, and the values of dissolved inorganic nitrogen in each station ranged from 3.43 to 60.64 μM, with an average of 19.07 μM.

3.2. *Identification of Dominant Species*

The dominant species of sampled organisms were defined according to Xu and Chen [32], by a Y value when it was higher than 0.015 in this study. Table 1 shows that the average abundance, OR, and Y values of various dominant species during the *P. donghaiense* bloom. It is found that the dominant organisms belonged to five main key categories, namely small jellyfishes, copepods, chaetognaths, tunicates, and planktonic larvae. *Muggiaea atlantica* (Y = 0.426) was shown to be the most dominant species in the whole process of *P. donghaiense* bloom. The dominance followed in declining order was *Zonosagitta nagae* (Y = 0.161), *Calanus sinicus* (Y = 0.053), copepoda larvae (Y = 0.024), *Clytia* sp. (Y = 0.022), and *Doliolum denticulatum* (Y = 0.017) in the overall HAB process. However, in the growth phase, *M. atlantica* (Y = 0.421) was the most dominant species followed by *C. sinicus* (Y = 0.148), *Zonosagitta* larvae (Y = 0.059), *Z. nagae* (Y = 0.058), *Clytia* sp. (Y = 0.049), and *D. denticulatum* (Y = 0.044) in declining order. It is noteworthy that in the maintenance phase there were only two dominant species, namely *M. atlantica* (Y = 0.562) and *Z. nagae* (Y = 0.292). In the dissipation phase, however, copepoda larvae (Y = 0.562) became the first dominant species, followed by *Z. nagae* (Y = 0.135), and *M. atlantica* (Y = 0.095) in declining order. Combined with dominance (Y > 0.05) and occurrence rate (OR > 50%), *M. atlantica*, *Z. nagae*, and *C. sinicus* were the most important species in the zooplankton community during this HAB incident (Table 1).

Table 1. The average abundance (A, ind. m^{-3}), occurrence ratio (OR, %), and dominance (Y) of dominant species during the *P. donghaiense* bloom.

Scienctific Classification	**Growth Phase**			**Maintenance Phase**			**Dissipation Phase**		
	A	**OR**	***Y***	**A**	**OR**	***Y***	**A**	**OR**	***Y***
Muggiaea atlantica	47.56	100.00	0.421	37.14	100.00	0.562	5.05	83.33	0.095
Clytia sp.	6.75	82.35	0.049	-	-	-	-	-	-
Calanus sinicus	18.91	88.24	0.148	-	-	-	-	-	-
Zonosagitta nagae	8.64	76.47	0.058	19.32	100.00	0.292	6.49	91.67	0.135
Doliolum denticulatum	12.13	41.18	0.044	-	-	-	-	-	-
Zonosagitta larvae	10.29	64.71	0.059	-	-	-	-	-	-
Copepoda larvae	-	-	-	-	-	-	28.73	66.67	0.433

3.2.1. *Muggiaea atlantica*

During the whole process of this *P. donghaiense* bloom, the total abundance of *M. atlantica* varied from 0.25 ind.$\cdot$m^{-3} (station 5.19-1) to 704.00 ind.$\cdot$m^{-3} (station 5.13-2), with an average of 33.43 ind.$\cdot$m^{-3}. The occurrence ratio was 96.43% (Figure 3A, Table 1). In the growth and maintenance phases, *M. atlantica* was found in sampled collected from all stations (OR = 100.00%). The average abundances were 47.56 and 37.14 ind.$\cdot$m^{-3}, respectively. In the dissipation phase, the average abundance was 5.05 ind.$\cdot$m^{-3}, with the occurrence ratio being 83.33%. According to statistical analysis, the average abundance of *M. atlantica* in the growth and maintenance phases were significantly higher than that in the dissipation phase (Supplemental Table S4, ANOVA, $p < 0.05$).

3.2.2. *Sagitta nagae*

During this investigation, the total abundance of *Z. nagae* varied from 0.56 ind.·m^{-3} (station 5.15-6 and 5.19.5) to 118.33 ind.·m^{-3} (station 5.14-1) with an average of 13.32 ind.·m^{-3}. The relevant occurrence ratio was 91.07% (Figure 3B, Table 1). The average abundances of *Z. nagae* were 8.64, 19.32, and 6.49 ind.·m^{-3} in the growth, maintenance, and dissipation phases respectively. The occurrence rates were 76.47, 100.00, and 91.67%, respectively. According to statistical analysis, there were no significant differences in the average abundances of *Z. nagae* between the three phases of bloom (Supplemental Table S4, Kruskal–Wallis, $p > 0.05$).

3.2.3. *Calanus sinicus*

According to the collected results, the total abundance of *C. sinicus* varied from 0.36 ind.·m^{-3} (station 5.20.3) to 81.25 ind.·m^{-3} (station 5.9-5) with an average of 6.83 ind.·m^{-3}. The occurrence rate was 58.93% (Figure 3C, Table 1). In the growth phase, the average abundance of *C. sinicus* was 18.91 ind.·m^{-3}, OR was 88.24%. In the maintenance and dissipation phases, the average abundances decreased rapidly and with the values of 2.02 ± 0.75 and 0.55 ± 0.22 ind.·m^{-3}, OR were less than 50%. According to statistical analysis, the average abundance in the growth phase was significantly higher than those in the maintenance and dissipation phases (Supplemental Table S4, Kruskal–Wallis, $p < 0.05$).

3.3. Zooplankton Community Structure

According to results of the 56 stations (Figure 4A), the abundance of zooplankton varied from 1.84 ind.·m^{-3} (station 5.10-2) to 833.00 ind.·m^{-3} (station 5.13-2) with an average of 75.62 ind.·m^{-3}. For the growth phase of *P. donghaiense* bloom, the abundance of zooplankton ranged from 1.84 ind.·m^{-3} to 274.47 ind.·m^{-3} (station 5.10-3), with an average of 113.00 ± 19.17 ind.·m^{-3}. For the maintenance phase, the abundance of zooplankton ranged from 5.00 ind.·m^{-3} (station 5.13-3) to 833.00 ind.·m^{-3}, with an average of 66.06 ± 30.50 ind.·m^{-3}. For the dissipation phase, the abundance of zooplankton ranged from 2.50 ind.·m^{-3} (station 5.19-1) to 404.44 ind.·m^{-3} (station 5.19-6), with an average of 44.20 ± 32.83 ind.·m^{-3}. The average abundance of zooplankton in the growth phase was significantly higher than that in the maintenance and dissipation phases (ANOVA, $p < 0.05$). In addition, a total of 42 species of zooplankton (including 10 species of larvae), belonging to six phyla (Cnidaria, Ctenophora, Arthropoda, Annelida, Chaetognatha, and Chordata), were identified during the study period (Supplemental Table S4). They comprised small jellyfishes, copepods, chaetognaths, tunicates, and planktonic larvae. Figure 4B shows the species number of zooplankton at each station. It varied from 2 (station 5.10-2) to 16 (station 5.9-2) with an average of 7. According to statistical analysis, the average species number in the growth phase was significantly larger than those in the maintenance and dissipation phases (ANOVA, $p < 0.05$).

Figure 5A shows the abundance of main zooplankton groups in different phases of *P. donghaiense* bloom. The average abundances of small jellyfishes were 58.85 ± 16.65 ind.·m^{-3} and 40.34 ± 25.71 ind.·m^{-3} in the growth and maintenance phases respectively. They were significantly higher than that in the dissipation phase (ANOVA, $p < 0.05$). The average copepods abundance was 18.97 ± 5.83 ind.·m^{-3} in the growth phase. It was significantly higher than that in the maintenance phase (2.09 ± 0.76 ind.·m^{-3}) and the dissipation phase (0.55 ± 0.22 ind.·m^{-3}) (Kruskal–Wallis, $p < 0.05$). The average chaetognaths abundance was 8.68 ± 3.74, 19.32 ± 5.48, and 6.49 ± 3.71 ind.·m^{-3} in the growth, maintenance, and dissipation phases respectively. Statistically, there was no significant differences (Kruskal–Wallis, $p > 0.05$). The average tunicates abundance was 12.50 ± 6.91, 2.21 ± 1.77, and 1.84 ± 1.65 ind.·m^{-3} in the growth, maintenance, and dissipation phases respectively. There were also no significant differences (Kruskal–Wallis, $p > 0.05$). The average planktonic larvae abundance was 13.60 ± 3.25, 1.95 ± 0.52, and 29.19 ± 26.46 ind.·m^{-3} in the growth, maintenance, and dissipation phases respectively. Statistically, the abundance in the maintenance phase was significantly lower than those in the growth and dissipation phases (Kruskal-Wallis, $p < 0.05$). Figure 5B shows the species number of main groups in the different phases. It was found that the species number of small jellyfishes was highest, with 14, 8, and 6 in the growth, maintenance, and dissipation phases respectively. The proportions of major zooplankton groups in the different phases of HAB were analyzed in depth (Figure 6). It was found that the proportions of small jellyfishes were 52.08, 61.07, and 13.88% in the growth, maintenance, and dissipation phases respectively. The proportions of chaetognaths were higher in the maintenance and dissipation phases than those in the growth phase. In contrast, the proportions of copepods and tunicates were higher in the growth phase than in the maintenance and dissipation phases. Surprisingly, the proportion of planktonic larvae was 66.04% in the dissipation phase, which shows a certain randomness. Nevertheless, further analysis showed that there was 320 ind.·m^{-3} copepoda larvae in the 5.19-6 station, which accounted for nearly 80% of the total abundance, while the abundance in most stations only ranged from 0.36 to 12.22 ind.·m^{-3}. Therefore, it is obvious that zooplankton community structure, which was jellyfishes- and copepods-dominated in the first instance, gradually changed to jellyfishes- and chaetognaths-dominated, and finally to copepod larvae- and chaetognaths-dominated during the different phases of *P. donghaiense* bloom.

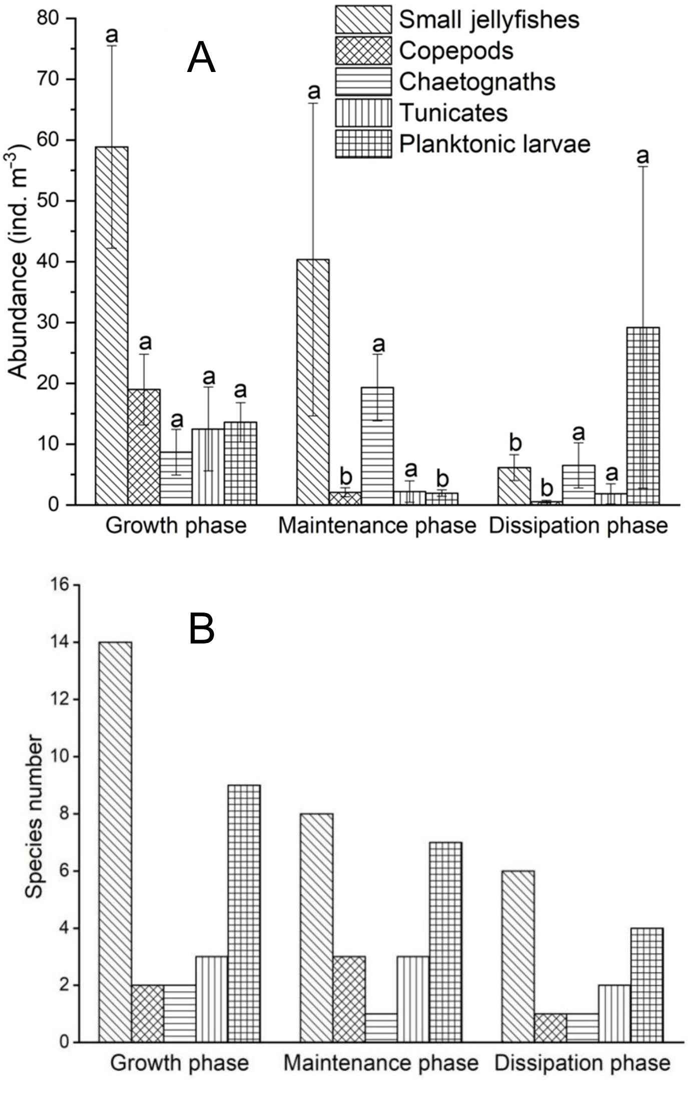

Figure 5. The abundance of zooplankton (total and main group, (**A**)) and changes of diversity (total number and main group, (**B**)) in different phases of *P. donghaiense* bloom. Data were presented as the mean values ± SE, with the different letters indicating significant ($p < 0.05$) differences among the different phases.

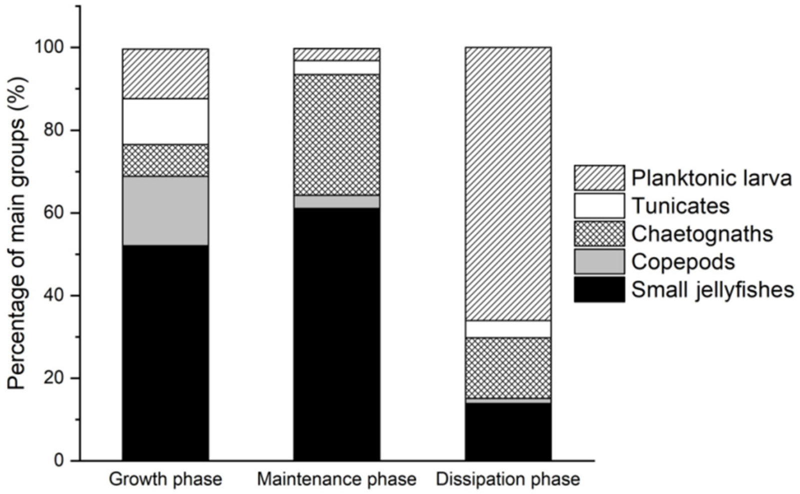

Figure 6. Percentages of major zooplankton groups (small jellyfishes, copepods, chaetognaths, tunicates, and planktonic larvae) in different phases of the *P. donghaiense* bloom.

The values of the Simpson index (*C*) at each sampling station varied from 0.21 to 0.85 with an average of 0.44; the Shannon index (H') varied from 0.52 to 2.71 with an average of 1.63; while the Pielou evenness index (J') varied from 0.17 to 0.95 with an average of 0.63 (Supplemental Table S5). It is noteworthy that the average values of the Simpson index (*C*) gradually changed from 0.44 to 0.45 and 0.43 during the growth, maintenance, and dissipation phases. No significant difference during the three phases was, however, found (Figure 7). The average values of the Shannon index (H') were 1.77, 1.55, and 1.62, while the Pielou evenness index values (J') were 0.56, 0.65, and 0.71 in the growth, maintenance, and dissipation phases respectively. Moreover, there was no significant difference in the three different phases of HAB (Figure 6), similar to the results of the Simpson index.

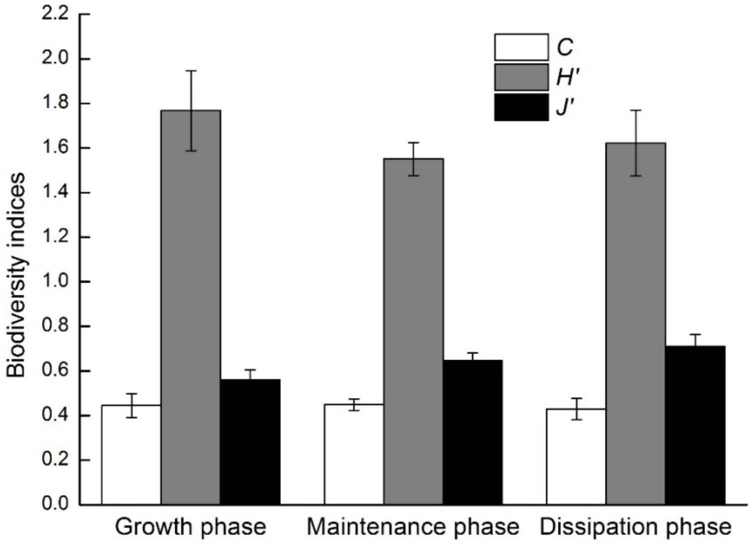

Figure 7. The indices of simplicity (*C*), diversity (H'), and evenness (J') in different phases of the *P. donghaiense* bloom; the data were presented as the mean values ± SE.

In addition, an MDS ordination of the 56 samples in the growth, maintenance, and dissipation phases of *P. donghaiense* bloom were plotted from Bray Curtis similarities on log-transformed abundances (Figure 8). The analyses indicated that the similarities of the zooplankton community showed a clear trend over the three phases, that most of the samples in the growth and maintenance phases are gathered together, and that the samples in the dissipation phase are slightly scattered.

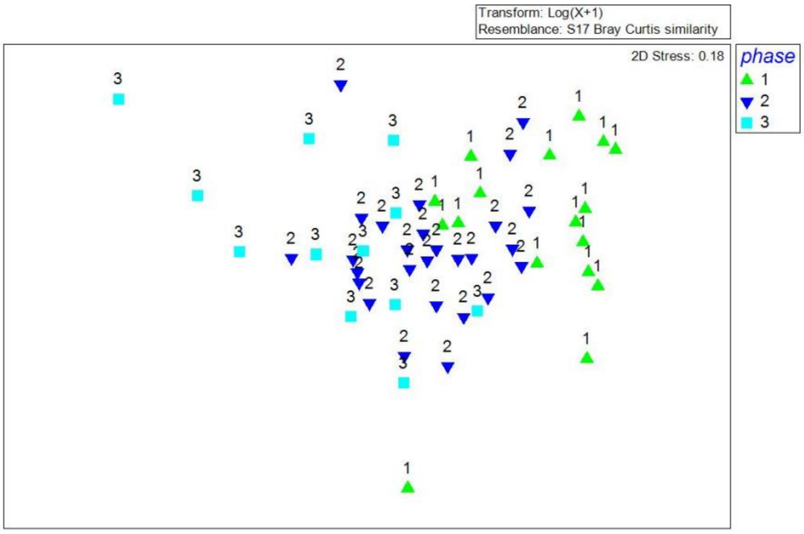

Figure 8. MDS ordination of 56 samples in the growth (1), maintenance (2), and dissipation (3) phases of *P. donghaiense* bloom using the Bray Curtis similarities on log-transformed abundance data.

3.4. Correlation between Abundance of Zooplankton and Environmental Factors

The abundances of zooplankton and environmental variables during the different phases positively or negatively correlated with environmental factors (Supplemental Table S6). In the growth phase, the abundances of total zooplankton, *M. atlantica*, and *C. sinicus* positively or negatively correlated with values of depth of sample, temperature, pH, salinity, dissolved oxygen, dissolved inorganic phosphorus, dissolved inorganic nitrogen, and the abundance of *P. donghaiense*, but the correlations between them were not significant ($p > 0.05$). However, for the other dominace species *Z. nagae*, there was a significant negative correlation between its abundance and temperature and pH ($p < 0.05$), but no significant positive or negative correlation with other environmental factors ($p > 0.05$). In the maintenance phase, the abundance of total zooplankton negatively correlated with the value of dissolved oxygen and the abundance of *P. donghaiense* ($p < 0.05$), the abundance of *Z. nagae* negatively correlated with the abundance of *P. donghaiense* ($p < 0.05$) as well, and for the other dominace species *M. atlantica*, and *C. sinicus*, there are no significant positive or negative correlations with other environmental factors ($p > 0.05$). In the dissipation phase, there are no significant positive or negative correlations between the abundances of zooplankton and environmental variables.

4. Discussion

The current study is the first attempt to study and compare the zooplankton community changes in the whole process of *P. donghaiense* bloom happened in ECS. The hypothesis that the different development phases of HAB would shift the zooplankton community structure is shown to be valid. Our results also reveal that (1) the average abundance of zooplankton decreased significantly with the development of this bloom and, (2) the dominant species progressively changed from '*M. atlantica* + *C. sinicus*' to '*Z. nagae* + *M. atlantica*'. Results suggest that harmful dinoflagellate bloom caused by *P. donghaiense* would produce detrimental effects on individual population number as well as the community composition of zooplankton. Relevant results fill the gap of ecological picture of *P. donghaiense* in ESC and relevant information would be important for formulating an ecological management plan and control and prevention strategies for HAB in China, as well as other countries in the world with similar environmental situations.

The *P. donghaiense*-dominated bloom observed in the southern coast of Zhejiang Province in May 2016 fulfilled the main criteria of a complete process of HAB, as described by Shen et al. [16]. Consequently, this massive, persistent, and multispecific bloom would undoubtedly affect the population dynamics of zooplankton, ecological community structure and food web. The potential influences to caught fishery and aquaculture should be further assessed with mechanism academically verified. Dominant species are often the key species limiting the stability of zooplankton community. In this study, the dominant species of zooplankton changed from *M. atlantica* to *C. sinicus*, then *Zonosagitta* larvae, *Z. nagae*, *Clytia* sp., *D. denticulatum*, *M. atlantica*, and *Z. nagae*, finally copepods larvae, *Z. nagae*, and *M. atlantica*. This represents community impacts of HAB in the growth, maintenance, and dissipation phase respectively (Table 1). The species *M. atlantica* and *Z. nagae* were found in the whole process of this bloom. *M. atlantica* was the first dominant species and the values of OR were 100.00% in the growth and maintenance phases, and *Z. nagae* was the second most dominant species and the values of OR were above 90.00% in the maintenance and dissipation phases (Table 1). This finding also can be explained by the fact that *P. donghaiense* bloom has no adverse effect on these two species and showed the decreases of the abundance in the dissipation phase due to the decease of food (*P. donghaiense*). Similar results were also observed by Lin et al. [13], indicating that there were no significant variations in the abundance of small jellyfishes and chaetognaths in nonbloom, peak-bloom, and decaying bloom areas. Interestingly, copepod larvae was the first dominant species (0.433) in the dissipation phase, its abundance (28.73 ind. m^{-3}) and OR (66.67%) being higher in this phase than in the growth (0.12 ind. m^{-3} and 17.65%) and maintenance phases (0.26 ind. m^{-3} and 18.52%). This indicated that the stress of *P. donghaiense* bloom on copepod larvae decreased significantly in the dissipation phase. Moreover, the changes of key zooplankton groups proportions (small jellyfishes, chaetognaths, and copepods) also showed that the zooplankton community structure changed from jellyfishes- and copepods-dominated to jellyfishes- and chaetognaths-dominated, and finally to copepod larvae- and chaetognaths-dominated during the whole *P. donghaiense* bloom. The changes in the growth and maintenance phases are in agreement with the findings of Lin et al. [13]. Generally, copepods are more sensitive to harmful dinoflagellate blooms, while small jellyfishes and chaetognaths are not [7,13,37].

In this study, the average abundance and species number of zooplankton in the growth phase was significantly higher than in the maintenance and dissipation phases (Figure 4; ANOVA, $p < 0.05$). Furthermore, the abundance and species number of main zooplankton groups showed the different changes in the different phases of *P. donghaiense* bloom (Figure 5), and the correlation between the abundance of zooplankton and *P. donghaiense* also showed that total zooplankton, *M. atlantica*, *C. sinicus*, and *Z. nagae* had a negative correlation between their abundance and *P. donghaiense* abundance (Supplemental Table S6). For example, the average small jellyfishes' abundance in the growth and maintenance phases was significantly higher than that in the dissipation phase (ANOVA, $p < 0.05$; Figure 5A), which may be caused by the shortage of food (phytoplankton such as *P. donghaiense*). Zheng et al. [38] indicated that jellyfish (the polyps and ephyrae of *Aurelia*) can feed on *P. donghaiense* and the ingestion rates of *Aurelia* increased with the increasing of microalgal cell densities. Sun et al. [39] used long-term monitoring data to evaluate changes in the abundance of small jellyfish between 1991 and 2009 in the Jiaozhou Bay, China, and reported that the abundance of small jellyfish was positively correlated with the density of dinoflagellates. In another field investigation of *P. donghaiense* bloom in the ECS, Lin et al. [13] divided the research area into three parts: nonbloom areas (the cell density of *P. donghaiense* lower than 10^7 cells·m^{-3}), peak-bloom areas (the cell density of *P. donghaiense* more than 10^9 cells·m^{-3}), and decaying bloom areas (the cell density of *P. donghaiense* more than 10^7 cells·m^{-3}). They found that the abundance of small jellyfishes on 25 and 26 April were lower than those in May, because most of the stations in this period are in nonbloom areas where the cell density of *P. donghaiense* was low. For chaetognaths, there were no significant variations in abundance in the growth, maintenance, and dissipation phases (Kruskal–Wallis, $p > 0.05$; Figure 5A), and this may be explained considering that chaetognaths feed on a wide range of species, including small jellyfish, copepods, cladocera, and phytoplankton [40–42]. Similar results have been reported recently by Lin et al. [13]—that there was no significant variation in the abundance of chaetognaths during over the course of the study. Therefore, to a certain extent, the *P. donghaiense* bloom had little toxic effect (allelopathic effect) on these colloidal zooplanktons (small jellyfishes and chaetognaths). However, the average copepods abundance in the growth phase was significantly higher than that in the maintenance phase and dissipation phase (Figure 5A; Kruskal–Wallis, $p < 0.05$), and a similar phenomenon occurred in another *P. donghaiense* bloom recently—that the abundance of copepods was clearly lower in peak-bloom and decaying bloom areas (Lin et al. [13]). There were multiple reasons proposed for this trend, including algal toxins or other substances [7,10,43,44], intact cells [9] and nutrient deficiencies [6,13,43,45]. *P. donghaiense* is considered to be a nontoxic dinoflagellate and does not release known phytotoxins [23], but there are some evidences that copepods exhibited significantly decreased viability or fecundity both in the laboratory and field studies (Lin et al. [5,13]), which may be in part due to the fact that *P. donghaiense* can release some unknown phtotoxions when the cell density is higher. Furthermore, nutritional insufficiency occurs when the prey lacks an essential element for growth in the grazer (e.g., copepods). For instance, as another *Prorocentrum* species, it was concluded that *P. minimum* was nutritionally insufficient, but not toxic to copepod *Acartia tonsa* [45]. For *P. donghaiense*, some essential fatty acids, such as arachidonic acid (20:4(n−6), ARA), eicosatetraenoic fatty acid (20:5(n−3), EPA) and amino acids (phenylalanine, lysine, and histidine) are low [24]. Lin et al. [13] also reported that the *C. sinicus* collected from bloom stations contained low quantities of ARA, EPA, 20:5(n−3)/22:6(n−3) (EPA/DHA), polyunsaturated fatty acids (PUFA), monounsaturated fatty acids (MUFA), and total saturated fatty acids. In short, the effects of HABs on zooplankton are often comprehensive, and further study is required to elucidate the roles of mechanisms related to algal toxins, nutrient deficiencies, and other factors. In general, the development speed of copepods is closely related to water temperature, and the fertilized eggs of copepods develop to hatch larvae in only 2–3 days under the environment of 22–23 °C [46]. Therefore, the whole *P. donghaiense* bloom process may affect the reproduction of copepods for 4–5 generations through factors such as algal toxins and nutrient deficiencies in 12 sampling days. Additionally, there is an abnormal phenomenon that the average number of planktonic larvae is higher in the dissipation phase (Figure 5A), which may be due to random sampling, and only one station (5.19-6) collected a high abundance of copepoda larvae, at 320 ind. m^{-3} (Figure 4A). Furthermore, only vertical tow plankton net type-I was used to collect zooplankton in this study, which could cause marked underestimation of the abundance of smaller zooplankton, especially larvae. For example, recent data have demonstrated that the average abundance of zooplankton larvae collected by a vertical tow plankton net type-I is 8.85 ind.$\cdot m^{-3}$, while the average abundance of zooplankton larvae collected by a type-II net is as high as 9585.15 ind.$\cdot m^{-3}$ on the coast of Shandong Province, China on November 2021 (unpublished data). In this regards, further studies about the zooplankton community should use more types of plankton nets to obtain more comprehensive data.

The linkage between biodiversity and community structure is a crucial issue in ecology, and some studies of plankton communities' stability proved to be related with species diversity [12,47–49]. During this *P. donghaiense* bloom period, the Simpson index (C) of total phytoplankton was the higher—significantly more so in the maintenance phase, than that in other phases—while the Shannon index (H') and Pielou evenness index (J') showed the opposite results (Shen et al. [16]). However, there were no significant differences of the biodiversity of zooplankton, such as in the Simpson index (C), Shannon index (H'), and Pielou evenness index (J') in the growth, maintenance, and dissipation phases (Figure 7). This may be explained considering that this kind of bloom only adversely affects its more sensitive groups (copepods will be poisoned to death or forced to leave the bloom area), and has little effect on some colloidal zooplankton (small jellyfishes and chaetognaths). In the same area, *Akashiwo sanguinea*-dominated algal blooms occurred in mid-June 2016, where the number of copepod species and their abundances in the bloom area were significantly less than those in the nonbloom area, which may be in part due to the fact that the dominant species, such as *A. sanguinea* and *Gonyaulax spinifera*, can secrete

Ichthyotoxins and Yessotoxins, and similar results about biodiversity also showed that there were no significant differences in the biodiversity indices of zooplankton between the bloom and nonbloom areas [50]. However, it is regrettable that the current research on dinoflagellate blooms is often in the form of cross-sectional voyage surveys (Lin et al. [13]) or a longer interval sampling method [12,51], and it is difficult to completely monitor the occurrence and disappearance of a bloom. Therefore, further research is needed to verify the possible impacts of the whole HABs process, including those interactions of diatoms and dinoflagellates on the growth conditions of zooplankton as well as the healthy development of marine ecosystems. The current study results form the basis of future research.

Finally, but not least, on the basis of present research we have developed a summary pattern to describe the effect of different stages of *P. donghaiense* bloom on the community structure of zooplankton in the ECS (Figure 9). In the growth phase, when 38 zooplankton species were identified with the abundances of small jellyfishes (*M. atlantica* and *Clytia* sp.), copepods (*C. sinicus*), chaetognaths (*Z. nagae*), tunicates (*D. denticulatum*), and planktonic larvae. Our data show that *P. donghaiense* bloom at this phase has a 'promoting effect' on some zooplankton species, such as *M. atlantica*, due to an increase in the food availability. The results also show that *P. donghaiense* is also toxic to some crustaceans, such as *C. sinicus*. It is probably because the allelopathic effect of *P. donghaiense* bloom is not enough to generate an adverse effect on the growth of these crustaceans. In the maintenance phase, however, the number of total zooplankton species dropped to 24, showing that only small jellyfishes and chaetognaths could comfortably survive. Relevant information could be relatively useful to fishermen. In the dissipation phase, while the abundance of *P. donghaiense* is very low (even lower than the growth phase, as shown in Figure 2), the influence of *P. donghaiense* and other microalgae may still have a lag effect on zooplankton, except for *Z. nagae*. At this stage, moreover, the abundance of other zooplankton groups is still at a low level, with results showing that only 14 species could be found. Our results, which represented the different responses of zooplankton population and ecological community in relation to various phases of HAB caused by *P. donghaiense*, coincided with the results of Lin et al. [13]. Hence, our results are likely to be applied to other waters (red tide high-incidence areas in China, such as the Yangtze River Estuary, Zhoushan Islands, Fujian Province coast, etc.) with high frequency and magnitude of HAB occurrence. Nonetheless, as advised by Tester and Steidinger (1997), our research provides very useful data for researchers who would like to understand more deeply the ecological succession process in marine environment with particular reference to the gradual community changes and fishery impacts in different phases (initiation, growth, maintenance, and dissipation phases) of an HAB.

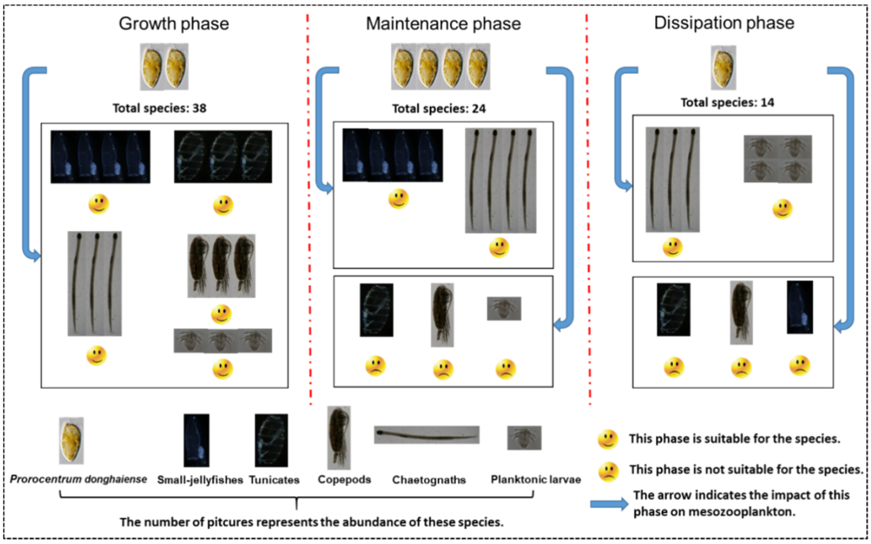

Figure 9. Responses of zooplankton community structure in relation to different phases of *P. donghaiense* bloom.

5. Conclusions

The present study demonstrated that zooplankton population and ecological community change gradually during the growth, maintenance, and dissipation phases of the *P. donghaiense* bloom process. The zooplankton community structure are proven to be significantly changed with jellyfishes and copepods dominating in the growth phase, jellyfishes and chaetognaths dominating in the maintenance phase and, copepod larvae and chaetognaths dominating in the final phase during the *P. donghaiense* bloom. In view of the adverse impact on the marine ecosystem caused by the large-scale outbreak of *P. donghaiense* bloom in the ECS, HABs will have a great negative impact on caught fisheries because zooplankton is an important bait for certain economic fishes.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jmse10020291/s1, Table S1: Sampling time and locations correspondent to dinoflagellate HAB; Table S2: Average cell abundance (CA, cells·m^{-3}) and dominance (Y) of the dominant phytoplankton species in the process of *P. donghaiense* bloom; Table S3: Environmental variables of depth of sample (DS), temperature (T), pH, salinity (S), dissolved oxygen (DO), dissolved inorganic phosphorus (DIP), and dissolved inorganic nitrogen (DIN) at each sampling station; Table S4: Average abundance (A, ind. m^{-3}), and occurrence ratio (OR, %) of species in the different phases, and the different letters in the *M. atlantica*, *C. sinicus*, and *S. nagae* indicate significant ($p < 0.05$) differences among the different phases; Table S5: Results of indices of simplicity (C), diversity (H'), and evenness (J') at each sampling station; Table S6: Correlation between abundance of zooplankton and environmental factors.

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