

RESEARCH ARTICLE

The Link Between Marine Thermal Discharges and *Nemopilema nomurai* Blooms Around Nuclear Power Plants

Jiawei Wu¹, Jie Kong¹, Edward A. Laws², Xin Liu^{1,3*}, Changyun Wang¹, Jixin Chen¹, Mianrun Chen³, Qingzhen Yao⁴, Yantao Wang⁵, Yu Zhen⁴, Chaolun Li⁵, and Bangqin Huang^{1,3}

¹State Key Laboratory of Marine Environmental Science, College of the Environment and Ecology, Xiamen University, Xiamen, China. ²Department of Environmental Sciences, College of the Coast and Environment, Louisiana State University, Baton Rouge, LA, USA. ³Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), Zhuhai, China. ⁴College of Chemistry and Chemical Engineering, Ocean University of China, Qingdao, China. ⁵Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China.

*Address correspondence to: liuxin1983@xmu.edu.cn

Recent research has shown that jellyfish blooms occur more frequently near nuclear power plants (NPPs), and a relationship between thermal discharges from the NPPs and the blooms has been hypothesized. There is, however, no direct evidence that links the thermal discharges with jellyfish blooms. In this study, we conducted 3 cruises (pre-bloom, bloom, and post-bloom) during July to September 2017 in the area surrounding the largest NPP in northern China. The water temperature near the cooling water outfall rose by 2 °C. Although we found no significant impact on phytoplankton abundance or community composition near the outfall, a broader analysis of monitoring data revealed significant correlations between temperature and the abundance of *Nemopilema nomurai*, cyanobacteria, and haptophytes. Temperature increases may have a stimulatory effect on key stages in the life history of jellyfish, and the abundance of jellyfish prey may be the factor that triggers jellyfish blooms. Blooms of jellyfish were accompanied by a decline of diatom dominance and an increase of the concentrations of small phytoplankton such as cyanobacteria and haptophytes. This study revealed for the first time a significant positive correlation ($R^2 = 0.39$, $P < 0.001$) between jellyfish abundance and concentrations of dissolved organic nutrients. This correlation suggested that the blooms of jellyfish resulted in the release of large amounts of organic nutrients. The results provided a comprehensive perspective and suggested a need for further study of the dynamics of planktonic ecosystems to link thermal discharges and jellyfish blooms.

Introduction

Human beings are currently faced with an increasing global demand for energy, the extremely severe challenges of climate change, and the urgent need for ecological and environmental protection. Although there are safety concerns about the release of radioisotopes during the nuclear fuel cycle, there has nevertheless been a desire to expand the nuclear power industry as a clean, safe, efficient, and low-carbon alternative to fossil fuel power plants [1]. In China, the Medium- and Long-Term Development Plan on Nuclear Power (2005–2020) and the “13th Five-Year” plan on national energy have both put forward the idea of active, continuous promotion of the development of nuclear power [2]. By 2020, more than 30 nuclear power plants (NPPs) had been put into operation in coastal provinces with high population densities and high levels of industrialization. The capacity of NPPs in operation in China

is expected to reach 40 GW [2]. There is now an urgent need to assess the impact on the marine environment around NPPs caused by thermal discharges from the power plants [3,4].

NPPs are generally built in coastal areas to meet the energy needs of coastal, high-intensity human activities and because coastal water is a convenient source of cooling water. The wisdom of siting NPPs in the coastal zone is questioned, however, by the following 2 considerations. First, when electricity is produced by boiling water, a large quantity of waste heat is discharged to the cooling water, and this thermal effluent increases the temperature of the receiving water and changes other physical and chemical properties in the discharge area [3–6]. Many studies have reported the impact of thermal discharges on the structure of biological communities and ecosystem functions in thermal discharge areas [1,7]. It has been reported that thermal pollution caused by discharges to cooling water has substantially impacted the structures of plankton, benthos, and fish communities [4,6].

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Among the many organisms sensitive to temperature change, the response of phytoplankton is rapid and easily documented [4]. Second, although the ocean is a convenient source of the cooling water that power plants need, the ocean can also pose a threat to the safe operation of NPPs. The damage to the Fukushima Daiichi NPP caused by a tsunami in 2011 and the associated release of radioactivity [8] are undoubtedly the best-known examples of the problems associated with siting NPPs adjacent to the ocean. In addition, blooms of jellyfish have less dramatically but much more frequently interfered with the operation of NPPs in recent years by blocking cooling water intakes [3].

A previous study has indicated that jellyfish blooms (mainly *Nemopilema nomurai*) usually occur in the Yellow Sea during the warm season [9]. Studies have suggested a possible link between temperature changes and jellyfish blooms [10]. However, the unequivocal identification of cause-and-effect relationships in natural ecosystems is very challenging. The thermal discharges from power plants and the jellyfish blooms that occur around them provide an excellent opportunity to determine whether there might be a cause-and-effect relationship between them. Temperature is important to the life cycle of jellyfish [11–14]. Somatic growth, podocyst formation, and excystment increase with increasing temperature and are dramatically affected by food supply when temperatures are warm [9]. Small changes in ambient temperature can have a significant impact on the mortality of jellyfish at some stages in their life history and thus on the magnitude of jellyfish blooms [11,13,14]. The effects of temperature thus involve the direct effect of temperature on the growth rates of jellyfish and the indirect influence of temperature on water movement and the supply of food (e.g., plankton) for the jellyfish. Sun et al. [9] have suggested that high temperatures (15 to 27.5 °C) and abundant plankton biomass should result in high productivity of polyps and contribute significantly to subsequent blooms of *N. nomurai*.

In fact, phytoplankton, zooplankton, and jellyfish form a well-known food chain. By feeding directly on zooplankton and large phytoplankton that they capture with their tentacles, jellyfish impacts phytoplankton biomass and community structure [15,16]. This feeding may also produce a trophic cascade effect. By feeding on zooplankton, jellyfish may indirectly regulate the abundance of small phytoplankton [15,16]. However, an increase of jellyfish biomass and feeding activity leads to an increase in the supply of autochthonous nutrients released into the water by the jellyfish and thereby affects phytoplankton biomass and community composition through bottom-up control [17]. The rate of nutrient release by jellyfish in the field has been estimated on the basis of the results of laboratory culture experiments, but direct evidence from field observations has been lacking [18]. The effects of thermal discharges and jellyfish blooms on phytoplankton communities are therefore unclear.

In this study, we selected 29 observation stations in a small area around the Hongyanhe NPP (HNPP; 6.7-GW capacity) in Liaoning, China. The latitude of this power plant is the highest of any NPP in China. The area is characterized by a temperate monsoon climate, and the average ambient air temperature is 11 °C. The water temperature in the study area ranges between 12 and 14 °C. The impact on the environment of the thermal effluent discharged by the HNPP may thus be more apparent than it would be at lower latitudes. The HNPP was the first NPP, and it is currently the largest energy project in the region. There are 4 units in operation, each with a capacity of 1061 MW. Two more similar units are under construction. The water intake of

the NPP is located on the eastern side of the Bohai Sea in Liaodong Bay, which is a semi-enclosed embayment. The Bohai Rim is 1 of the 3 major economic belts in China, and it is characterized by a high population density and intensive human activities. The waters around Liaodong Bay are more seriously impacted by human activities than the open ocean [19]. In recent years, jellyfish blooms and red tides that have occurred in this region have been a major problem for NPPs [19,20].

To determine what relationship might exist between the thermal discharges from the power plant and these blooms, we carried out 3 field cruises during July to September 2017 (pre-jellyfish bloom, jellyfish bloom, and post-jellyfish bloom). We posed the following scientific questions: (a) What are the impacts of the thermal discharges from the NPP on the temperature regime and biological community in Liaodong Bay, (b) are there any relationships between the jellyfish blooms and phytoplankton blooms, and (c) is there a plausible cause-and-effect relationship between the thermal discharges from the HNPP and the jellyfish blooms?

Materials and Methods

Study area and sampling design

The study area was the part of Liaodong Bay in the vicinity of the HNPP (Fig. 1). Information about the distribution of the world's NPPs was obtained from the International Atomic Energy Agency (IAEA) Power Reactor Information System (PRIS) database, provided by the IAEA. The HNPP is located in northeastern China on the Liaodong Peninsula, which is connected to mainland China to the northeast and is otherwise surrounded by marine waters. Four nuclear power units with pressurized water reactors (CPR1000) were built during phase I of the construction, and 2 similar units were constructed during phase II. The heat exchangers in the units use a once-through cooling system in which seawater provides the cooling.

The bottom shoals abruptly near the plant, and the isobaths lie roughly parallel to the coastline. The area of Liaodong Bay near the plant experiences an irregular semidiurnal tide. The mean tidal range over the years has been 1.33 m, the mean spring tide range has been 1.53 m, and the mean neap tide range has been 1.08 m. Tidal movement has consisted mainly of reversing currents. The currents during the rising tide and ebb tide move toward the northeast and southwest, respectively. There is good dispersion in the nearshore area.

On the basis of the terrain characteristics, we set up 29 sampling sites (A1 to A4, B1 to B4, C1 to C4, D1 to D4, E1 to E5, F1 to F4, and G1 to G4) along 7 onshore–offshore transects in the nearshore area surrounding the HNPP (Fig. 1B). Among the sites, D4 was closest to the outfall from the NPP, and a significant elevation of the water temperature was apparent at D4 (Fig. 2). Results of previous studies [21] have shown that jellyfish blooms often occur near the HNPP in the summer (July to August). We therefore conducted 3 cruises to the region in July, August, and September of 2017.

Sampling

An acoustic doppler current profiler (ROWE Technologies, USA) was used to characterize the hydrological environment around the HNPP. The longitude and latitude of sampling stations were measured with a handheld global positioning system device. Seawater temperature and salinity were measured with

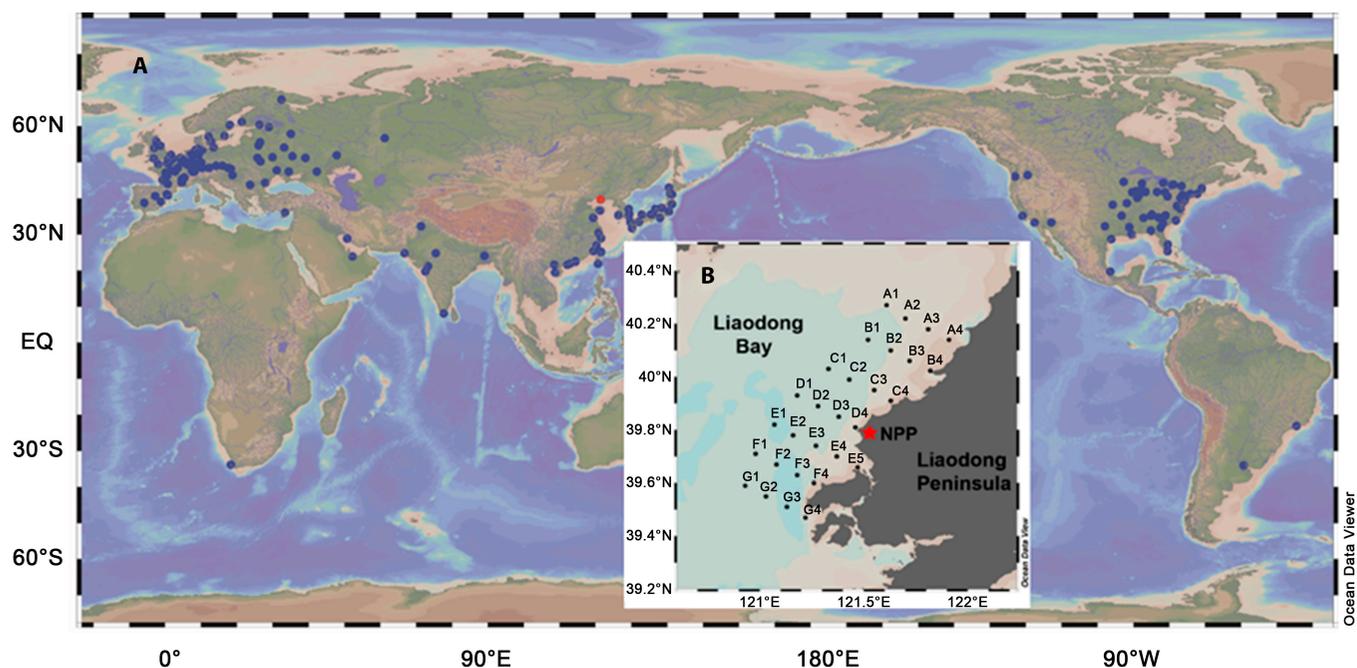


Fig. 1. Study sea area and sampling station. Dots on the world map show existing or under construction nuclear power plants (NPPs), and the red dot (A) shows the location of this study. The red star (B) represents the location of Hongyanhe NPP and black dots (B) show the sampling stations all around.

a RBR420 conductivity–temperature–depth instrument (RBR, Canada).

Duplicate seawater samples from each station were filtered through an acid-washed, cellulose acetate membrane (0.45- μm pore size) and were stored in 2 acid-washed, 100-ml polyethylene bottles: 1 bottle was kept at 4 °C for analysis of silicate concentration; the other was kept at –20 °C for analysis of the concentrations of other nutrients. The temperature, salinity, and nutrient concentrations in July and August have been published previously [22]. Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_3^- -N, NO_2^- -N, and NH_4^+ -N. All sampling and analytical methods followed the Chinese national seawater analysis protocols. The dissolved nutrient concentrations in the seawater samples were determined using a QuAAtro automatic nutrient analyzer (produced by Bran+Lubbe, Germany). The detection limits of each nutrient were 0.02, 0.03, 0.02, and 0.02 $\mu\text{mol/l}$ for NO_3^- -N, NH_4^+ -N, NO_2^- -N, and PO_4^{3-} -P, respectively [23]. The boric acid–persulfate oxidation method was used to measure the total dissolved nitrogen (DTN) and the total dissolved phosphorus (DTP). DTN was calculated as the sum of DIN and dissolved organic nitrogen (DON). DTP was calculated as the sum of PO_4^{3-} -P and dissolved organic phosphorus (DOP) [24]. For analysis of chlorophyll *a* (Chl *a*) concentration, 200 to 400 ml of seawater was filtered onto 25-mm-diameter GF/F filters. Chl *a* was extracted with acetone and determined using a Turner Trilogy fluorometer [25]. For measurement of other pigment concentrations, 400 to 800 ml of seawater was filtered onto 25-mm-diameter GF/F filters. Pigments were extracted with N, N-dimethylformamide and measured by high-performance liquid chromatography following the procedures of [26].

Sampling of phytoplankton was carried out in accordance with the Code for Marine Survey. The survey was carried out with a shallow-water II plankton trawl. The trawl was pulled vertically from the bottom to the surface. The samples were fixed with Lugol's solution and stored in the laboratory. To

identify diatom species, a 0.5-l water sample was collected and mixed with Lugol's iodine solution for observation with a microscope. Phytoplankton cells were concentrated with 100-ml settlement columns for 24 h. An inverted fluorescence microscope (Leica DMIRB, LYCRA, Germany) was then used to identify and count cells according to the methodology described in [27]. The small, juvenile, and adult *N. nomurai* medusa samples were collected with the drift nets of different mesh sizes [28]. According to the abundance and life history of *N. nomurai*, the drift net of the mouth area in June that was 40 m \times 5 m (mesh size: 0.2 cm) was used. While in July and September, the drift net of the mouth area that was 60 m \times 8 m (mesh size: 5 cm) was used. The drift net was placed across the current flow with a system of floats and sinkers, towing for 0.5 h. The amount of the medusae was counted, and their bell diameters were measured after collection. The abundance of *N. nomurai* medusa was calculated as follows:

$$A = N / \text{net} \quad (1)$$

where *A* is the medusa abundance (individual (ind.) net⁻¹), *N* is the total number of medusae, and net is the number of nets that was used to sample the medusae.

Data analysis

The distribution maps of temperature, salinity, Chl *a* concentration, and jellyfish abundance were made with Ocean Data View 4.7.8 [29]. The mean values of parameters including jellyfish abundance (*N. nomurai*; ind. net⁻¹), temperature (°C), salinity, and concentrations of dissolved reactive phosphorus (DRP; μM), NH_4^+ -N (μM), NO_3^- -N (μM), DOP (μM), DON (μM), and Chl *a* ($\mu\text{g l}^{-1}$) were compared by analysis of variance (ANOVA) followed by Tukey HSD (honestly significantly different) test.

A redundancy analysis (representational difference analysis (RDA)) and Spearman correlation analysis were carried out via the “Vegan” [30], “Psych” [31], and “Minerva” [32] packages in R 3.6.3 software [33] to identify relationships among parameters including latitude, longitude, water depth, and surface values of temperature, salinity, DRP, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, DOP, DON, Chl *a* concentration, and jellyfish abundance (*N. nomurai*). Hellinger transformation of phytoplankton groups, construction

of principal coordinates of neighbor matrices (PCNM variables) by latitude and longitude, and standardization of environmental factors were carried out before the RDA. The function ordistep in vegan was used to perform forward model selection with the permutation test for RDA.

The corr.test() in the ‘Psych’ package was used to calculate Spearman correlation coefficients among variables, and the *P* values were corrected with the false discovery rate (FDR)

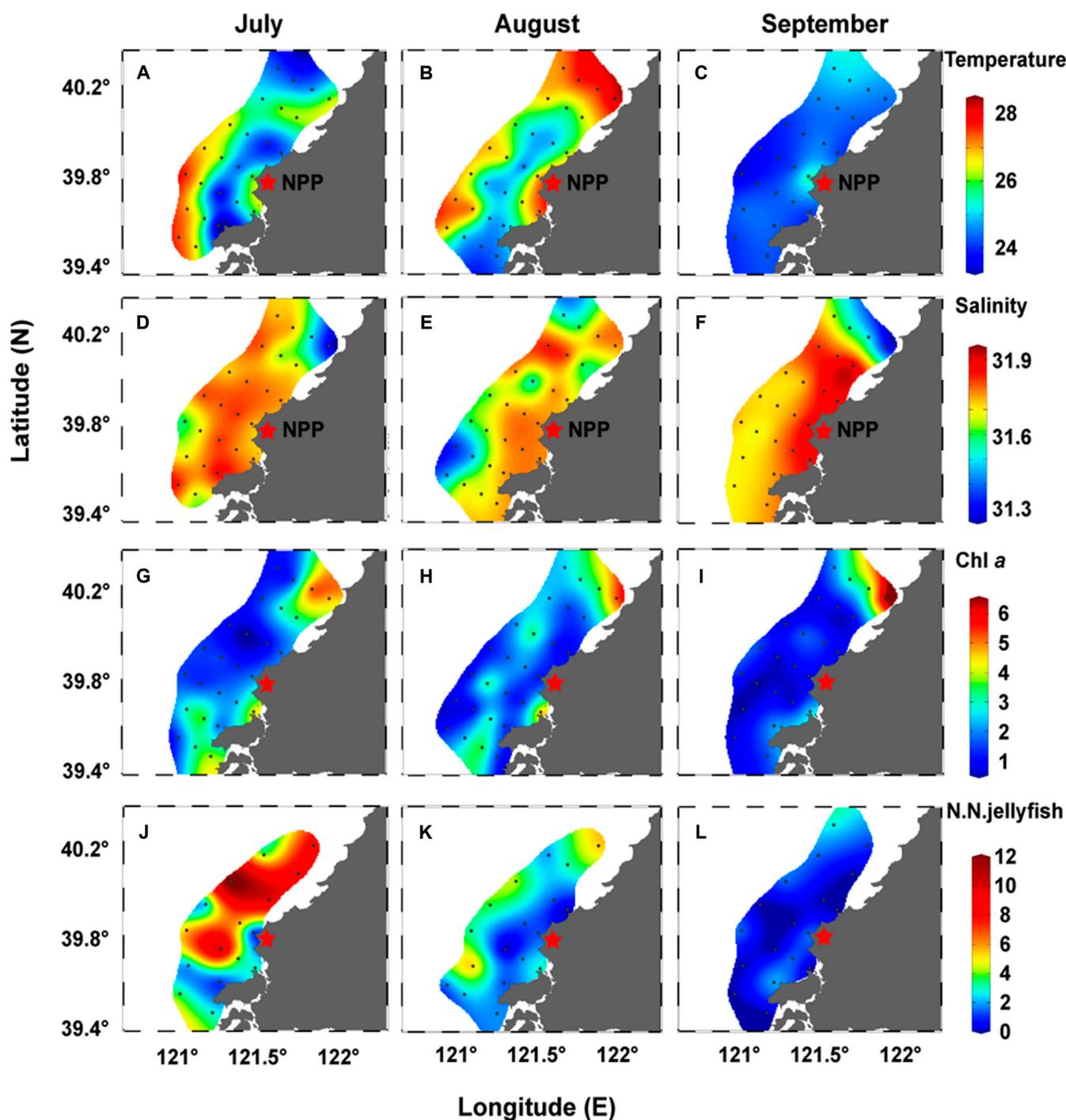


Fig. 2. Surface distribution characteristics of water temperature (A to C) ($^{\circ}\text{C}$), salinity (D to F), chlorophyll *a* concentration (G to I) ($\mu\text{g l}^{-1}$), and jellyfish abundances (J to L) (*N. nomurai* (N.N.); ind. net $^{-1}$) during the cruises in July, August, and September 2017, respectively. The abundance of jellyfish is square root transformed.

method. Maximal information-based nonparametric exploration (Minerva) analysis was applied using the 'Minerva' package (1,000 iterations, P value FDR correction) to calculate the maximal information coefficient (MIC) and P values. Nonsignificant Spearman correlations with significant P values in the Minerva analysis were defined as nonlinear correlations. 'Gephi' [34] was used to visualize significant associations. In RDA, the Hellinger transformation of phytoplankton groups, construction of PCNM variables by latitude and longitude, standardization of environmental factors (z -score transformation), and stepwise variable selection were performed [35]. The phytoplankton community composition was the response variable, and environmental factors were the explanatory variables.

Results

Variations of environmental parameters

Differences of the temperature and salinity among the nearshore stations around the HNPP were caused mainly by regional circulation and tides (Fig. 2A to F). The average temperature in July was 25.0 °C, and the maximum temperature was 27.6 °C. The average temperature in August was 26.1 °C, which was the highest among the 3 months, and the maximum was 28.2 °C. The average surface seawater temperature was significantly lower in September than in July ($P < 0.001$) and August ($P < 0.001$; Fig. 3A). The temperature was higher at station D4 (nearest the outfall of the HNPP) than at any of the surrounding stations during the 3 months (Fig. 2A to C). Although the area affected by the outfall was not large, the maximum temperature difference between D4 and surrounding stations was 2 °C.

The average salinities during the 3 months were 31.75, 31.67, and 31.79, respectively, and they were not significantly different (Fig. 3B). There was also no significant difference between the salinity at station D4 and the surrounding stations. The average concentrations of Chl *a* during July, August, and September were 2.37, 2.14, and 1.53 µg/l, respectively (Fig. 3H). The average Chl *a* concentration at the surface was significantly lower in September than in July ($P < 0.05$) and August ($P < 0.01$), but there was no significant difference between the Chl *a* concentration at station D4 and the surrounding stations during the 3 months.

Jellyfish and nutrients

As expected, we found a significantly higher abundance of jellyfish during the July cruise, when the average abundance was 41.9 ind. net⁻¹ (Figs. 2J and 3I). The maximum abundance of 170 ind. net⁻¹ was observed at station C1, northeast of the HNPP. The average abundance of jellyfish was significantly lower in August than in July, and the abundance was lowest in September (Figs. 2K and L and 3I). The concentrations of NH₄-N and DON were also significantly higher in July than in August, and they were significantly higher in August than in September (Fig. 3D and G). The results for DOP were consistent with the DON results, although the decline from July to August was not significant (Fig. 3F). The concentrations of DRP and NO₃⁻-N did not differ significantly among the 3 months, but they showed a weak downward trend from July to September (Fig. 3C and E).

To test our hypothesis, we performed statistical tests to determine whether there was a relationship between jellyfish abundance and nutrient concentrations. The results showed that there was a significant positive correlation between jellyfish abundance and DON and DOP concentrations in the surface seawater of

the study area in July, August, and September 2017 (Fig. 4). For DON, $R^2 = 0.39$ ($P < 0.001$), and for DOP, $R^2 = 0.12$ ($P = 0.008$).

Phytoplankton and jellyfish

The phytoplankton in the study area was mainly diatoms, cyanobacteria, cryptophytes, and dinoflagellates (Fig. 5). The community structure was similar in July and August, when it was dominated by diatoms, cyanobacteria, and cryptophytes. The dominance of diatoms was significantly higher in September than in July and August (Fig. 5C). These results clearly showed that there were temporal changes to the phytoplankton community from summer to early autumn.

A comparison of the spatiotemporal changes of jellyfish abundance and phytoplankton community structure revealed that there were marked differences of phytoplankton community structure in July at C1 and B3, where jellyfish blooms occurred (Fig. 5A). The dominant diatoms almost disappeared and were replaced by dinoflagellates, cyanobacteria, and haptophytes. However, this pattern was not observed at other sites of high jellyfish abundance (stations C3 and E3). Phytoplankton abundance and community composition seemed to be substantially affected by factors in addition to jellyfish abundance.

To identify those additional factors, we examined the Spearman correlation coefficients between surface seawater parameters in the study area and the abundances of both jellyfish and phytoplankton (Fig. 6). In Fig. 6, only significant correlations are marked. Red indicates a positive correlation, and blue indicates a negative correlation. The darker the color, the stronger the correlation. The results of the analysis again confirmed the positive correlations between jellyfish abundance and concentrations of NH₄⁺-N, DOP, and DON. We also found that jellyfish abundance was significantly and positively correlated with temperature and the abundances of dinoflagellates, haptophytes, and cyanobacteria. However, jellyfish abundance was significantly and negatively correlated with diatom abundance. The abundance of diatoms was significantly and negatively correlated with temperature, NH₄-N, DOP, and DON, whereas the abundance of dinoflagellates was significantly and negatively correlated with NO₃-N.

Spearman correlation and RDA results

To help explain these complex relationships, we performed a network analysis of the Spearman correlations among all surface water parameters in the study area (Fig. 6). We used the 'Minerva' package for the Minerva analysis (1,000 iterations, P value corrected by FDR method) and obtained MIC and P values. Nonsignificant Spearman correlations but significant P values in Minerva analysis were defined as nonlinear correlations. Temperature and dissolved organic nutrients were significantly and positively correlated with jellyfish abundance, whereas the correlations with phytoplankton varied among classes of phytoplankton. These results were consistent with the left panel of Fig. 6, which shows that jellyfish were significantly and positively correlated with small phytoplankton (cyanobacteria and haptophytes), significantly and negatively correlated with diatoms, but related to dinoflagellates in a nonlinear manner.

We applied RDA to identify the mechanisms responsible for the spatiotemporal distribution of the phytoplankton community. Phytoplankton community composition was taken as the response variable and environmental factors as the explanatory variables. Longitude and latitude were used to construct the

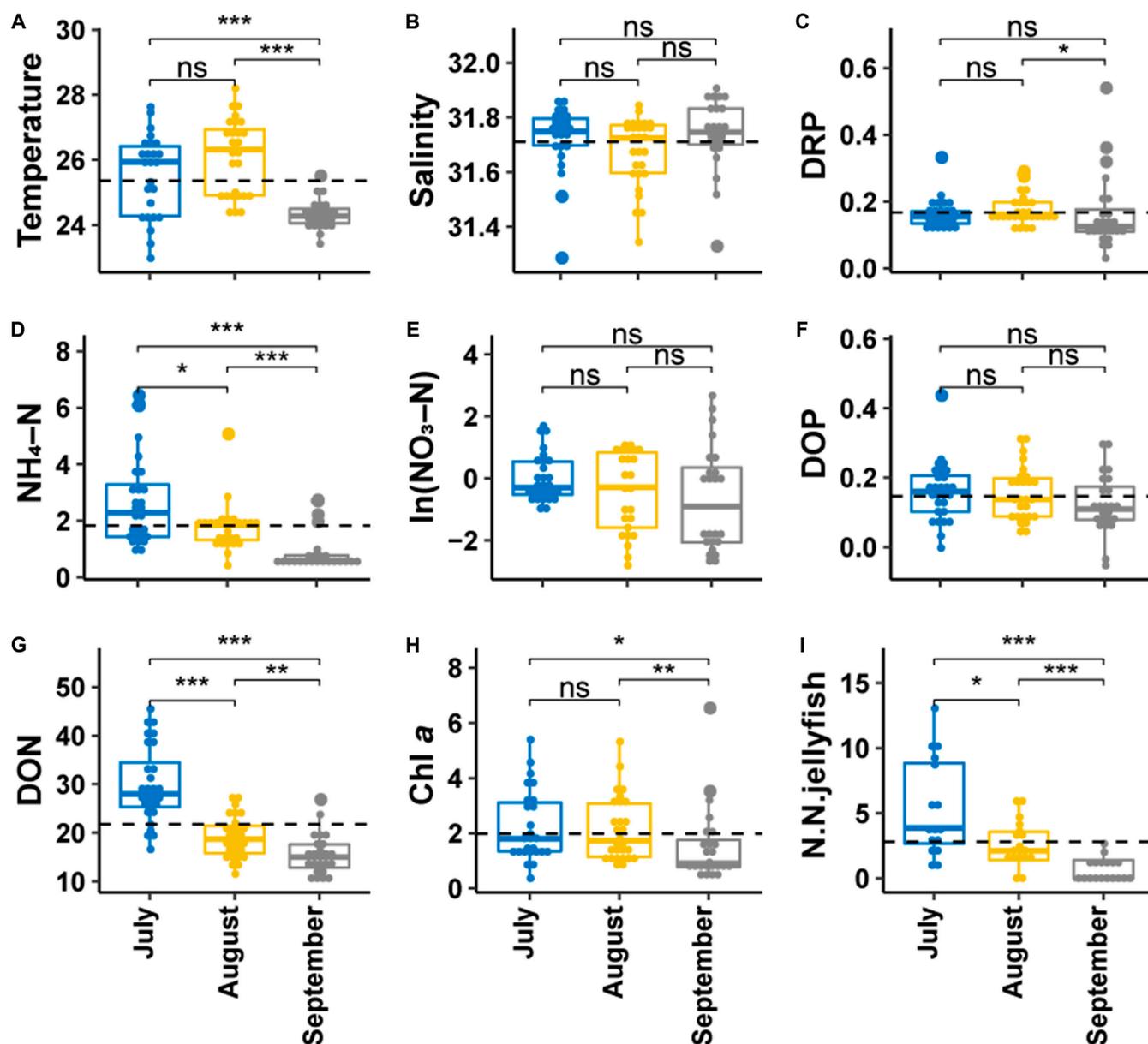


Fig. 3. The mean comparison and difference analysis of surface environmental factors during the cruises in July, August, and September 2017. Parameters include (A) temperature, (B) salinity, (C) dissolved reactive phosphorus (DRP; μM), (D) ammonium ($\text{NH}_4\text{-N}$; μM), (E) nitrate ($\text{NO}_3\text{-N}$; μM), (F) dissolved organic phosphorus (DOP; μM), (G) dissolved organic nitrogen (DON; μM), (H) chlorophyll *a* concentration ($\mu\text{g l}^{-1}$), and (I) jellyfish abundance (*N. nomurai*; ind. net⁻¹). Statistical analysis was conducted with ANOVA (Tukey HSD test). The abundances of jellyfish are square root transformed. * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$; ns, not significant.

PCNM variable (Fig. 7). The results showed that 2 principal components, RDA1 and RDA2, could explain more than 50% of the variance of the samples. The arrangement of the phytoplankton samples in July, August, and September, respectively, from left to right in the RDA1 dimension, showed that there had been a temporal succession of phytoplankton from small cells such as cyanobacteria, haptophytes, and cryptophytes to a large phytoplankton such as diatoms. In the negative direction of RDA1, which was dominated by a small phytoplankton, the main contributors to cyanobacteria, haptophytes, and cryptophytes were temperature and DON, which were closely related to the discharge of thermal effluent and jellyfish abundance, respectively. RDA2 was affected mainly by salinity, and PCNM1 was impacted by spatial variability.

Discussion

Impact of thermal discharges from the HNPP

Our study revealed that discharges of cooling water from the HNPP significantly elevated temperature in the area surrounding the outfall. In all 3 months, the water temperature at D4 were elevated by 2 °C relative to nearby stations (Fig. 2). Our results were consistent with the results of satellite remote sensing used to monitor and study the impacts of the HNPP on the trend of temperature changes. On the basis of verified methods for estimating the average temperature of the water, 3 kinds of data (MODIS, HJ-1B, and Landsat-8) have revealed the thermal plume of the HNPP [36]. The dispersion of the thermal plume leads to the mixing of warm and cold water and results in a

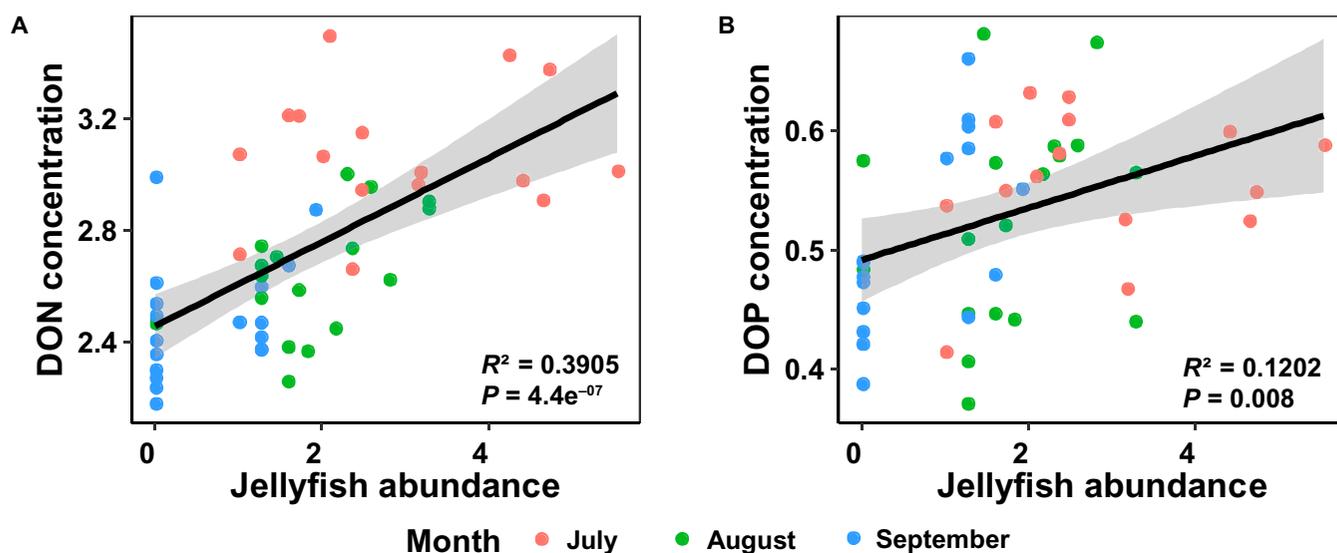


Fig. 4. (A and B) Scatter diagram of jellyfish abundance (*N. nomurai*; ind. net⁻¹, natural logarithmic transformation) and dissolved organic nutrient concentration (cube root transformation) in the study area. The black line is a linear regression curve, and the gray area shows 95% confidence interval.

large area of temperature elevated by less than 2 °C and a small area of temperature elevated by more than 2 °C. Wang et al. [37] have applied an aerial remote-sensing monitoring system based on an unmanned aerial vehicle platform to monitor the thermal discharge in the same area. Their results have shown that the water temperature at the outfall reaches nearly 25 °C, which is 10 °C higher than the water temperature at the edge of the zone of mixing. High-temperature cooling water extended in a concentric pattern away from the outfall. With dispersion, the thermal effluent was increasingly mixed with cold water, and the water temperature decreased accordingly. The water temperature dropped to 21 °C in the zone of mixing about 200 m from the outfall.

Although the above studies indicate that the thermal effluent from the HNPP has a significant impact on the local environment, the moderate elevation of the temperature at D4 in this study did not have a significant impact on the structure of the phytoplankton community. Even though the temperature rose by as much as 2 °C at D4, we found no significant changes in the phytoplankton biomass and community structure there compared with similar stations nearby (Fig. 5). We suspect that the phytoplankton community in the study area was dominated by eurythermal species in the summer. The direct effect of temperature increase of about 2 °C on the phytoplankton community may not be marked in the summer in this area. Indirect effects of a temperature increase on the phytoplankton might include effects on thermal stratification, diffusion of nutrients, and rates of zooplankton feeding. The apparent absence of any net effect on the phytoplankton might reflect the fact that D4 was far enough from the outfall that any effects of thermal pollution on the phytoplankton were imperceptible. Another possibility is that the effect of thermal effluent was mainly at the level of species, and differences between higher-order taxa were not significant. This possibility would have been overlooked by our assessment methods. Our study was based on the analysis of photosynthetic pigments, which cannot quantitatively distinguish phytoplankton at the phylum or class levels. A follow-up to this study would be to identify the species composition of the phytoplankton through a combination of microscopic observations and molecular methods.

To evaluate the effects of thermal effluent on phytoplankton communities in a larger context, we examined publications on the effects of thermal effluents from NPPs on phytoplankton communities and found that most of the studies have confirmed that impacts of thermal effluent include one or more of the following (Table). First, there are spatial differences in the effects of thermal effluent on phytoplankton. Changes of the temperature affect the rate of photosynthesis and the activity of photosynthetic enzymes [38–40]. Studies have shown that phytoplankton productivity is negatively correlated with water temperature in the zone of mixing, but not in the vicinity of the cooling water intake [38]. The discharge of thermal effluent causes thermal stratification, which leads to changes in vertical hydrodynamics, and a high temperature significantly affects phytoplankton abundance and community structure [41]. Lo et al. [42] have shown that phytoplankton species composition differs at the cooling water intake and outfall of an NPP. Furthermore, the long-term effects of thermal effluent can lead to changes of phytoplankton species composition and even the community structure of other taxa such as zooplankton and benthic organisms in the area around an NPP [7,42–44].

Second, there are seasonal differences in the effects of thermal effluent on phytoplankton. The area of elevated temperature is greater in winter than in summer. During the winter and spring, the increase of temperature stimulates the growth and reproduction of phytoplankton. However, in summer, the growth rates of phytoplankton are adversely affected in areas where the elevation of temperature is moderate (2 to 4 °C) or high (4 to 7 °C) [45]. A recent study has reported that thermal effluent causes severe winter algal blooms in Xiangshan Bay [46].

Third, the effect of thermal effluent on phytoplankton community structure is variable. Thermal effluent in Daya Bay has affected the phytoplankton community structure, and the long-term trend has been a replacement of the formerly dominant diatoms with dinoflagellates [47]. Temperature rise can prolong the season of active phytoplankton growth, exacerbate eutrophication, and change the dominant species [48]. The response of phytoplankton to an increase of water temperature differs markedly between warm and cold seasons. In the study by Ye et al. [49],

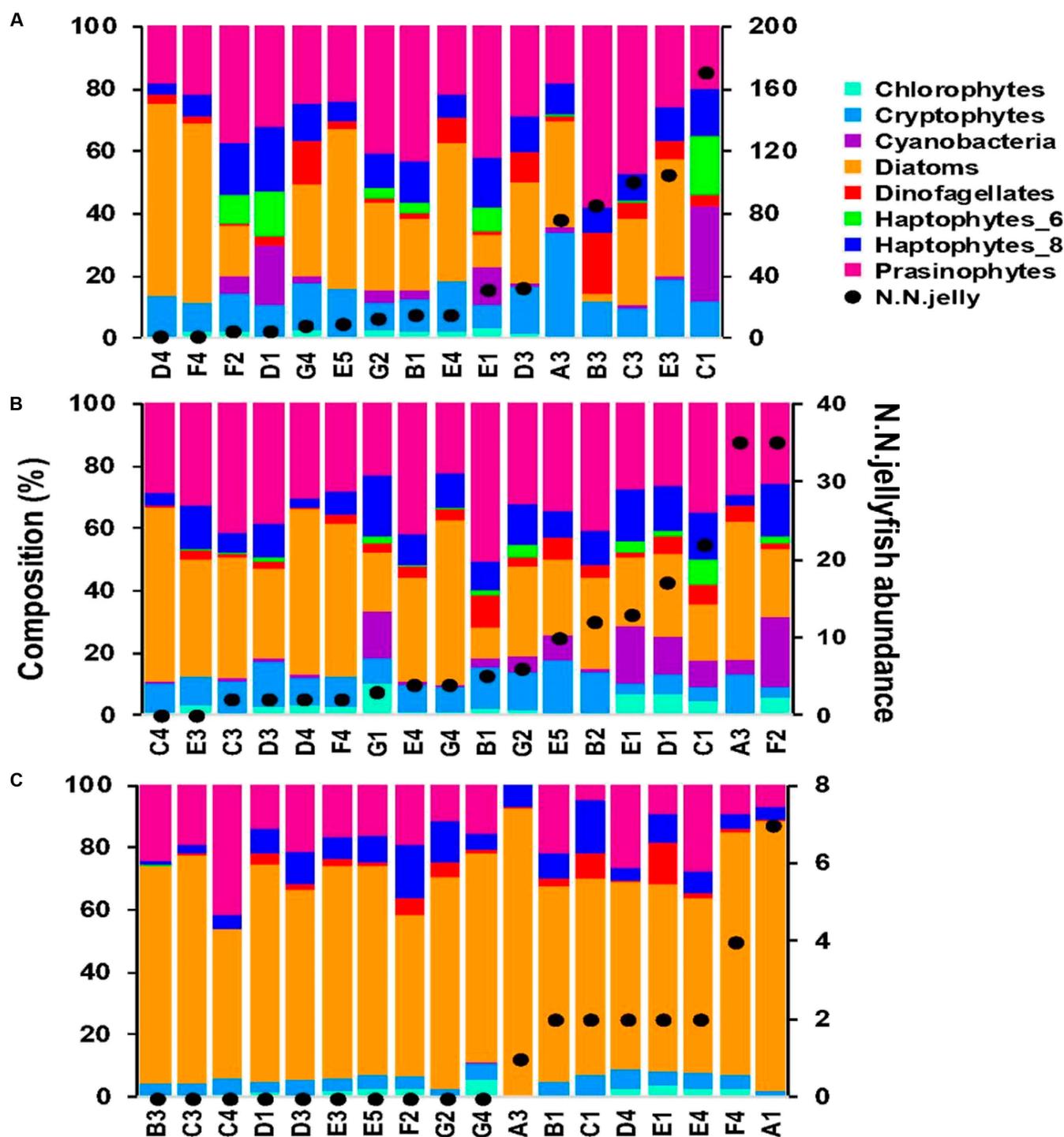


Fig. 5. (A to C) Surface phytoplankton community structure based on photosynthetic pigment analysis and CHEMTAX calculation along with jellyfish abundance (*N. nomurai*; ind. net⁻³) during the cruises in July, August, and September 2017.

those differences were reflected by differences of biomass, but the dominant species did not change.

In general, thermal effluent and other factors can be expected to affect phytoplankton. For example, the area affected by thermal effluent can be affected by tides, and the area of elevated temperatures may be larger at high tide than at low tide [45]. The threshold temperature for impacts on phytoplankton may differ as a function of tidal patterns [39]. The effects of thermal

effluent on phytoplankton may also be modified by factors such as the mechanical load on high pressure, salinity, and residual chlorine in the thermal effluent [38,49].

The threat of jellyfish blooms in the sea surrounding the HNPP

In recent years, the increasingly frequent and even annual occurrences of jellyfish blooms have affected fisheries and tourism

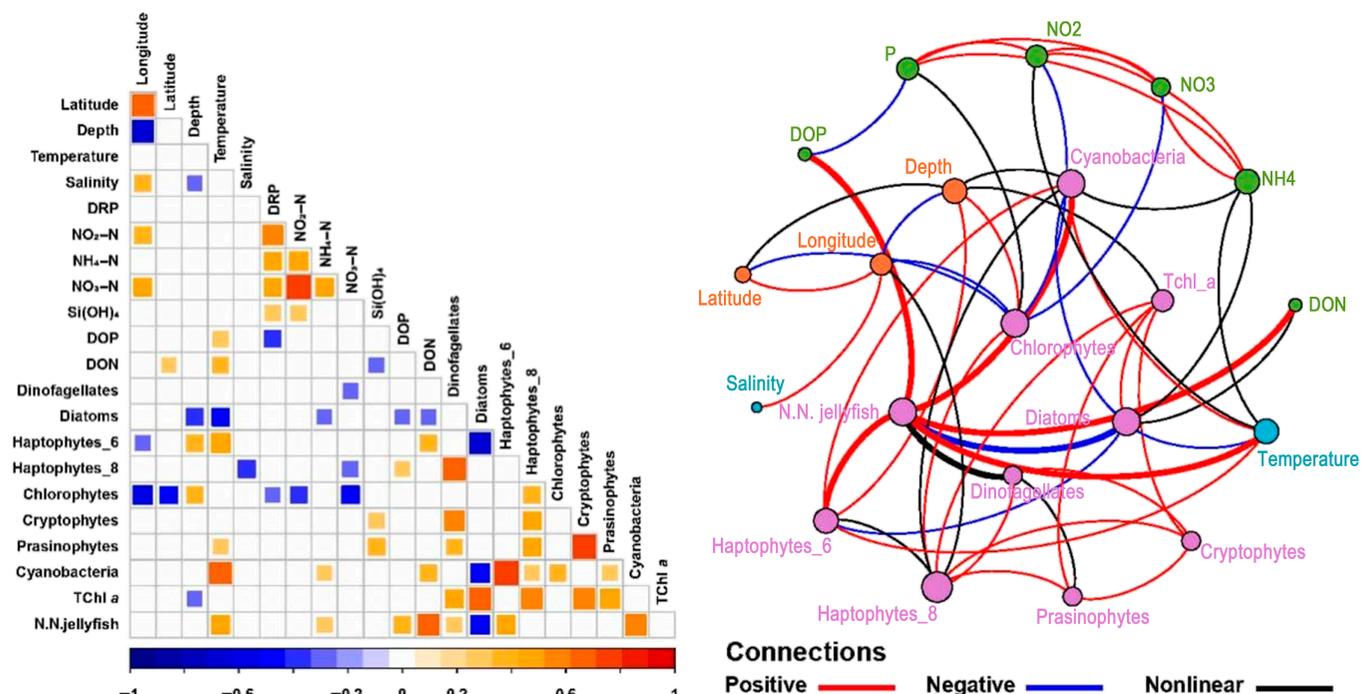


Fig. 6. Spearman correlation (left panel) and maximal information-based nonparametric exploration analysis (Minerva) (right panel) between parameters. Only the results of significant correlation ($P < 0.05$) were drawn. Parameters include the latitude, longitude, water depth, and surface values in temperature, salinity, DRP (μM), $\text{NH}_4\text{-N}$ (μM), $\text{NO}_3\text{-N}$ (μM), DOP (μM), DON (μM), chlorophyll a concentration ($\mu\text{g l}^{-1}$), and jellyfish abundance (*N. nomurai*; ind. net $^{-1}$).

along many coastlines [50]. Because jellyfish feed on zooplankton, during large blooms, they compete with commercial fish species for food, and they sting commercially valuable fish. The result has been a decline in commercial fish catches [50,51]. Coastal tourism has also been adversely affected by jellyfish blooms that have discouraged tourists from visiting the coast [50,51]. Jellyfish blooms have also led to the shutdown of some coastal fossil fuel power plants and NPPs as well as desalination plants [51].

Warming has been speculated to be one of the causes of the jellyfish blooms [9,52]. The thermal effluent from NPPs provides an excellent opportunity to explore whether increases of water temperature are related to jellyfish blooms. This study provided the first direct evidence of a significant positive correlation between jellyfish abundance and DON (Fig. 4), as well as significant correlations of jellyfish abundance with temperature and the abundances of diatoms, cyanobacteria, and dinoflagellates. These results from a natural system provide some clues and reflect the complexity of natural ecosystems. The multiple effects that we observed reflect a complex and interrelated system with interacting components that include temperature, jellyfish, nutrients, and the phytoplankton community (Fig. 8).

One of the key stages of the jellyfish life cycle is the polyp stage, which importantly affects the population in the medusa stage. Jellyfish polyps have good reproductive potential and survival capability [53,54]. The polyps multiply by asexual reproduction, and they produce a stack of medusoid structures that can bud off to replenish the number of medusae [55]. The germination rate of the polyps in the sea around Taiwan has decreased with the increase of temperature, but the rates of transversion and release of medusae have increased. There is

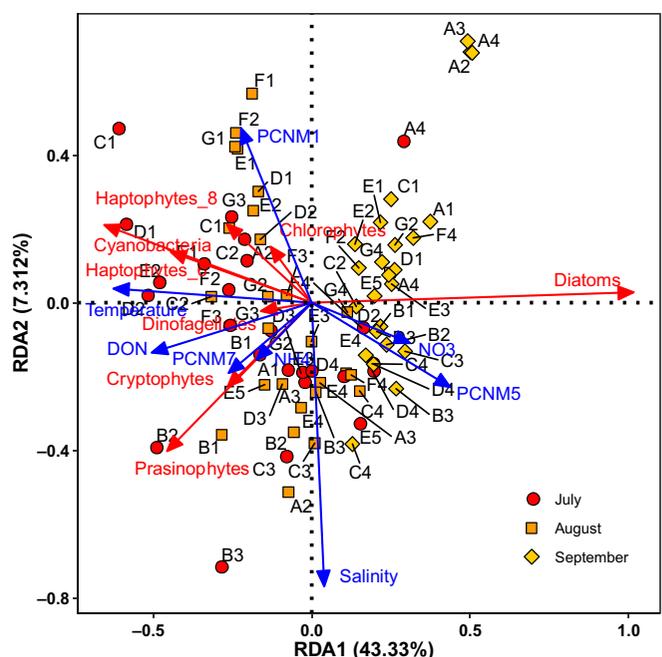


Fig. 7. Response of phytoplankton community to environmental change indicated by representational difference analysis (RDA). Parameters include the latitude, longitude, water depth, and surface values in temperature, salinity, DRP (μM), $\text{NH}_4\text{-N}$ (μM), $\text{NO}_3\text{-N}$ (μM), DOP (μM), DON (μM), chlorophyll a concentration ($\mu\text{g l}^{-1}$), and jellyfish abundance (*N. nomurai*; ind. net $^{-1}$). Hellinger transformation of phytoplankton groups, construction of principal coordinates of neighbor matrices (PCNM variables) by latitude and longitude, standardization of environmental factors, and variable preselection were included.

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Table. Impact of thermal emission on phytoplankton (+, positive effect; –, negative effect; O, impact; X, no impact or no study).

Area	Location	Latitude	Temporal scale	Influence biomass	Influence community structure	Sources
Asia	Daya Bay	22°N	Seasons	Summer – Winter + Spring +	X	(Jiang and Wang 2020)
	Xiangshan Bay	29°N	Season	$T > 0.8\text{ °C}$ – $T < 0.4\text{ °C}$ X	X	(Yang and Dai 2013)
	Zhanjiang Bay	21°N	Seasons	+	O	(Li, Li et al. 2014)
	Daya Bay	22°N	Years	–	O	(Li, Liu et al. 2011)
	Daya Bay	22°N	Seasons	High T+ – Low T+ +	High T+ – Low T+ +	(Ye, Chen et al. 2018)
	Ningde Nuclear Power Plant	26°N	Years	–	–	(Lin, Zou et al. 2018)
	Xiangshan Bay	29°N	Years	+	–	(Jiang, Du et al. 2019)
	Jinshan and Wanli, Northern Taiwan	25°N	Seasons	Seasonal O Spatial O	Seasonal O Spatial O	(Lo, Hsu et al. 2016)
	Kuosheng Bay, Northern Taiwan	25°N	Years	–	O	(Chuang, Yang et al. 2009)
	Obra	22°N	Year	–	–	(Srivastava, Ambasht et al. 1993)
North America	Bay of Bengal	12°N	Months	X	X	(Poornima, Rajadurai et al. 2005)
	Veracruz, Gulf of Mexico	21°N	Years	–	O	(Martinez-Arroyo, Abundes et al. 2000)
Europe	Venice lagoon	45°N	Season	+	X	(Socal, Bianchi et al. 1999)
	Loviisa archipelago, Gulf of Finland	60°N	Years	+	O	(Ilus and Keskitalo 2008)

no transversion at a temperature of 20 °C [11]. The temperatures of the waters around Taiwan where the *Aurelia aurita* were found ranged from 19 to 32 °C during the year, and warm water temperatures would likely stimulate the reproduction of *Aurelia aurita* [11]. However, the genitalization of the *Aurelia aurita* in Jiaozhou Bay has been reported to stop at 17 °C, and the temperature for sphenoid formation there is 10 to 17 °C [56]. In this study, the thermal effluent warmed the water near the outfall by about 2 °C. The results of these previous studies suggest that the thermal effluent might have enhanced the survival rate of the polyp stage and the growth rate of the medusa stage of the jellyfish and, thus, stimulated the blooms of jellyfish.

From the perspective of the bottom-up control, studies have shown that the metabolic activity of jellyfish during a bloom can release large amounts of organic matter and nutrients that stimulate the growth of phytoplankton [57]. After the jellyfish bloom, many jellyfish die and decompose, and the dissolved organic matter and inorganic nutrients are released into the water as the jellyfish decompose, and the organic matter that is catabolized by bacteria can stimulate blooms of phytoplankton [58]. Field observations during the post-bloom period have revealed

evidence of increased nutrient concentrations [17]. Some culture experiments in the laboratory have also indicated that increases of jellyfish biomass can accelerate the recycling of nutrients and thereby stimulate algal blooms [11,13,14]. Previous studies have speculated that jellyfish outbreaks release large amounts of nutrients (especially organic nutrients and phosphorus) that affect phytoplankton communities via bottom-up control [17]. However, it has been difficult to establish a cause-and-effect relationship between jellyfish blooms and increases of nutrient concentrations based on field studies in open waters. Forty-three days of continuous observations of a jellyfish bloom in a lagoon, a relatively closed-water environment, have provided evidence consistent with the conjectured cause-and-effect relationship [18]. Our study was the first to provide evidence that dissolved organic nutrient concentrations vary as a function of jellyfish abundance and the composition of phytoplankton communities (Figs. 6 to 8).

Under these conditions, the growth of harmful dinoflagellates may be stimulated because diatoms, which require silicate and are unable to exploit the N and P [59]. About 50% of the nitrogen released by the decomposition of jellyfish becomes DIN and

DON [60]. Some of the DON can be directly utilized by phytoplankton [61], and the rest of the DON is converted to ammonium by bacterial mineralization and then taken up by phytoplankton [62]. During the development of a jellyfish bloom, the jellyfish release large amounts of inorganic nutrients that promote the growth of diatoms. During the mature stage of the jellyfish bloom, the abundance of diatoms decreases [17]. These results of earlier studies are consistent with the phenomenon that we observed: The development of the jellyfish bloom was positively correlated with DON concentrations, and the demise of the bloom benefitted small phytoplankton but not diatoms (Fig. 8).

Because jellyfish feed directly on zooplankton and large phytoplankton, a jellyfish bloom reduces the pressure on small phytoplankton from competition and grazing via top-down control (Fig. 8). Our previous research work has focused on the jellyfish bloom area outside the Yangtze River estuary and has revealed that a sharp increase in the jellyfish population affects the community structure of phytoplankton because the jellyfish feed on relatively large cells and can also alleviate the grazing pressure of zooplankton on phytoplankton. The jellyfish therefore indirectly promote the growth of small phytoplankton via top-down control [18,17]. If feeding by jellyfish releases relatively large amounts of nutrients, then the size distribution of the phytoplankton shifts to nanophytoplankton (2.0 to 20 μm); if feeding by jellyfish releases relatively small amounts of nutrients, then the size distribution of phytoplankton shifts to picophytoplankton (0.2 to 2.0 μm) [16,63]. However, if the abundance of copepods is greatly reduced because of grazing by fish or jellyfish, then microphytoplankton (20 to 200 μm) would be expected to dominate [16,63]. The implication is that predator-prey

relationships may cause nonlinear effects that are sometimes difficult to predict. In addition, there are nutrient cascade effects. The combined effects of predation/grazing via top-down control and nutrient recycling can therefore be very complex. Observations have indicated that jellyfish blooms cause nanophytoplankton to become dominant. However, the mechanisms and the dynamics of the internal processes that lead to this effect may be complex. Future studies will be needed to clarify the magnitudes of these interactions and their effects.

Conclusions

In this study, we used a Spearman correlation analysis and RDA of environmental and biological results of sampling near the outfall of the HNPP to answer 3 questions (Fig. 8). The first question asked what the impacts were of the thermal discharges from the NPP that were on the temperature regime and biological community in Liaodong Bay. We found that the thermal effluent from the HNPP significantly elevated the temperature near the outfall, but the temperature increase was only 2 °C, the area of the elevated temperature was small, and there was no significant impact on the phytoplankton community structure at the station nearest the outfall. There may have been an effect of the thermal effluent on the species composition of the phytoplankton community, but there was no discernible effect on the phytoplankton community composition at the taxonomic levels that we were able to document. A more in-depth analysis could involve a study of species composition with a combination of microscopic observations and molecular biological methods.

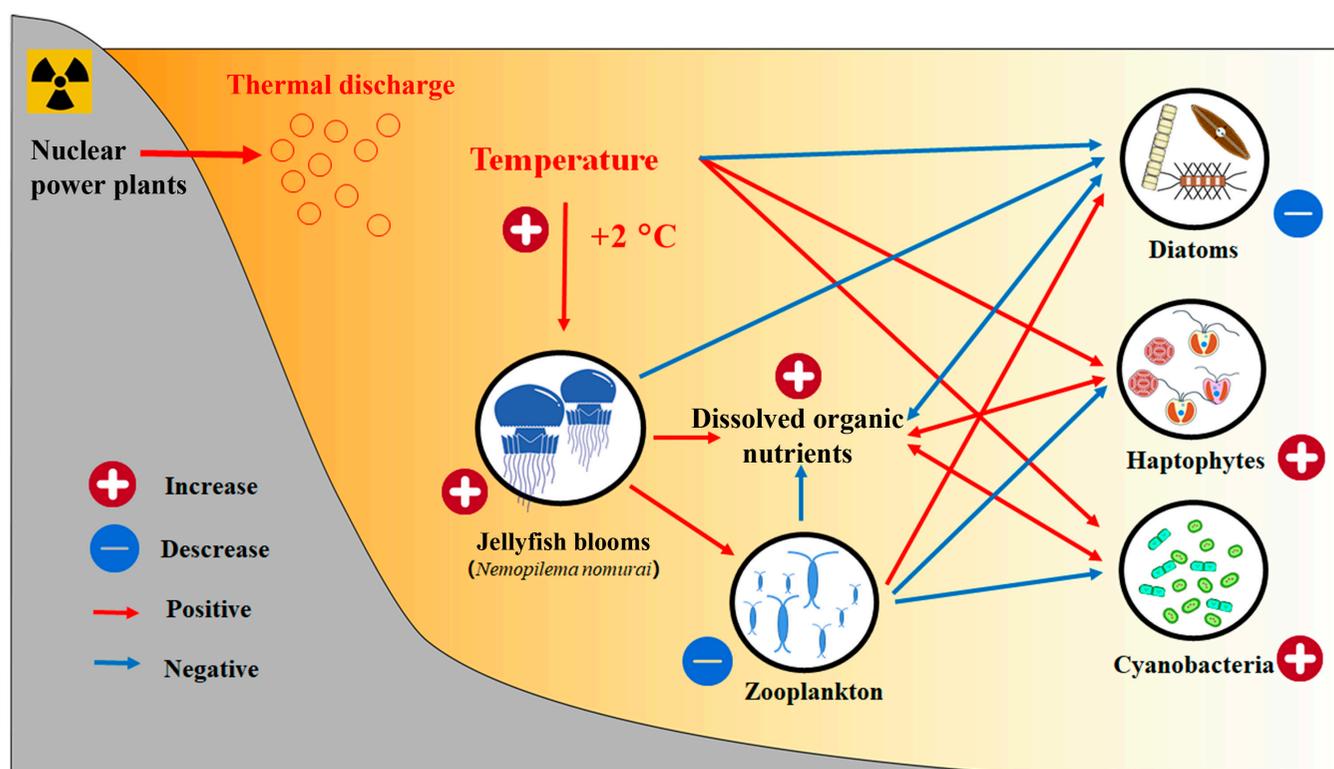


Fig. 8. The interactions among the temperature change from thermal discharge of NPPs, jellyfish blooms (*N. nomurai*), dissolved organic nutrients, zooplankton, and phytoplankton (diatoms, cyanobacteria, and haptophytes). + in red and white means increase, - in blue and white means decrease, and arrows in red and blue means positive and negative effects, respectively.

The second question asked whether we could identify a cause-and-effect relationship between jellyfish blooms and phytoplankton blooms. Our results showed that jellyfish abundance was positively correlated with the abundances of cyanobacteria and dinoflagellates and was negatively correlated with the abundance of diatoms. Jellyfish outbreaks may therefore lead to phytoplankton blooms through a top-down and/or bottom-up process. The third question asked whether there was any connection between these biological blooms and the thermal discharge from the HNPP. Our results showed that jellyfish abundance was positively correlated with temperature. The study revealed for the first time a significant positive correlation between jellyfish abundances and DON concentrations. Our analyses suggested that there might be a complex system of interactions involving temperature, jellyfish abundance, nutrient concentrations, and phytoplankton communities that reflected, inter alia, jellyfish life history, top-down control, bottom-up control, and trophic cascades. Future studies of these interactions should be carried out to clarify the internal processes and mechanisms.

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Data Availability

All data are available in the main text or contact the corresponding author (X.L.).

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