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Distribution Patterns of Large Jellyfish and Their Effects on the Zooplankton Community in the Northern Chinese Coastal Seas during the Summer of 2021

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Abstract: The northern Chinese coastal seas have been observed to constitute a large jellyfish blooming hotspots during the last decades. The spatial distribution of the abundance and biomass of large jellyfish was investigated in this area through a bottom trawl survey during the summer of 2021. Nemopilema nomurai, Cyanea spp., Aurelia coerulea, Aequorea spp., and Ulmaridae (undefined sp.) were identified during the investigation. The realized niches of the three most abundant species (N. nomurai, Cyanea spp., and A. coerulea) were measured through the maximum entropy (MaxEnt) model to explain their spatial distribution patterns. Nemopilema nomurai was used as a representative species to estimate the feeding rate and feeding pressure of large jellyfish on the zooplankton. During N. nomurai blooms, the potential consumption of zooplankton by N. nomurai was enormous and even exceeded the zooplankton productivity in regions where N. nomurai assembled in this study. Reductions in absolute and relative abundance were noted in small copepods at mid-bloom and bloom stations compared to non-bloom stations. The realized niches of large jellyfish and their relationships with the zooplankton in this study would be helpful for understanding their biogeographic distribution and ecological roles in the northern Chinese coastal seas under future climate change scenarios.

Keywords: jellyfish bloom; spatial distribution; realized niches; ecological roles

1. Introduction
In recent decades, large jellyfish blooms have been reported in various marine areas, and fluctuations in the population size of large jellyfish have attracted increasing worldwide attention due to their detrimental impact on marine fisheries and aquaculture [1–4]. Large jellyfish blooms are thought to be influenced by changes in the coastal environment resulting from both climate change and anthropogenic disturbances [5–8]. The global ecosystem is undergoing rapid and widespread change, and climate change will continue to increase [9]. Predicting the population variations of large jellyfish under future scenarios is critical to managing fishery resources and marine ecosystem health.

The northern Chinese coastal seas (i.e., the northern East China Sea (nECS), Yellow Sea (YS), and Bohai Sea (BS)) are one of the largest jellyfish blooming hotspots [10–14]. There has been a general increase in blooms of large jellyfish in summer and autumn in this area, such as Nemopilema nomurai, Cyanea spp., and Aurelia coerulea, over the past few decades. However, this trend has reversed or paused in the past 10 years, with a decline in jellyfish abundance observed during this period [10–13,15]. Scientists have conducted a large number of field studies on the northern Chinese coastal seas and laboratory experiments...
to demonstrate the population dynamics and spatial–temporal distribution [11,13,16], bloom mechanisms [17–19], and ecological roles of large jellyfish [12,20,21]. Among them, *N. nomurai* is one of the most dominant species, with an extensive distribution in this area, and it has exhibited high interannual variability in its population size since the consecutive outbreaks in 2002 [11,13,16,22]. Compared to *N. nomurai*, *Cyanea* spp. is a warmer-water species that is distributed mainly in the East China Sea and BS [10,11]. *Cyanea* spp. has a complex trophic relationship with other zooplankton. The stable isotope result showed that there was an intraguild predation of *C. nozakii* on *N. nomurai* and small medusae in the nECS [20]. *Aurelia coerulea* is a cosmopolitan scyphomedusan that blooms mainly in harbors and inshore areas, including Jiaozhou Bay and the BS, in the Chinese seas [10,23]. Due to the lack of a whole and systematic survey of large jellyfish in the northern Chinese coastal seas, an overall analysis of large jellyfish in this area is limited. According to previous research, the interannual variation of the large jellyfish population was related to climate variability [5–7,24]. The Pacific Decadal Oscillation (PDO), a significant climate mode that controls the North Pacific ecosystems [25], moves into a negative phase in 2020 after an oscillation (https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst.v5.pdo.dat, accessed on 1 December 2022). Thus, this study is also an important data supplement to the mechanisms research of large jellyfish interannual variation.

Research on the realized niches of plankton is beneficial to better reveal the relationships between environmental variables and plankton, which is valuable for understanding the mechanisms of their temporal and spatial distribution, as well as their population variation under climate change [26–28]. The realized niches, which could be inferred from species distribution data and associated environmental data through the maximum entropy (MaxEnt) model, describe the environmental and biotic conditions occupied by a species [26]. Compared to the fundamental niche, where a species could persist according to its physiology, the realized niche includes the effects of ecological interactions as a subset of the fundamental niche where the species is found [27]. This method has been used to explain the response of plankton to fluctuations in multiple environmental variables—for example, the ecological response of phytoplankton species to environmental variables in the North Atlantic [27], the mechanisms explanation for biogeographic patterns of phytoplankton communities in the South China Sea [28], the comparison of copepod niches between the North Atlantic and Southern Ocean [29], and the future global distribution map of *Craspedacusta sowerbii* under climate change scenarios [30].

In addition to population variations, interest in the ecology of large jellyfish has expanded during the last three decades due to the frequent appearance of these gelatinous organisms and their consequences on ecosystems [31,32]. The fluctuations in large jellyfish populations may affect fishery stocks by affecting the zooplankton community composition [2,3,15,33]. The results of gastric content and stable isotope analyses showed that large jellyfish predominantly prey on micro- and mesozooplankton such as copepods, ciliates, and fish eggs and may act as potential competitors with zooplanktivorous fish [20,34,35]. Mature *Cyanea nozakii* individuals feed mainly on zooplankton, with copepods being an important food source [20]. The feeding rate and feeding pressure of *N. nomurai* on the standing stock and production rate of zooplankton during the blooming period in the nECS and southern YS in summer 2006 and 2007 were estimated, indicating that the potential consumption of zooplankton at *N. nomurai* assemblage areas was enormous and damaging to the zooplankton community [36]. The number of fish species and catch per unit effort (CPUE) declined in summer 2003 (a bloom year with large jellyfish ≥14 × 10³ kg·h⁻¹) compared to 1999–2001 (non-bloom years with large jellyfish ≤3 × 10³ kg·h⁻¹) in large-jellyfish-dense regions of the nECS [37]. Thus, it is recognized that the high feeding pressure of large jellyfish blooms could control the abundance of zooplankton via top-down control [20,38–41]. Although an important fishing ground, there is a lack of research on the relationship between large jellyfish and zooplankton in the northern Chinese coastal seas—for example, on the community composition, spatial distribution, and abundance fluctuation of large jellyfish and zooplankton.
Here, a comprehensive, large-scale fishery survey was designed and conducted in summer 2021 in the northern Chinese coastal seas. By investigating environmental variables, the species composition, abundance, and biomass, realized niches of large jellyfish, abundance, production rate, and composition of zooplankton, and grazing rate of N. nomurai on zooplankton, the following scientific issues were tested. The first research goal was to construct the distribution patterns of large jellyfish in summer 2021 in the surveyed area and to provide a database for studying the interannual variations in large jellyfish population size. The second research goal was to characterize the realized niches for large jellyfish, which will be helpful to understand their biogeographic distribution in this area and to forecast possible consequences of climate change. The third research goal was to determine whether the large jellyfish bloom would have a negative effect on the zooplankton community.

2. Materials and Methods

2.1. Study Area

The bottom trawl survey was conducted in the northern East China Sea (ECS), Yellow Sea (YS), and Bohai Sea (BS) aboard the R/V “Beidou” from August 2nd to September 11th, 2021, to investigate the characteristics of the large jellyfish population and its relationship with the zooplankton community. The sampling stations during the cruise are shown in Figure 1. The sampling depth ranged from 13 to 83 m. To compare the ecological characteristics of large jellyfish in different regions, the whole study area was divided into three parts from south to north: the nECS, YS, and BS (Figure 1).

Figure 1. Sampling sites (triangles) within three sectors of the study area. nECS: northern East China Sea, YS: Yellow Sea, BS: Bohai Sea, LZB: Laizhou Bay, LDB: Liaodong Bay.

2.2. Sampling

Large jellyfish individuals were collected using a bottom trawl net with a total length of 83.2 m, an opening circumference of 167.2 m (836 mesh × 20 cm), an opening height of 7 m, an opening width of 22 m, and a 10 cm mesh size cod-end with a 2.4 cm mesh liner [11]. During trawling, the towing speed was approximately 3 kt·h⁻¹ (5.556 km·h⁻¹), and the duration of the trawl hauled at each station was approximately 0.5 h. As soon as the trawl was hauled onboard, the species and number of large jellyfish were enumerated, and the bell diameter of each specimen was unintentionally measured. The abundance and biomass of each large jellyfish were estimated according to Zhang et al. [11] and expressed as ind·km⁻² and kg·km⁻², respectively.

Zooplankton (>160 μm) samples were collected vertically at ~1 m·s⁻¹ from the bottom to the surface of the water column using a plankton net (mesh size 160 μm, 50 cm mouth diameter, 0.2 m² mouth area) in the nECS and southern YS. The zooplankton samples were immediately preserved in 5% neutral formalin and then digitized with a ZooScan (Hydroptic, Occitanie, France) digital imaging system with an 11 × 24 cm scanning frame.
and 4800 dpi. Following that, the samples were examined using Zooprocess software, and all individuals were counted, quantified, and identified [42]. Plankton Identifier software was used for automatic recognition through supervised learning [43]. To understand the ecological role of large jellyfish and their relationship with zooplankton, the zooplankton community was classified into seven functional groups in this study: giant crustaceans (euphausiids, luciferidae, amphipods, etc.), large copepods (>1000 µm), small copepods (<1000 µm), tunicates, chaetognaths, medusae (hydromedusae, siphonophore, ctenophore, etc.), and other organisms, according to the zooplankton functional groups [44] and the prey size of *N. nomurai* [40]. The abundance of each zooplankton group was calculated and expressed as ind.·m$^{-3}$.

Environmental data including temperature (°C), salinity, and chlorophyll a concentration (mg·m$^{-3}$) were sampled at the sea bottom layer at each station throughout the whole cruise using a Seabird-25 PLUS conductivity–temperature–depth (CTD). “Sea bottom layer” refers to the deepest depth that the CTD instrument could lower to.

### 2.3. Data Analysis

#### 2.3.1. Realized Niches of Large Jellyfish

The realized niches of large jellyfish were calculated through the maximum entropy models (MaxEnt; https://biodiversityinformatics.amnh.org/open_source/maxent/, accessed on 1 September 2022, version 3.4.4) that combine large jellyfish with corresponding environmental data [27,28,45]. The MaxEnt method is a statistical machine-learning technique that utilizes species presence-only records along with corresponding environmental data to estimate the functional relationships with the full environmental data as background. Data on species absence, abundance and biomass are not required in MaxEnt [45]. Before modeling, pair plots of environmental variables were used to check for collinearity with the R package ‘GGally’, using an |r| > 0.70 to remove multiple collinearity [46]. According to the results of the collinearity analysis, depth and temperature, as well as depth and chlorophyll a concentration, exhibited a high degree of collinearity with |r| > 0.70 (Figure S1). Thus, the environmental variables used to calculate the realized niches of large jellyfish in this study were temperature, salinity, and chlorophyll a concentration. Two sets of models were constructed through MaxEnt software: one set using all of the environmental factors to assess the model feasibility, and another set including only one environmental factor at a time to characterize how the species responded to each environmental condition individually, as advised by the MaxEnt software tutorial [27,45]. During the MaxEnt analysis, 75% of the presence data was randomly selected for model training, and the rest was used to test the model performance. The MaxEnt analysis performed 100 bootstrap resampling replicates for each species and recorded the logistic probability. All the other adjustable parameters in the MaxEnt software were kept at their default settings. The model formations were created as follows:

$$p(y = 1|x) = p(y = 1) f_1(x) / f(x)$$

where $p(y = 1|x)$ was estimated through the MaxEnt method, representing the conditional probability of finding the species in a particular environment. $p(y = 1)$ was the probability that the species would be found in a random sample, regardless of the environment. $f(x)$ and $f_1(x)$ were the probabilities estimated for the environmental variables of all the stations (considered background data) and for the environmental variables of the stations where the species were known to exist, respectively. The accuracy of the MaxEnt model was confirmed by receiver operating characteristic (ROC) curve analysis and further summarized by the area under the ROC curve (AUC). The AUC value of the MaxEnt model ranges from 0 to 1, and an AUC closer to 1 indicates a better model fit [27,47].

The mean realized niche (u) and breadth of the realized niche (σ) were defined based on the univariate response function $f(x)$ derived from the MaxEnt software, representing a simple description of the realized niche of a species [27]. Furthermore, the realized niches for pairs of environmental variables were compared, two variables at a time, to examine
the similarities and differences across all large jellyfish species [28]. The mean and breadth of the realized niche were calculated as follows:

\[ u = \frac{\int xf(x)dx}{\int f(x)dx} \]  

(2)

\[ \sigma^2 = \frac{\int (x-u)^2f(x)dx}{\int f(x)dx} \]  

(3)

2.3.2. The Feeding Pressure of Large Jellyfish on Zooplankton

Considering that N. nomurai accounted for more than 95% of the biomass of large jellyfish in summer 2021 in the nECS and southern YS, N. nomurai can be used as the representative research target to represent the feeding rate of large jellyfish and their feeding pressure on the standing stock and production rate of zooplankton, as well as the relationship between fluctuations in the population size of large jellyfish and zooplankton communities. The feeding rate \( F_{\text{jelly}} \) (mg C m\(^{-2}\) d\(^{-1}\)) included the amount of carbon required for metabolism and the amount required for individual growth [40].

\[ F_{\text{jelly}} = K \times R \times RQ_{\text{jelly}} \times 24 \times WW_{\text{jelly}} / A_e + g \times CW_{\text{jelly}} / A_e \]  

(4)

where \( F_{\text{jelly}} \) represented the feeding rate of N. nomurai, the conversion constant \( K \) was 0.375 mg C mg O\(_2\)\(^{-1}\) [36], and the respiration rate \( R \) was 17.15 mg O\(_2\) kg\(^{-1}\) h\(^{-1}\) [40]. The \( g \) represented the growth rate, which was set as 0.02 [36]. The \( WW_{\text{jelly}} \) represented the wet biomass (mg m\(^{-2}\)), and \( CW_{\text{jelly}} \) represented the carbon biomass (mg C m\(^{-2}\)), which was equivalent to 0.28% of the \( WW_{\text{jelly}} \) [36]. The assimilation efficiency \( (A_e) \) and respiratory entropy \( (RQ_{\text{jelly}}) \) were 0.8 [48].

The wet weight (\( WW_{\text{zoopl}} \), mg m\(^{-2}\)) of zooplankton was directly obtained in the laboratory using an electronic balance. The dry weight (\( DW_{\text{zoopl}} \), mg m\(^{-2}\)) was converted from the WW\(_{\text{zoopl}}\) according to Wiebe et al. [49], and the carbon weight (\( CW_{\text{zoopl}} \), mg C m\(^{-2}\)) was 40% of the \( DW_{\text{zoopl}} \) [50]. The zooplankton production rate \( (P_{\text{zoopl daily}} \text{, mg C m}^{-2}\text{d}^{-1}) \) was calculated according to Huo et al. [51]. The zooplankton productivity \( (P_{\text{zoopl}} \text{, mg C animal}^{-1}\text{h}^{-1}) \) was calculated through the respiration rates \( (R_{\text{O}_2}, \mu\text{L O}_2\text{animal}^{-1}\text{h}^{-1}) \), which depended on the dry weight of the zooplankton \( (DW_{\text{zoopl}}, \text{mg animal}^{-1}) \) and temperature \( (T, ^\circ\text{C}) \) of the habitat [52]. After that, the respiration rate \( (R_{\text{O}_2}) \) was expressed in terms of carbon units \( (R_C, \text{mg C animal}^{-1}\text{h}^{-1}) \), assuming an \( RQ_{\text{zoopl}} \) of 0.8 [53]. The gross growth efficiency and assimilation efficiency of zooplankton were considered to be 0.3 and 0.7, respectively [52]. The zooplankton productivity \( (P_{\text{zoopl}}) \) was equal to 0.75\( R_C \) [54]. The daily zooplankton production rate \( (P_{\text{zoopl daily}}) \) was equal to the productivity \( (P_{\text{zoopl}}) \) multiplied by the zooplankton abundance (ind./m\(^3\)), 24 h and depth (m). The calculation process of zooplankton production was as follows:

\[ \ln R_{\text{O}_2} = -0.2512 + 0.7886 \times \ln WW_{\text{zoopl}} + 0.0490 \times T \]  

(5)

\[ R_C = R_{\text{O}_2} \times RQ_{\text{zoopl}} \times 12 / (1000 \times 24) \]  

(6)

\[ P_{\text{zoopl daily}} = P_{\text{zoopl}} \times \text{Abundance} \times 24 \times \text{depth} \]  

(7)

The feeding pressure (%) of N. nomurai on the carbon biomass and production rate of zooplankton was as follows:

\[ F_{\text{biomass}} = F_{\text{jelly}} / CW_{\text{zoopl}} \times 100\% \]  

(8)

\[ F_{\text{production}} = F_{\text{jelly}} / P_{\text{zoopl daily}} \times 100\% \]  

(9)
where $F_{\text{biomass}}$ and $F_{\text{production}}$ represented the feeding pressure of $N. nomurai$ on the zooplankton carbon biomass and production rate, respectively. $CW_{200}$ and $P_{\text{zooldaily}}$ represented the carbon biomass and production rate of zooplankton, respectively. The feeding pressure of $N. nomurai$ on zooplankton estimates excluded stations with Noctiluca and phytoplankton blooms.

2.3.3. Statistical Analyses

A Kruskal–Wallis test was employed to examine the variations in environmental variables and large jellyfish populations among the three regions, as well as zooplankton and small copepod abundance under different population sizes of $N. nomurai$. A principal component analysis (PCA) was conducted within the R packages ‘Factoextra’ and ‘FactoMineR’ to portray the spatial patterns of the environmental factors [55]. Before the PCA, all the environmental variables were normalized to values between 0 and 1. All statistical analyses in this study were conducted using R software [55].

3. Results

3.1. Spatial Variation in Environmental Variables

The regional distribution of the depth, temperature, salinity, and chlorophyll a concentration in the surveyed area is shown in Table 1. All environmental variables were significantly (Kruskal–Wallis test, $p < 0.05$) different across the three regions. The temperature ranged from 7.71 to 27.50 °C, with the lowest value occurring in the Yellow Sea (YS). The salinity range in summer 2021 in the whole study area was 25.09–34.31. The chlorophyll a concentration ranged from 0.16 to 2.85 mg m$^{-3}$.

<table>
<thead>
<tr>
<th>Area</th>
<th>Number</th>
<th>Depth (m)</th>
<th>Temperature (°C)</th>
<th>Salinity</th>
<th>Chlorophyll a (mg m$^{-3}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>nECS</td>
<td>11</td>
<td>46.63 ± 14.79</td>
<td>24.36 ± 2.24</td>
<td>32.85 ± 2.21</td>
<td>0.37 ± 0.18</td>
</tr>
<tr>
<td>YS</td>
<td>50</td>
<td>52.88 ± 18.90</td>
<td>14.22 ± 5.94</td>
<td>32.11 ± 0.74</td>
<td>0.52 ± 0.47</td>
</tr>
<tr>
<td>BS</td>
<td>34</td>
<td>23.03 ± 9.21</td>
<td>23.24 ± 2.66</td>
<td>29.46 ± 4.78</td>
<td>0.79 ± 0.38</td>
</tr>
</tbody>
</table>

The first two principal component analysis (PCA) axes accounted for approximately 87.08% of the variability in the environmental variables across the three regions in summer 2021 (Figure 2). The Bohai Sea (BS) region was generally characterized by a high chlorophyll a concentration. The Yellow Sea (YS) region had a great depth and low temperature. The northern East China Sea (nECS) region was characterized by high salinity.

![Figure 2](image-url)  
**Figure 2.** Plots of the principal component analysis (PCA) for the environmental variables throughout the regions. nECS: northern East China Sea, YS: Yellow Sea, BS: Bohai Sea, Temp: temperature (°C), Sal: salinity, Chl: chlorophyll a concentration (mg m$^{-3}$), Dep: depth (m).
3.2. Distribution of Large Jellyfish Abundance and Biomass

The principal species of large jellyfish collected during this cruise were as follows: *Nemopilema nomurai*, *Cyanea* spp., *Aurelia coerulea*, *Aequorea* spp., and Ulmaridae (undefined sp.). The geographical distribution of abundance and biomass varied among the large jellyfish species. *Nemopilema nomurai* was the dominant species and was widely distributed throughout the whole surveyed area, with an abundance and biomass of $876.18 \pm 1131.46$ ind.·km$^{-2}$ and $10,513 \pm 13,208.01$ kg·km$^{-2}$, respectively (Figure 3a,d). *Nemopilema nomurai* assembled mainly in the southern YS and central BS (Figure 3a,d). There were no significant differences in the abundance and biomass of *N. nomurai* among the three regions in summer 2021 ($\chi^2_{abun} = 3.65$, $p_{abun} > 0.05$, $\chi^2_{bio} = 1.04$, $p_{bio} > 0.05$, Figure 4a,d). Compared with *N. nomurai*, the distribution of *Cyanea* spp. was significantly different in the study area ($\chi^2_{abun} = 13.11$, $p_{abun} < 0.05$, $\chi^2_{bio} = 11.01$, $p_{bio} < 0.05$, Figure 4b,e). *Cyanea* spp. was distributed mainly in the BS, with an abundance and biomass of $469.53 \pm 1868.76$ ind.·km$^{-2}$ and $903.34 \pm 3523.20$ kg·km$^{-2}$, respectively (Figure 3b,e). The high abundance and biomass of *Cyanea* spp. were concentrated in Liaodong Bay in the northern part of the BS. *Cyanea* spp. sporadically distributed in the nECS and YS, with abundance and biomass ranging from 0.00 to 93.38 ind.·km$^{-2}$ and 0.00 to 399.82 kg·km$^{-2}$, respectively (Figure 3b,e). *Aurelia coerulea* was distributed mainly in the BS, with an abundance and biomass of $13,314.37 \pm 43,946.48$ ind.·km$^{-2}$ and $4190.57 \pm 15,768.42$ kg·km$^{-2}$, respectively (Figure 3c,f). *Aurelia coerulea* congregated in large numbers in Laizhou Bay in the southern part of the BS and occurred at only one station in the YS in the surveyed area (Figure 3c,f). There were significant differences in the abundance and biomass of *A. coerulea* among three regions in summer 2021 ($\chi^2_{abun} = 34.21$, $p_{abun} < 0.05$, $\chi^2_{bio} = 34.08$, $p_{bio} < 0.05$, Figure 4c,f). Furthermore, *Aequorea* spp. and Ulmaridae (undefined sp.) were only sporadically distributed in the region of the YS (Figure S2).

![Figure 3. Distribution pattern of abundance (ind.·km$^{-2}$) and biomass (kg·km$^{-2}$) of Nemopilema nomurai (a,d), Cyanea spp. (b,e), and Aurelia coerulea (c,f) in summer 2021 in the northern Chinese coastal seas.](image-url)
3.3. Realized Niches of Large Jellyfish

By combining presence-only records of large jellyfish with corresponding environmental data, the response of each large jellyfish to important environmental variables was estimated using MaxEnt models. The AUC values for *N. nomurai*, *Cyanea* spp., and *A. coerulea* obtained from the 100 bootstrapped resampling were 0.655, 0.819, and 0.912, respectively (Table 2). Generally, the distribution of large jellyfish in summer 2021 in northern Chinese coastal seas was influenced by temperature and salinity, although there were considerable species-specific differences. Among them, salinity was the more important factor for *N. nomurai* and *A. coerulea*, whereas temperature was more important for *Cyanea* spp. (Table 2, Figure S3). As salinity increased, the probability of *N. nomurai* occurrence increased in the approximate range of 28–31, being insensitive to salinity at salinity of 31–34 (Figure S3b). In contrast to that of *N. nomurai*, the occurrence probability of *A. coerulea* decreased with salinity in the approximate range of 29–33 (Figure S3h). The distribution pattern of *Cyanea* spp. was significantly influenced by temperature, exhibiting a unimodal distribution in which the occurrence probability increased and then decreased with increasing temperature until ~26 °C. The occurrence probability of *Cyanea* spp. exhibited a high plateau at a temperature of approximately 20 °C (Figure S3d). Chlorophyll a concentration was the least important environmental variable, accounting for less than 20% of the general importance in the distribution of large jellyfish in this study (Table 2).

Table 2. The mean permutation importance (%) of the environmental variables in the MaxEnt analysis. AUC: area under the ROC curve, Temp: temperature (°C), Sal: salinity, Chl: chlorophyll a concentration (mg·m⁻³).

<table>
<thead>
<tr>
<th>Species</th>
<th>AUC</th>
<th>Variable</th>
<th>Percent Contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nemopilema nomurai</td>
<td>0.655</td>
<td>Temp</td>
<td>23.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sal</td>
<td>57.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chl</td>
<td>19.1</td>
</tr>
<tr>
<td>Cyanea spp.</td>
<td>0.819</td>
<td>Temp</td>
<td>70.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sal</td>
<td>13.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chl</td>
<td>15.4</td>
</tr>
<tr>
<td>Aurelia coerulea</td>
<td>0.912</td>
<td>Temp</td>
<td>27.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sal</td>
<td>67.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chl</td>
<td>4.7</td>
</tr>
</tbody>
</table>
The niches of large jellyfish differed greatly in terms of temperature and salinity (Figures 5 and 6), while for chlorophyll a concentration, the niches of large jellyfish were narrow and centered around intermediate environmental conditions. *Nemopilema nomurai* was distinguished from other species by its broad temperature niche breadth ($\sigma_{\text{Temp}} = 6.46$ °C), low mean temperature niche ($\mu_{\text{Temp}} = 18.05$ °C), and high mean salinity niche ($\mu_{\text{Sal}} = 31.84$). *Cyanea* spp. was distinct from the other species by its intermediate mean temperature niche ($\mu_{\text{Temp}} = 21.01$ °C) and broad salinity niche ($\sigma_{\text{Sal}} = 1.21$). The niche of *A. coerulea* was distinguishable from those of other species in terms of temperature and salinity. Its temperature niche was narrow ($\sigma_{\text{Temp}} = 2.56$ °C), with a high mean temperature niche ($\mu_{\text{Temp}} = 23.52$ °C) and a low mean salinity niche ($\mu_{\text{Sal}} = 30.44$).

**Figure 5.** Realized niches of the univariate environmental variables for (a) temperature (°C), (b) salinity, and (c) chlorophyll a concentration (mg m$^{-3}$) for *Nemopilema nomurai*, *Cyanea* spp., and *Aurelia coerulea*. Colored lines indicated the 95% confidence intervals for each parameter from 100 bootstrapped resampling.

**Figure 6.** Mean niches of paired environmental variables for large jellyfish. (a) Temperature and salinity, (b) temperature and chlorophyll a concentration, (c) salinity and chlorophyll a concentration. Colored lines indicated the 95% confidence intervals for each parameter from 100 bootstrapped resampling.
3.4. Relationship between Large jellyfish and the Zooplankton Community

The zooplankton community in this study was composed of giant crustaceans, large copepods (>1000 μm), small copepods (<1000 μm), tunicates, chaetognaths, small medusae, and other organisms. The abundance distributions of these zooplankton taxa are shown in Figure 7. The average abundance of total zooplankton was 3690.05 ± 2329.29 ind./m³. The small copepods were the dominant zooplankton group in terms of abundance in summer 2021 in the nECS and southern YS, comprising 72.93 ± 12.39% of the total zooplankton abundance.

![Figure 7](image)

Table 3 shows the standing stock and production rate of zooplankton, as well as the feeding rate of *N. nomurai* and their feeding pressure on zooplankton in summer 2021 in the nECS and southern YS. The average carbon biomass of zooplankton in the study region was 453.37 ± 301.67 mgC·m⁻², ranging from 51.09 to 1267.85 mgC·m⁻². The average production rate was 59.38 ± 33.42 mgC·m⁻²·d⁻¹, with a range of 9.54 to 121.04 mgC·m⁻²·d⁻¹. The feeding rate of *N. nomurai* in this study was 21.05 ± 18.75 mgC·m⁻²·d⁻¹, and the feeding rate ranged from 0.00 to 62.94 mgC·m⁻²·d⁻¹ when the capture rate of *N. nomurai* was 0.1. If all the zooplankton samples collected by the plankton net were assumed to be prey of *N. nomurai* and the capture rate of *N. nomurai* was 0.1, then the feeding pressure of *N. nomurai* on the standing stock of zooplankton was 7.70 ± 8.04%, with a range of 0.00
to 25.51%. The feeding pressure of *N. nomurai* on the production rate of zooplankton was 55.16 ± 55.52%, with a range of 0.00 to 183.45%.

**Table 3.** The standing stock (mgC·m⁻²) and production of zooplankton (mgC·m⁻² d⁻¹) and the feeding rate (mgC·m⁻² d⁻¹) and feeding pressure per day (%) of *Nemopilema nomurai* on the standing stock and production rate of zooplankton in summer 2021 in the northern Chinese coastal seas.

<table>
<thead>
<tr>
<th>Capture Rate</th>
<th>Mean</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standing stock of zooplankton</td>
<td>453.37</td>
<td>51.09–1267.85</td>
</tr>
<tr>
<td>Production rate of zooplankton</td>
<td>59.38</td>
<td>9.54–121.04</td>
</tr>
<tr>
<td>Feeding rate</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>0.1</td>
<td>21.05</td>
<td>0.00–62.94</td>
</tr>
<tr>
<td>0.4</td>
<td>5.26</td>
<td>0.00–15.74</td>
</tr>
<tr>
<td>Feeding pressure on standing stock</td>
<td>0.1</td>
<td>7.70</td>
</tr>
<tr>
<td>0.4</td>
<td>1.92</td>
<td>0.00–6.38</td>
</tr>
<tr>
<td>Feeding pressure on production rate</td>
<td>0.1</td>
<td>55.16</td>
</tr>
<tr>
<td>0.4</td>
<td>13.79</td>
<td>0.00–45.86</td>
</tr>
</tbody>
</table>

High values of a zooplankton abundance occurred at stations off the Changjiang estuary and the Shandong Peninsula (Figure 7). There was a non-overlap in the spatial distribution between the high population size of *N. nomurai* and zooplankton abundance (Figure 3a,d and Figure 7). According to the abundance of *N. nomurai*, the stations in the nECS and southern YS were divided into non-bloom stations (<500 ind·km⁻²), mid-bloom stations (500–1000 ind·km⁻²), and bloom stations (>1000 ind·km⁻²). Compared to the non-bloom stations, significant decreases were noted for zooplankton and small copepods at the mid-bloom stations and bloom stations (Figure 8). The absolute and relative abundances of small copepods were 2138.15 ind·m⁻³ and 70.71% at the bloom stations and 2020.29 ind·m⁻³ and 73.91% at the mid-bloom stations, which were less than 4143.02 ind·m⁻³ and 78.94% at the non-bloom stations, respectively (Figure 9).

*Figure 8.* Abundance of zooplankton and small copepods under different population size of *Nemopilema nomurai* in August and September 2021 in the northern East China Sea (nECS) and southern Yellow Sea (YS).
4. Discussion

4.1. Distribution of Large Jellyfish Abundance and Biomass

*Nemopilema nomurai* was extensively distributed in summer 2021 in the surveyed area (Figure 3a,d), with a broad range of temperature niches and a high mean salinity niche (Figure 5a,b). *Nemopilema nomurai* was the dominant species of large jellyfish in terms of abundance and biomass in this study. Based on historical long-term data from the southern Yellow Sea (YS), the *N. nomurai* population was at a mid-bloom level [13,56] (our unpublished data). A previous study demonstrated that *N. nomurai* abundance ranged from 34 to 4951 ind.·km$^{-2}$ in the southern YS [13]. The abundance and biomass of *N. nomurai* in the YS were 888.38 ± 1005.45 ind.·km$^{-2}$ and 11,008.805 ± 12,284.80 kg·km$^{-2}$ (Figure 4a,d), respectively, in summer 2021, which was similar to those in 2013 [13]. *Nemopilema nomurai* assembled in the central Bohai Sea (BS), with abundance and biomass values as high as 4878.19 ind.·km$^{-2}$ and 75,346.77 kg·km$^{-2}$, respectively (Figure 3a,d). There were no *N. nomurai* individuals collected in Laizhou Bay in this study (Figure 3a,d). The maximum entropy (MaxEnt) results showed that occurrence probability of *N. nomurai* increased with salinity in the approximate range of 28–31 (Figure S3b), indicating saltier water may be
beneficial to the distribution of *N. nomurai*. This may be one of the reasons for the rare occurrence of *N. nomurai* in Laizhou Bay, a low-salinity coastal water mass.

Compared to *N. nomurai*, *Cyanea* spp. was considered to be a warm-water species with a higher mean temperature niche (Figures 5a and 6a) that was distributed mainly in the northern East China Sea (nECS) and BS in this study (Figure 3b,e). The abundance and biomass of *Cyanea* spp. in the nECS were 23.19 ± 34.61 ind.-km$^{-2}$ and 86.13 ± 144.27 kg·km$^{-2}$, respectively (Figure 4b,e). Compared to the distribution of *Cyanea* spp. in the nECS in late August 2006 [11], *Cyanea* spp. was more widespread and closer to the pelagic zone in summer 2021. *Cyanea* spp. was distributed mainly in the BS and assemblaged in Liaodong Bay in this study, with abundance and biomass values as high as 9058.92 ind.-km$^{-2}$ and 18,765.13 kg·km$^{-2}$, respectively (Figure 3b,e), while *N. nomurai* individuals were collected at only a few stations in summer 2021 in Liaodong Bay (Figure 3a,d) compared to those in September 2014 [14] and June 2016 [57]. The assemblage of *Cyanea* spp. may be one of the reasons for the low *N. nomurai* population size in Liaodong Bay in this study (Figure 3b,e). The results of the stable isotope analysis revealed that *N. nomurai* comprised 9.54% of the diet of larger *Cyanea nozakii* individuals, which indicated that there was an intraguild predation relationship between these two species [20]. A similar phenomenon also occurred in Liaodong Bay in July 2004; the number of *N. nomurai* individuals decreased dramatically, whereas the number of *C. nozakii* individuals increased significantly [58].

Compared to *N. nomurai* and *Cyanea* spp., *Aurelia coerulea* had a high mean temperature and a low mean salinity niche (Figure 6a), and assembled mainly in Laizhou Bay in the BS and occurred at only one station in the YS in this study (Figure 3c,f). According to a previous study, *A. coerulea* appeared at only a few stations in Laizhou Bay with a low biomass in July 2011 and broke out in October 2011 with a biomass value as high as 45,454 kg·km$^{-2}$ at individual stations [59]. In this study, the highest biomass of *A. coerulea* in Laizhou Bay was 86,410.58 kg·km$^{-2}$, indicating that the population size was larger than that in 2011. The regional temperature may be one of the reasons for the differences in *A. coerulea* population size in Laizhou Bay between 2021 and 2011. The average sea surface temperature of the BS from July to September 2021 was higher than that of 2011 based on the sea surface temperature data from MODIS-Aqua (https://oceancolor.gsfc.nasa.gov/, accessed on 1 December 2022). The increased temperature may have a direct effect on the asexual reproduction and metabolic rate of *Aurelia* species and has been recognized as a major factor affecting their population scale [60]. High temperatures were also beneficial to earlier blooms of *A. coerulea* in the Korean Peninsula [7]. This phenomenon has been reported in other regions as well. The population size of *Aurelia* spp. in the northern Gulf of Mexico appeared to be larger than their long-term averages when sea surface temperatures were higher than average from July to September [6]. Markedly large blooms of *Aurelia* spp. were found in anomalously warm years due to enhanced medusae growth [61].

The realized niches for the three most abundant large jellyfish, namely *Nemopilema no- murai*, *Cyanea* spp., and *Aurelia coerulea*, were characterized by combining their distribution data and environmental data (Figures 5 and 6). The temperature and salinity were more important environmental factors than chlorophyll a concentration in the distribution of large jellyfish (Table 2). These realized niches can be utilized for analyzing the distribution patterns of large jellyfish, providing valuable insights into their biogeography and community dynamics in response to climate change. The investigated large jellyfish exhibit a typical life cycle, consisting of a pelagic medusa stage and a benthic polyp stage [12,17,19,60]. Important to note is that the realized niches estimated in this study pertained to the environmental conditions inhabited by large jellyfish in the pelagic stage. Due to the challenge of accurately identifying benthic polyp locations and the paucity of sample data, the benthic polyp stage was not taken into consideration in this study. Additionally, factors such as predation, competition, and prey availability may also influence the population size of large jellyfish [8,19–21]. In the future, assessment of the large jellyfish population in northern
Chinese coastal seas should consider both benthic and pelagic stages, as well as biotic and abiotic variables, to achieve more precise predictions.

4.2. Relationship between Large Jellyfish and the Zooplankton Community

Previous studies have shown that blooms of large jellyfish imposed relatively high predation pressure on micro- and mesozooplankton \[36,40,62,63\]. The abundance and biomass of large jellyfish in this study were estimated through a bottom trawl survey \[11\]. Unfortunately, there was no corresponding capture rate as a reference for this method to evaluate the abundance and biomass of large jellyfish \[36\]. Taking into account the swimming ability of large jellyfish and their vertical distribution in the water column, the capture rate of large jellyfish in bottom trawls in this study was assumed to be similar to that of pelagic fishes \(0.1–0.4\), and a capture rate of 0.1 was used to estimate the maximum abundance and biomass, while a capture rate of 0.4 was used to estimate the minimum abundance and biomass \[11,36,64\]. Given that \textit{N. nomurai} accounted for over 95% of the biomass of large jellyfish in August and September 2021 in the nECS and southern YS, \textit{N. nomurai} was used as the representative research target to study whether the large jellyfish blooms in summer would have a negative impact on the zooplankton community.

In this study, the feeding pressure of \textit{N. nomurai} on the standing stock and production rate of zooplankton was 7.70% and 55.16%, respectively, when all the zooplankton samples collected by the plankton net were assumed to be prey of \textit{N. nomurai} and the capture rate of \textit{N. nomurai} was 0.1 (Table 3). At the stations where the \textit{N. nomurai} assembled, their feeding pressure on zooplankton exceeded the zooplankton productivity rate, indicating that the potential consumption of \textit{N. nomurai} on zooplankton was significant. If the capture rate of \textit{N. nomurai} was 0.4, their feeding rate and feeding pressure on the standing stock and production rate of zooplankton were a fourth as much as those when the capture rate of \textit{N. nomurai} was 0.1 (Table 3). During the large jellyfish bloom period near Tsushima Island in late July 2005, the feeding pressure of medusae on mesozooplankton was approximately 24% \[40\]. During the \textit{N. nomurai} outbreak in early September 2006 in the southern YS, the average feeding pressure of \textit{N. nomurai} on the standing stock and production rate of zooplankton was 6.4% and 76.6%, respectively \[36\]. As their mouthlet diameters expand to ca. 1 mm when the ephyra become medusae, the prey of \textit{N. nomurai} was restricted to micro- and mesozooplankton \[40\]. The gastric pouch of \textit{N. nomurai} near Oki Island, Shimane Prefecture, in November 2005 contained many copepods and gastropod shells \[40\]. Stable isotope analysis showed that small copepods comprised over 30% of the diet of \textit{N. nomurai} in August 2016 in the YS \[60\]. This indicated that the feeding pressure of \textit{N. nomurai} would be more pronounced on micro- and mesozooplankton compared to the hypothesis that all the zooplankton samples collected were assumed to be the prey of \textit{N. nomurai}. Thus, it is interesting to determine whether the \textit{N. nomurai} population could impact the zooplankton community during the summer. Sun et al. \[41\] showed that the potential predator–prey relationship between small jellyfish and \textit{Calanus sinicus} eggs and nauplii may be the reason for their non-overlapping geographical distribution in the northern YS. The composition of zooplankton communities may be impacted by the population size of \textit{N. nomurai} in this study. Compared to non-bloom stations, decreases in absolute and relative abundance were noted in small copepods at mid-bloom stations and bloom stations in summer 2021 in the nECS and southern YS (Figures 8 and 9). There was a non-overlapping regional distribution between the areas of high abundance of \textit{N. nomurai} and those of small copepods (Figures 3a and 7), which also indicated that the \textit{N. nomurai} blooms may exert a high feeding pressure on these small organisms and alter the zooplankton communities.

Long-term field research revealed that large jellyfish aggregations were often accompanied by a decline in zooplankton and fishery population size. During 1982–1984 and 1991–1994, when \textit{A. coerulea} abundance varied between 0.3 and 23 individuals per 100 m\(^3\), there was a negative relationship between \textit{A. coerulea} and zooplankton biomass in Kiel Fjord \[65\]. The total abundance of zooplankton fluctuated greatly in the summer when \textit{A. coerulea} aggregated in Jiaozhou Bay. According to long-term observations at fixed
stations, the highest value of total zooplankton abundance was lower in *A. coerulea* bloom years than in other years [66,67]. This impact of large jellyfish on zooplankton was a critical factor in the energy transfer from primary producers to higher trophic levels, impacting the ecosystem function and fisheries recruitment [44,68,69]. Mass occurrence of medusae, along with overfishing, caused a collapse of fisheries such as the anchovy fishery in the Black Sea in 1989 [70] and the Pacific herring fishery in the Bering Sea in 2010 [36]. The energy consumed by jellyfish accounted for approximately 30% of the combined fish–jellyfish energy consumption in recent years (since 1999) in the Northern California Current and the Black Sea [71]. To date, limited information was available on the relationship between the population fluctuations of large jellyfish and the abundance and community composition of zooplankton in the northern Chinese coastal seas. As mentioned above, the predation pressure of large jellyfish during bloom on zooplankton was potentially high. It is theoretically possible that during years of large jellyfish blooms, the production of zooplankton available for fishery resources may decrease, potentially impacting the sustainable development of fisheries. More field investigations and other tools such as models are necessary to accurately analyze the effects of large jellyfish blooms on zooplankton and fishery resources in the future.

5. Conclusions

The large jellyfish groups collected in summer 2021 in the northern Chinese coastal seas included *Nomepilema nomurai*, *Cyanea* spp., *Aurelia coerulea*, *Aequorea* spp., and Ulmaridae (undefined sp.). Among them, *N. nomurai* was the dominant species in terms of abundance and biomass, followed by *Cyanea* spp. and *A. coerulea*. *Aequorea* spp. and Ulmaridae (undefined sp.) were only sporadically distributed in the Yellow Sea (YS). Based on historical long-term data from the southern YS, the *N. nomurai* population in summer 2021 was at a mid-bloom level. Through the maximum entropy (MaxEnt) method, the realized niches of the three most abundant large jellyfish species (*N. nomurai*, *Cyanea* spp., and *A. coerulea*) were fitted to explain their distribution patterns in the study area and responses to multiple environmental variables. The realized niches of large jellyfish differed substantially in terms of temperature and salinity. The feeding pressure of *N. nomurai* on zooplankton exceeded zooplankton productivity at the stations where *N. nomurai* assembled. Reductions in absolute and relative abundance were noted in small copepods at mid-bloom stations and bloom stations compared to non-bloom stations, indicating that blooms of large jellyfish may have an important influence on zooplankton abundance and community composition through top-down control.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15060729/s1, Figure S1: Pairplots of environmental variables, Figure S2: Distribution pattern of abundance (ind. km$^{-2}$) and biomass (kg km$^{-2}$) of *Aequorea* spp. (a,c) and Ulmaridae (b,d) in 2021 summer in the northern Chinese coastal seas, Figure S3: Univariate response functions of large jellyfish to environmental variables using the MaxEnt method.

Author Contributions: D.G., F.Z. and S.S. contributed to administration, conception, and design of the study. D.G. and P.W. executed the field investigation and sampling. D.G. carried out the sample processing, organized the database, and performed the statistical analysis. D.G., F.Z. and S.S. led the writing of this study. All authors have read and agreed to the published version of the manuscript.

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