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Characteristics and particularities of bacterial community variation in the offshore shellfish farming waters of the North Yellow Sea

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Bacteria in coastal waters drive global biogeochemical cycling and are strongly related to coastal environmental safety. The bacterial community in offshore shellfish farming waters of North China has its own characteristics and particularities, while the knowledge is limited. In this study, the bacterial community characteristics, the particularities of bacterial community in the waters with surface cold patches (SCPs) and the variation of pathogenic bacteria were investigated in the offshore shellfish farming waters in the North Yellow Sea (NYS) from 2017 to 2019. For all studied samples, Desulfobacterales acted as the keystone species taxon in microbial co-occurrence networks, and the proportional abundance of Actinobacteriota was found to be as low as 1.3%. The abundance of *Marinobacter* and *Synechococcus* was remarkably prominent in 13 genera with nitrogen-transforming function. The top two different bacterial functions in the spatial analysis (between the waters with SCPs and the ambient waters) were xenobiotics biodegradation and metabolism and metabolism of cofactors and vitamins, which were same with that in the seasonal analysis (between spring and summer). The abundance differences of most pathogenic bacteria analyzed in this study (11 out of 12 genera) also had the same variation dynamics between the spatial analysis and the seasonal analysis. An ANN predictive model for *Vibrio* abundance was constructed for *Vibrio* forecasting, with acceptable predictive accuracy. According to the above results, the bacterial community in the shellfish aquaculture waters in this study was characterized by the enhancing ability of nitrogen removal. Temperature was concluded as the predominant environmental factor to drive the variation of bacterial community function and pathogenic bacteria patterns in the offshore shellfish farming waters with SCPs. The results of this study will further our understanding of the bacterial community characteristics in offshore shellfish farming waters, and help for *Vibrio* forecasting and coastal environmental safety in aquaculture seawater.

KEYWORDS

shellfish aquaculture, bacterial community, *Vibrio*, surface cold patches, predictive model

Introduction

Bacteria are important components in the marine ecosystem, driving global biogeochemical cycling (Falkowski et al., 2008). They play important roles in maintenance and sustainability of microbial food webs and contribute to the rapid adjustment towards marine environmental changes and deterioration (Dash et al., 2013). The marine planktonic bacteria, especially those distributed near the coast, are of importance in people's life due to their close relationships to human and animal's health, industry and tourism, as about 60% of the world's population residing within 100 km of the coast (Vitousek et al., 1997).

Shellfish have been considered as "keystone species" and "ecosystem engineers" in coastal environment (Gutiérrez et al., 2003; Newell, 2004). The shellfish aquaculture industry, which is always located near the coast, has greatly developed in recent years to meet the growing global demand for protein (eg. 17.7 million tons in 2018) and contribute to world economic development (FAO, 2020). Shellfish are known to modify microbial assemblages by filtering water and transferring nutrients in the water system. On one hand, shellfish aquaculture can reduce water turbidity and improve nutrient recycling in anthropogenic impacted coastal environment, thus acting as an excellent nutrient bioextraction system in eutrophic areas. On the other hand, the suspension filtering and deposition through shellfish aquaculture are always involved in nutrient flux regulation and plankton speciation, which sometimes stimulates the growth of red tide species of plankton (Dumbauld et al., 2009; He et al., 2017). The increasing farming areas and stocking density have raised considerable concern, due to their influence on the marine environment (Yuan et al., 2010; Han et al., 2013). Even though there were some reports about the microbiome in the coastal environment, the bacterial community dynamics concluded from different studies are not always in strong agreement, because of different biogeographic and environmental features (Hartwick et al., 2019). The effect of shellfish aquaculture on the microbial community is quite complex, and the understanding of bacterial community characteristics in offshore shellfish farming waters is very limited.

The North Yellow Sea (NYS) is closed to a continental margin of major economic importance in China and Korea with unique oceanographic characteristics. Shellfish aquaculture is an important industry in the NYS and plays critical roles in the development of the marine economy. It is located near the coastal areas, especially around the islands off the coast, rearing Yesso scallop (*Patinopecten yessoensis*), Pacific oyster (*Crassostrea gigas*) and bay scallop (*Argopecten irradians irradians*), etc. In recent years, aquaculture and industrial wastes run-off and atmospheric deposition also affected the nutrient concentrations in the NYS, further leading to the change of microbial community and dynamics and even hypoxic dead zones (Lin et al., 2005; Tang, 2009). The NYS is always considered as one of the most complicated continental sea areas in the world, due to the seasonal variation of strong currents, wind stress and nutrient-enriched freshwater outflows in the shallow sea area (Hur et al., 1999). The Yellow Sea is also well known because of the Yellow Sea Cold Water Mass, which is a basin-scale water mass of relatively low temperature lying under the seasonal thermocline. Surface cold patches (SCPs) could be observed scattering around the Yellow Sea Cold Water Mass in boreal summer, in contrast to the ambient waters with relative higher sea surface temperature (Xia and Guo, 1983; Zou et al., 2001). The environmental particularity of SCPs was speculated to result in different bacterial communities in shellfish farming waters, while the principal environmental parameter involved in this was not clear. The dynamics of bacterial community variation in the NYS or even in its offshore shellfish farming waters are attracting increasing interest in recent years.

Pathogenic bacteria in coastal waters are strongly related to the health of human and animals. The environmental problems caused by microbiome change and the infections caused by pathogenic bacteria have been reported frequently in shellfish farming waters (Azandégbé et al., 2012; He et al., 2017). Among various potential pathogenic bacteria, the prevalence patterns of *Vibrio* spp. in marine environment are attracting widespread concern, since they include some pathogenic species that could infect to human and other organisms, such as *V. parahaemolyticus* and *V. vulnificus*. Pathogenic species of *Vibrio* spp. in seawater can cause seafood-borne illnesses through consumption of contaminated seafood and cause wound infections by exposure of an open wound to seawater, probably resulting in diarrhea, septicemia and even death (Hsieh et al., 2008). The forecasting of *Vibrio* abundance and breakout would help to prevent human illness by identifying and reporting the forecasting information and making it publicly available (Froelich et al., 2013; Izumiya et al., 2017).

In short, investigating the characteristics and dynamics of bacterial community variation and potentially pathogenic bacteria in the offshore shellfish farming waters in the NYS would contribute to coastal environmental safety. To achieve this, in the present study, seawater samples were collected from two offshore shellfish farming areas (the waters with SCPs and the ambient waters) in the NYS from every March to August in 2017-2019 with the aims to (1) illuminate the characteristics of bacterial community in the offshore shellfish farming waters and its seasonal dynamics; (2) reveal the particularities of bacterial community in the waters with SCPs; (3) analyze the variation patterns of pathogenic bacteria abundance and develop a predictive model for *Vibrio* abundance level.

Material and methods

Sample collection

Two sampling regions (location X and location Z) were set for the offshore Yesso scallop farming waters in the NYS (Figure S1). The geographic coordinates of location X and Z are N39°17’44”–E122°40’38” and N39°1’7”–E122°42’2”, respectively. According to Lü et al. (2010), the location X could be considered as within SCPs and the location Z was among the ambient region with relative higher sea surface temperature, because our three-year data also showed that the surface water temperature in summer in location X was generally 2-3°C lower than that in location Z. There were three sampling sites included in each region as three parallels. The sampling experiments were carried out from March to August in 2017-2019, as March to August was the main period of scallop farming. In this study, spring was defined from March to May, and summer from June to August. Seawater samples were collected at 3 m of depth where scallops were suspension-cultured and were then stored at 4°C within 1 h before further processing as previous description (Yu et al., 2019a; Yu et al., 2019b).

Determination of water parameters

Water temperature (T), salinity (Sal), pH and dissolved oxygen (DO) were monitored using an YSI Professional Plus meter (YSI, Yellow Springs, Ohio, USA) *in situ*. According to the procedures of the National Specification for Marine Monitoring (SOA of China, 2007), the concentration of TAN, NO_2–N, NO_3–N, PO_4-P and SiO_4-Si of the water were analyzed using indophenol blue spectrophotometric method, N-(1-naphthyl)-ethylenediamine dihydrochloride spectrophotometric method, Zn-Cd reduction method, Phosphomolybdenum blue spectrophotometric method and Silicon molybdenum yellow Spectrophotometry method, respectively. The concentration of Chl-*a* was measured with spectrophotometry after extraction with acetone (Lorenzen, 1967).

DNA extraction and high–throughput sequencing

One liter of seawater was filtered using 0.22 μm pore size membranes (Sagon, Shanghai, China) to enrich the microbial cells for each sample, which was then used for genomic DNA extraction using the Water DNA Kit (Omega, GA, USA) following the manufacturer’s instruction. DNA quality and quantity were analyzed by 1% agarose gel electrophoresis and NanoDrop spectrophotometer (Thermo Fisher Scientific, DE, USA). The high-throughput sequencing of the V3–V4 hypervariable region of 16S rDNA genes was performed using the Illumina HiSeq platform by Novogene (Beijing, China) with low-quality reads filtered.

Amplicon sequence analysis

The raw reads of the 16S rDNA sequence were processed using Quantitative Insights into Microbial Ecology (QIIME 2) pipeline (Bolyen et al., 2019). Paired-end reads were imported, then trimmed and denoised using DADA2 to remove chimeras and obtain amplicon sequence variants (ASVs). The abundance of nitrogen-transforming bacteria was calculated as log10 (relative abundance proportion * 10000 + 1). Taxonomy was assigned at the single nucleotide level to the ASVs using a feature classifier against a trained SILVA 138 SSU database. Alpha diversity and beta diversity were evaluated using the Shannon diversity index and unweighted UniFrac distances, respectively.

Statistical analysis

MicrobiomeAnalyst (http://www.microbiomeanalyst.ca) was used to compare the abundance and diversity of the bacterial community and to generate visual exploration, with ASV data and the metadata files (Chong et al., 2020). The functional profiles and metabolic pathways of the bacterial communities were predicted using Phylogenetic Investigation of Communities by Reconstruction of Unobserved States

(PICRUSt) 2 software (Douglas et al., 2020). KEGG database was used for the annotation of predicted genes. STAMP software was used for differential analysis of functional profiles (Parks et al., 2014). The co-occurrence ecological network was analyzed using the online Molecular Ecological Network Analysis (MENA) pipeline (http://ieg2.ou.edu/MENA) (Deng et al., 2012), and the network construction was performed using Cytoscape software (Shannon et al., 2003). Redundancy analysis (RDA) was conducted to reveal the effect of environmental factors on the abundance and diversity of bacterial communities using CANOCO software (version 5) (Šmilauer and Lepš, 2014). Correlations between the *Vibrio* abundance and environmental factors were investigated through Spearman's correlation analysis and Pearson's correlation analysis using SPSS 26 (SPSS Inc. Chicago, IL) statistical software package. P-value<0.05 was considered statistically significant. P-value<0.01 was considered extremely significant.

Construction of the predictive model

A predictive model was constructed for the level of *Vibrio* abundance in this study. First, the co-occurrence relationships between the *Vibrio* abundance and the bacterial abundance at order level were investigated using MENA pipeline to get the order taxa (VAO) that were directly associated with the *Vibrio* variation. Second, all tested environmental factors and the VAO abundance were analyzed for their correlation with the *Vibrio* abundance in the next month using Spearman's correlation analysis and Pearson's correlation analysis, to get the factors (VAF, including environmental factors and order taxa) that had significant associations with *Vibrio* variation in the next month in both results of correlation analysis. Third, three levels of *Vibrio* relative abundance were set as High Level (proportional abundance ≥ 2%), Moderate Level (2% > proportional abundance ≥ 0.5%), and Low Level (proportional abundance< 0.5%). The multi-layer feed-forward artificial neural network (ANN) modeling was used to construct and test the neural networking by SPSS 26, using the VAFs as input variables and the *Vibrio* level in the next month as output variable. The feasible ANN model was constructed by trial and error. The ANN was classified into three layers, including input, hidden and output layers. The three layers processed signals and searches to obtain the best linear and nonlinear relationships between the input and output data. In this model, about 70% of the input data was used for training, with the remaining 30% used for testing. Levenberg–Marquardt algorithm was applied for modeling and calculating the weights among the input, hidden and output layers through modifying the learning rate and the number of hidden layers and neurons.

Results

Composition, function and co-occurrence of bacterial community

High-throughput sequencing of 16S rDNA was performed to obtain 12,988,676 sequences, which were clustered into 16,747 ASVs. A total of 415 orders across 56 phyla in all samples were detected through direct taxonomical classification and annotation. Proteobacteria (58.6%), Bacteroidetes (18.6%), Cyanobacteria (12.3%), Firmicutes (3.4%) and Verrucomicrobiota (2.0%) were dominant phyla in seawater accounting for 95.0% of the total abundance (Figure 1A). The average proportional abundance of Actinobacteriota was 1.3%. The abundance of nitrogen-transforming bacteria was investigated, and 13 genera were found in our samples (Figure 2). Among them, *Marinobacter* and *Synechococcus* were consistently present in all samples, and their abundance was markedly higher than that of the other nitrogen-transforming bacteria.

The KEGG pathways that the bacterial community involved were predicted to explore the potential biosynthetic and ecological functions. By searching against the KEGG database using PICRUSt2, a total of 188 third-level pathways were identified, including Valine, leucine and isoleucine biosynthesis, C5-Branched dibasic acid metabolism and Biosynthesis of ansamycins, etc. After grouping into second-level pathways, 36 pathways were determined, including carbohydrate metabolism, infectious disease and replication and repair, etc. For the further grouped first-level pathways, six types were identified (Figure 1A). The co-occurrence analysis was performed to investigate the interaction relationships among specific taxa and to construct the microbial co-occurrence networks. A total of 114 orders (belong to 22 phyla) were included in the network construction (Figure 1B). In general, complex co-occurrence relationships were showed for the whole bacterial community in this result. Among all orders listed in this work, the orders in Proteobacteria processed dominate positions in co-occurrence relationship, which occupied 48.1% of the co-occurrence degree in the whole microbiota. Desulfobacterales was suggested to be the keystone species taxon, as it was most directly associated among all orders in this network.

For the composition variation of bacterial community between spring and summer, some apparent patterns could be observed among different years, indicating that bacterial compositions differed in interannual patterns (Figure 3A). In the PCA analysis of bacterial beta diversity, the bacterial community differed obviously between spring and summer (Figure 3B). This difference could be investigated more clearly in the analysis among different months. Progressive changes could be outlined in bacterial community patterns from March

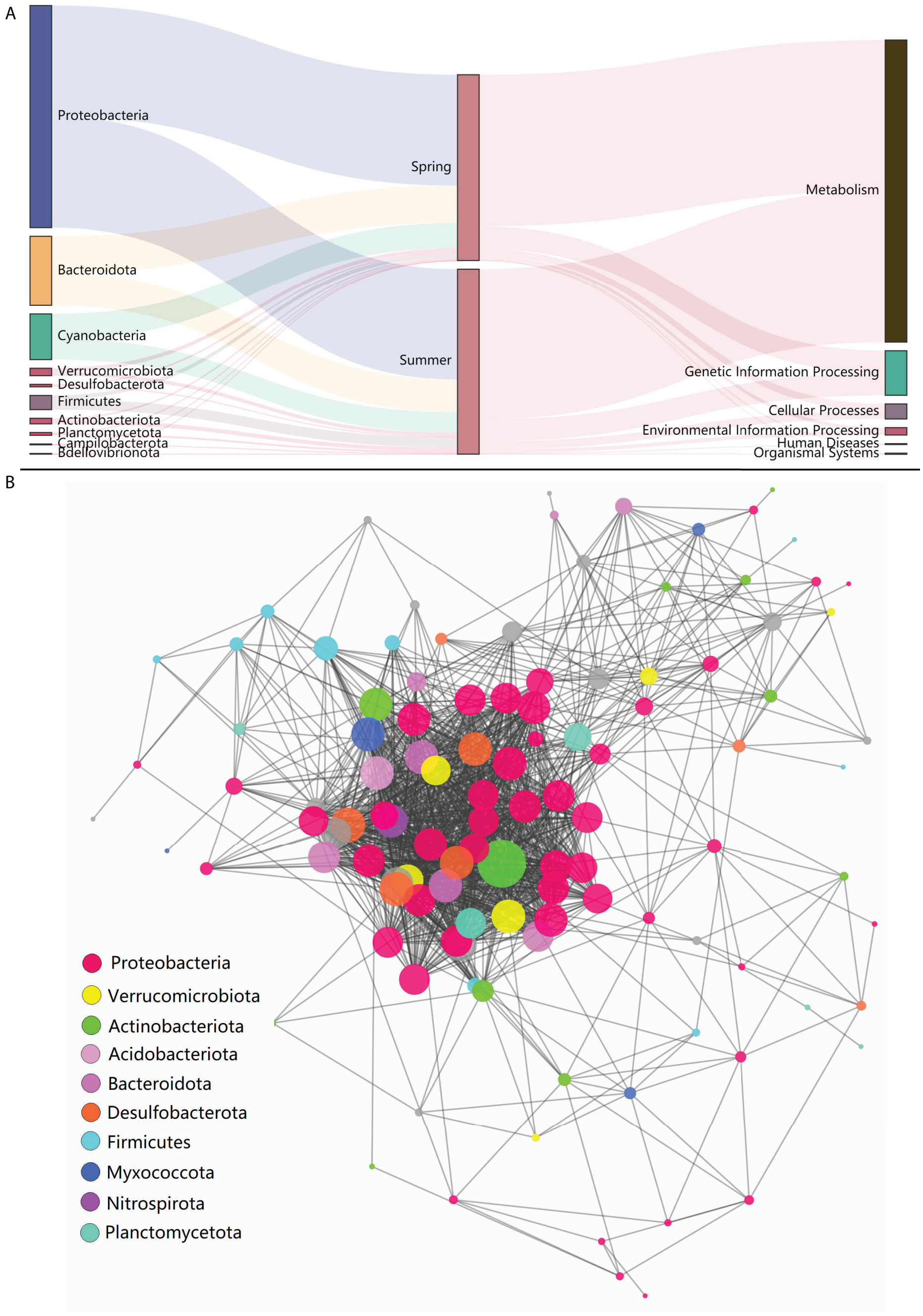

FIGURE 1
Composition, function and co-occurrence of bacterial community. **(A)** Distribution profiles of phylum taxa and functional pathways of the bacterial community; **(B)** Microbial co-occurrence networks at phylum-order level.

to August (Figure 3B). Microbiota comparisons were conducted between spring and summer by LEfSe analysis. Firmicutes and Bacteroidota were identified as discriminative features at phylum level (Figure 3C). Seven genus taxa were identified as discriminative features at genus level, in which *Vibrio* genus was found to be significantly abundant in summer (Figure 3C).

The variation of bacterial functional patterns was pronounced at seasonal scales, and the seasonal variation could be discriminated from PCA analysis (Figure 3D). The differently predicted pathways between spring and summer were mainly related to metabolism and cell functional pathways, in which the top two different pathways were xenobiotics biodegradation and

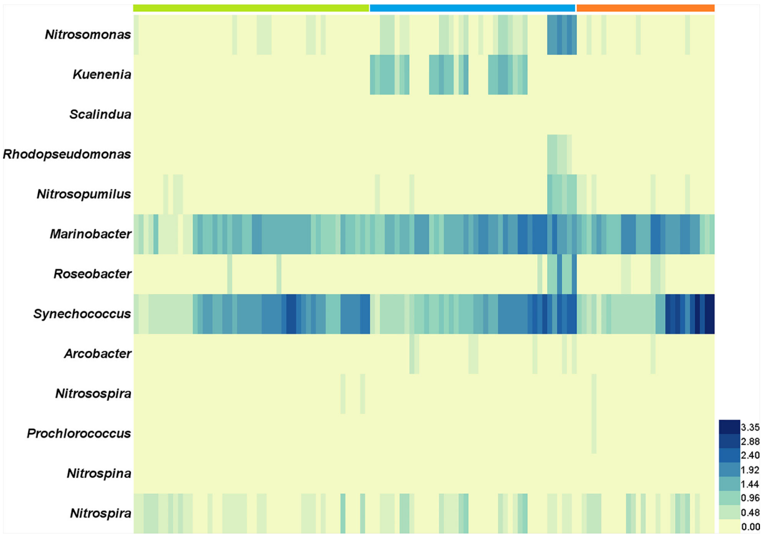

FIGURE 2
The abundance variation of 13 genera of nitrogen-transforming bacteria in the offshore shellfish farming waters. The x-axis is samples in chronological order. Green: 2017; blue: 2018; orange: 2019.

metabolism and metabolism of cofactors and vitamins (Figure 3E). The pathways related to infectious disease were also found to be differently enriched between spring and summer.

The composition and function characteristics of bacterial community in the waters with SCPs

The difference in alpha diversity was non-significant between the two locations (Figure 4A). Differences could be found in some of the most dominant phyla between locations, that the samples from location X had a higher relative abundance of Bacteroidota and Actinobacteriota, and lower relative abundance of Firmicutes (Figure 4B). The differences became even more pronounced in specific seasons or months. For instance, in summer, the variation of six phyla, such as Actinobacteriota, Planctomycetota and Patescibacteria, etc., had significantly different patterns between the two locations (Figure 4C). When further focused on the situation of August, Actinobacteriota was identified as the only discriminative feature at phylum level between the two locations by LEfSe analysis. The functional patterns of the bacterial community did

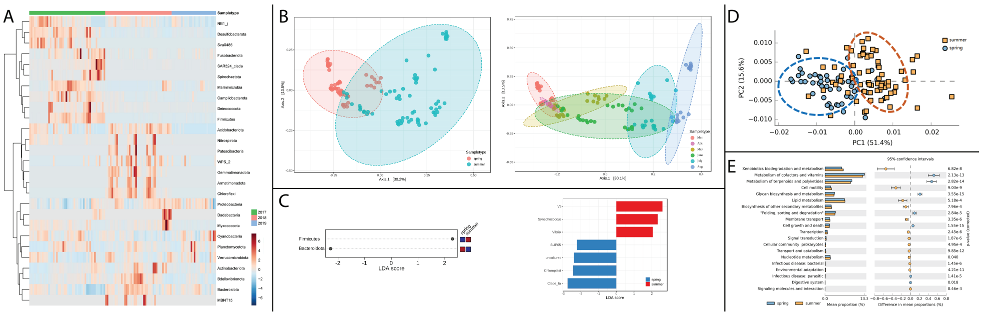

FIGURE 3
Temporal variation of bacterial community and function in shellfish farming areas. **(A)** Annual abundance heatmap at phylum level; **(B)** Seasonal (left) and monthly (right) variation of alpha diversity; **(C)** Discriminative features of bacterial community at phylum level (left) and genus level (right); **(D)** Principal components analysis (PCA) of bacterial functional characterization; **(E)** The functional pathways in significantly temporal variation patterns.

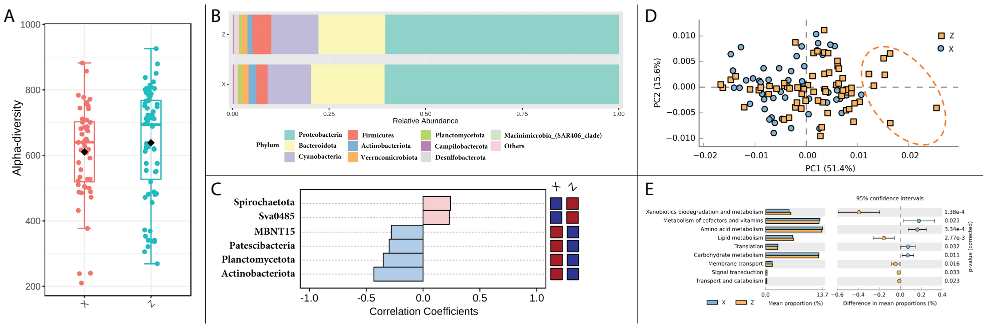

FIGURE 4
Spatial variation of bacterial community and function in shellfish farming areas. **(A)** Bacterial alpha diversity; **(B)** Bacterial relative abundance in phylum level; **(C)** The phyla in significantly spatial variation patterns. **(D)** Principal components analysis (PCA) of bacterial functional characterization; **(E)** The functional pathways in significantly spatial variation patterns.

not differ markedly between locations, but still showing a few differences that could be observed in PCA analysis on PC1 axis, which explained 51.4% of the total variation (Figure 4D). The differently predicted pathways between locations were mainly enriched in metabolism pathways, in which the top two different pathways were xenobiotics biodegradation and metabolism and metabolism of cofactors and vitamins (Figure 4E).

Variation patterns of pathogenic bacteria abundance

During the sampling period of different months, the *Vibrio* abundance generally increased with warming temperature (Figure 5). In order to fully investigate the seasonal variation of potential pathogenic bacteria, the abundance of 12 genera of

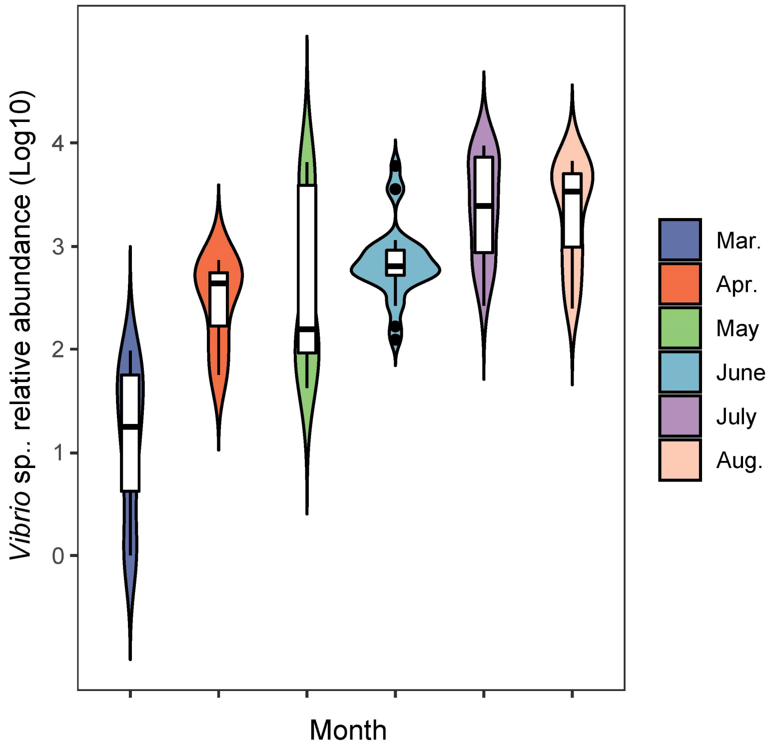

FIGURE 5
The monthly variation of *Vibrio* abundance in shellfish farming areas.

common pathogenic bacteria were analyzed (Figure 6). For the comparison between spring and summer, the average abundance of five genera were higher in spring than in summer (fold of (log10 abundance): 1.02-2.70), including *Shewanella*, *Pseudomonas*, *Streptococcus*, *Campylobacter* and *Escherichia*. The average abundance of the other seven genera were lower in spring than in summer (fold of (log10 abundance): 0.34-0.97), including *Vibrio*, *Aeromonas*, *Photobacterium*, *Francisella*, *Staphylococcus*, *Clostridium* and *Legionella*. For the comparison between the two locations, the average abundance of four genera were higher in location X than in location Z (fold of (log10 abundance): 1.02-1.41), including *Shewanella*, *Streptococcus*, *Campylobacter* and *Escherichia*. The average abundance of eight genera were lower in location X than in

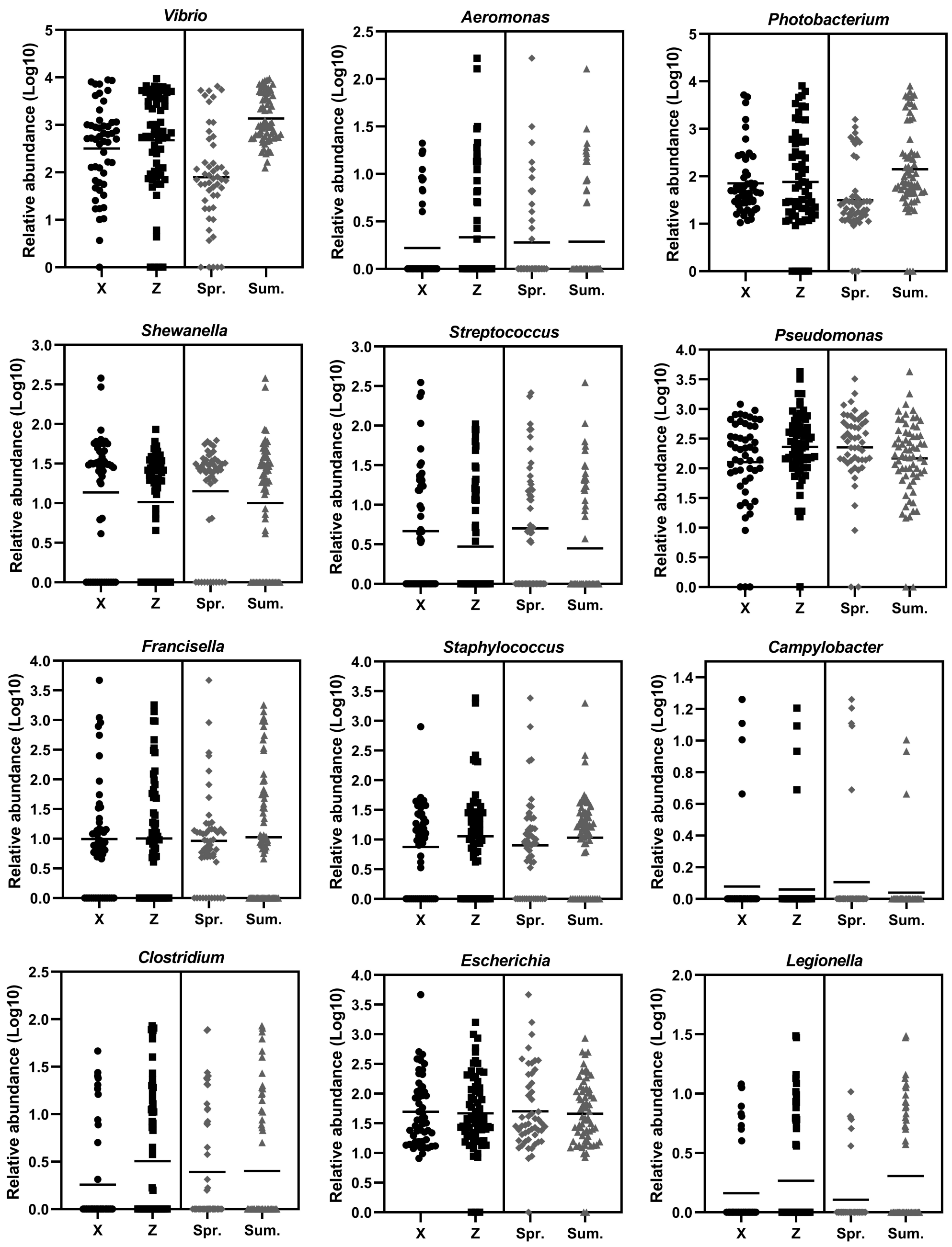

FIGURE 6
The temporal and spatial variation of the abundance of 12 genera of potential pathogenic bacteria. X indicates location X. Z indicates location Z. Spr. indicates spring. Sum. indicates summer.

location Z (fold of (log10 abundance): 0.51-0.99), including *Vibrio*, *Pseudomonas*, *Aeromonas*, *Photobacterium*, *Francisella*, *Staphylocockus*, *Clostridium* and *Legionella*.

Relationships between environmental factors and bacterial community

The relationships between the environmental factors and bacterial community were analyzed and were presented in the RDA biplot (Figure 7A). The first and second RDA axes explained 45.88% and 12.14% of the total variation, respectively. The top three significant environmental factors that constrained the bacterial community were DO, T and Chl-*a*, with the explaining rate of 33.6%, 33.4% and 28.3%, respectively. T and Chl-*a* had a strong negative influence on the abundance of most phyla taxa located in the upper right quadrant and the lower right quadrant, while DO had a strong positive influence instead. WPS-2 generally had an opposite relationship with environmental factors compared to some other phyla that had a positive relationship with DO and a negative relationship with T and Chl-*a*. T and DO almost had no influence on the abundance of SAR324. For specific pairs of environmental factors, T and DO had opposite influences on the bacterial community, while Chl-*a* and SiO_4 had similar influences on the bacterial community. Through Spearman's correlation analysis and Pearson's correlation analysis, the environmental factors that were significantly associated with the *Vibrio* abundance in both analyses were identified, including T, DO, Chl-*a*, SiO_4, PO_4 and Si/N (Figure 7B). The environmental factors that had correlation coefficients above 0.5 in both analyses were T and SiO_4.

Prediction for *Vibrio* abundance level

Before the construction of ANN model, 41 VAOs were found to be directly associated with the *Vibrio* abundance. After the correlation analysis, 32 VAFs were found to be significantly associated with the *Vibrio* abundance in the next month. One hidden layer and 8 neurons in the hidden layer were finally used for the ANN model training, with structure exhibition in Figure 8A. The predictive accuracy was shown in Table S1. The mean predictive accuracy for training samples was 95.8%, with each sub-accuracy above 85%. The mean predictive accuracy for testing samples was 96.4%, with each sub-accuracy above 85%. The prediction probability can also be seen in Figure 8B, which showed acceptable performance of the ANN model for the *Vibrio* abundance level prediction.

Discussion

Characteristics of bacterial community in the offshore shellfish farming waters and its seasonal dynamics

The bacterial phyla dominant in our samples were investigated and were generally consistent with previous studies, in which Proteobacteria, Bacteroidetes, Cyanobacteria and Actinobacteriota, etc. were characterized as the top ubiquitous phyla in the Yellow Sea or other adjacent sea areas (Yu et al., 2018; Kim et al., 2019). However, the proportional abundance of Proteobacteria in this study (58.63%) is relatively higher than that in some other studies (generally below 50%) (He et al., 2017; Yu et al., 2018). The higher abundance of

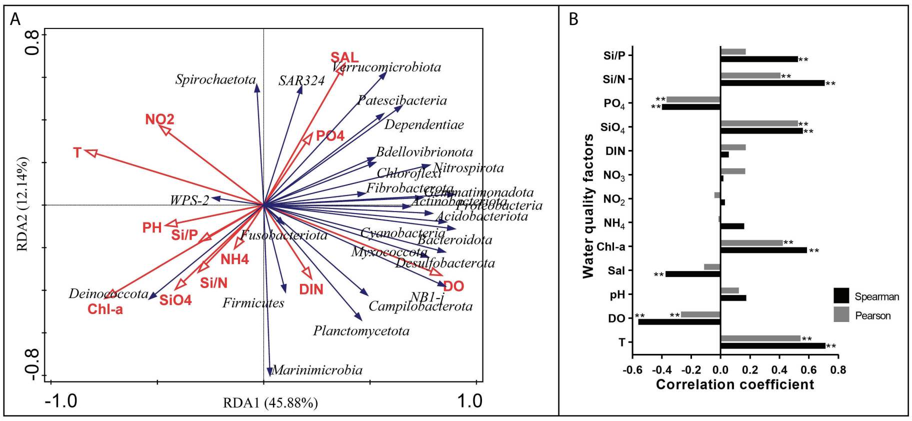

FIGURE 7
Relationships between environmental factors and bacterial community. **(A)** RDA ordination plot for the first two principal dimensions of the relationships between the phylum taxa abundance and environmental factors in shellfish farming areas. **(B)** The correlation between *Vibrio* abundance and environmental factors using Spearman's correlation analysis and Pearson's correlation analysis. "**" represent an extremely significant difference (P<0.01).

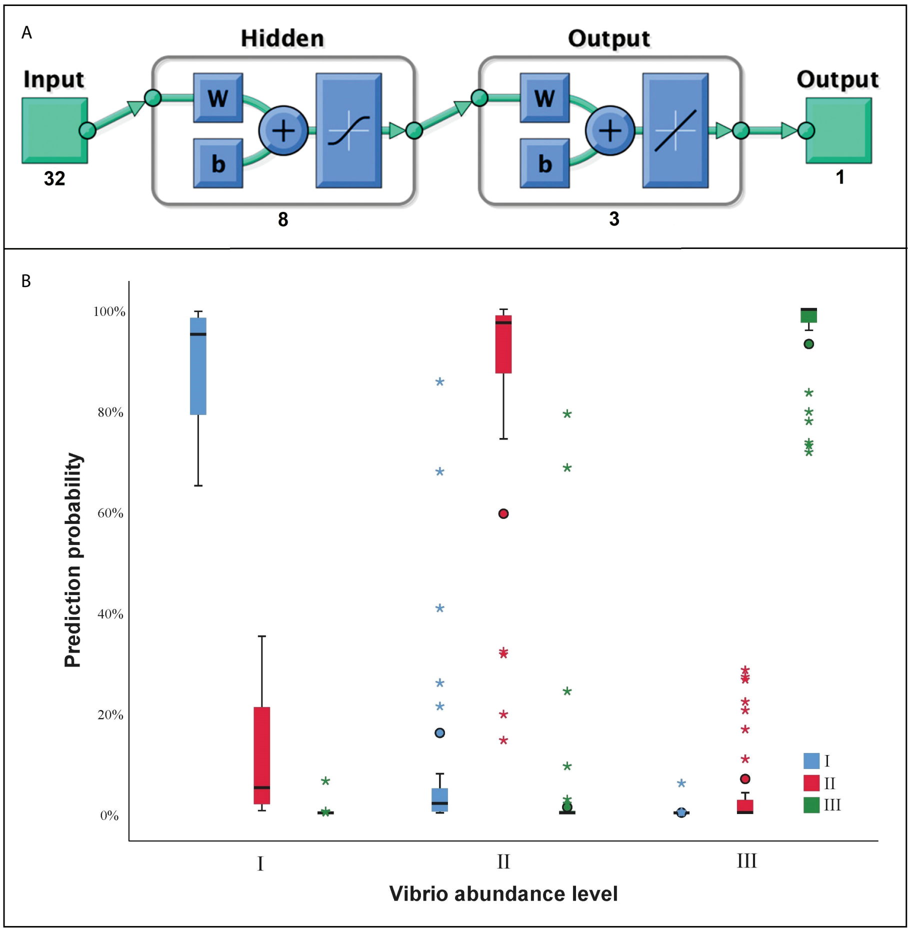

FIGURE 8
The artificial neural network (ANN) for *Vibrio* abundance prediction. **(A)** The structure of ANN layer; **(B)** The prediction probability of ANN model at three abundance level of *Vibrio*. "I, II, III" indicate the three levels of prediction.

Proteobacteria is in agreement with their dominant positions in co-occurrence relationships of microbiota in this study. Proteobacteria is always the dominant bacterial taxon in seawater, and its further increase may preempt the space of other bacteria and reduce microbiota diversification.

The seasonal and monthly variation of the bacterial community was more pronounced than inter-annual variation, mainly due to the intra-annual environmental changes. This followed common sense and was in agreement with other reports. Kim et al. (2019) found that bacterial abundance closely fitted a chronological seasonal pattern in the bays of the Yellow Sea, and temporal patterns of microbial communities were also observed in the New Jersey coast and the Pearl River Estuary area (Nelson et al., 2008; Xie et al., 2018). The monthly progressive changes of bacterial community patterns were probably caused by one factor that was in continuously unidirectional changes, which was most likely the water temperature. Water temperature was always considered as the most important environmental factors that drove the bacterial community (Kim et al., 2019). We can also have this inference according to the results of RDA analysis. The relative high T and low DO in summer may play important roles in constraining and shaping the bacterial community. Except for T and DO, in the present study, Chl-*a* was another important environmental factor that was associated with bacterial community variation. Previous studies also reported that the Chl-*a* was the key predictor of microbiota, and some bacterial taxa were clearly correlated with Chl-*a* (Kim et al., 2019). It should be noted that shellfish aquaculture always has a great influence on the phytoplankton abundance and community, as phytoplankton is the main food source of shellfish. Thus, the bacterial community in the offshore shellfish farming waters would have specific structure patterns, resulted from the phytoplankton variation.

In the present study, Desulfobacterales acted as the keystone species taxon in co-occurrence relationships of microbiota and may function in nitrogen metabolism with further effect on other bacterial communities through nitrogen cycling. Desulfobacterales plays important roles in nitrogen cycling and removal, and could contribute about 12% of the genes in nitrogen pathways (Nie et al., 2021). Recently, dominant sulfate reducing microorganisms (SRM) within Desulfobacterales were also reported in the sediments of coastal oyster aquaculture ecosystems (Mara et al., 2021). The proportional abundance of Actinobacteriota (1.3%) in this study was obviously lower than that in other studies, in which it was reported up to 5%-20% (He et al., 2017; Yu et al., 2018). The abundance of Actinobacteriota has been proved to be strongly correlated with nitrogen cycling, and it can thrive under oligotrophic conditions and be suppressed with high organic matter and inorganic nutrient availability (Kulaš et al., 2021; Wang et al., 2021). The impact of shellfish farming on nitrogen cycling has been investigated in previous reports by analyses of water/sediment quality parameters (Erler et al., 2017; Jiang et al., 2020; Pan et al., 2021). The understanding of the bacterial community characteristics involved in nitrogen cycling in shellfish farming water is very limited. In order to further explore the details of nitrogen-transforming function of bacterial community, the commonly reported nitrogen-transforming bacteria (Kuypers et al., 2018) were investigated in our study. The presence of *Marinobacter* and *Synechococcus* was remarkably prominent in all 13 genera with nitrogen-transforming function. *Marinobacter* and *Synechococcus* were mainly responsible for the process and remove of organic nitrogen and NH_4^+ in seawater. The bacterial community characteristics involved in nitrogen cycling were rarely reported in the Yellow Sea (Bai et al., 2012; Yu et al., 2018; Jing et al., 2019; Yang et al., 2022). Together, the above results indicated that the bacterial community in the shellfish aquaculture waters in this study was characterized by the enhancing ability of nitrogen removal.

The particularities of bacterial community in the waters with SCPs

The bacterial community between the two locations had less variation compared to the seasonal variation. Greater temporal variation and less spatial variation of the bacterial community were also found in the Yellow Sea area and some aquaculture sea areas (He et al., 2017; Kim et al., 2019). Spatial differentiation may superficially mask the environmental effects only when the physicochemical factors are closely related to the spatial conditions. Otherwise, persistent environmental heterogeneity would cover the geographic difference and shape the microbial diversity directly at intermediate spatial scales (Crossland et al., 2005; Wang et al., 2015).

SCP is an important geographic feature of the Yellow Sea and some other seas. Its formation results from the upwelling, which carries the cold deep water up to the sea surface. The more water exchange in vertical direction may change the water environment and bring more nutrients and attachments from the bottom water layer to surface water layer (Lü et al., 2010; Huang et al., 2018; Lin et al., 2019). In our study, the bacterial community variation between the two locations had more significant differences in summer than that in spring. It was suggested that different geographic conditions may lead to the variation of the bacterial community, mainly through the environmental factor variation. Environmental factors always play key roles in the spatial variation of the bacterial community. For instance, the different concentration levels of Chl-*a* were reported to be in charge of the bacterial community diversity between two stations of the Yellow Sea (Kim et al., 2019).

Interestingly, consistency was found in two points between the spatial analysis (location X *vs* location Z) and the seasonal analysis (spring *vs* summer). First, the top two differently predicted pathways of microbial function in both spatial analysis and seasonal analysis were same, and they were xenobiotics biodegradation and metabolism and metabolism of cofactors and vitamins, which may indicate the occurrence of environmental stresses and resultant activation of stress responses (Huo et al., 2019; Ye et al., 2021). Second, 11 of the 12 common genera of pathogenic bacteria (except for *Pseudomonas*) had the same dynamic patterns in the spatial and seasonal analyses, in other words, if the abundance of one pathogenic bacterial genus was higher (or lower) in the waters with SCP than that in ambient waters, it was most likely that the abundance of the pathogenic bacterial genus was also higher (or lower) in spring than that in summer. Temperature was the predominant environmental factor that drove the seasonal dynamic of bacterial community variation between spring and summer. Temperature was also the most critical feature that distinguished the waters with SCP from ambient waters. As there are highly similar dynamic patterns of bacterial community variation between the seasonal and spatial analyses, it is reasonable to speculate that temperature is the predominant environmental factor to drive the variation of bacterial community function and pathogenic bacteria patterns in the offshore shellfish farming waters with SCPs.

Vibrio abundance variation and the predictive model construction

The *Vibrio* abundance generally increased with the elevated water temperature and showed clear seasonal patterns, consistent with some other reports (Hsieh et al., 2008; Vezzulli et al., 2009; Oberbeckmann et al., 2012; Froelich et al., 2015). The enrichment of the pathways related to infectious disease in summer suggested that the risk from pathogenic bacteria increased in summer and need more attention. Shellfish aquaculture was found to play important roles in shaping *Vibrio* characteristics (Joye and Anderson, 2008; Feinman et al., 2018), probably through disturbing the structure of phytoplankton and zooplankton, both of which served as determinants of *Vibrio* presence and abundance (Johnson, 2015). There were many reports about the *Vibrio* variation in water environment, in which the key environmental factors that affect *Vibrio* community were identified and the variation tendency of *Vibrio* was speculated based on environmental factors (Hsieh et al., 2008; Oberbeckmann et al., 2012; Johnson, 2015). In the present study, except for T, SiO_4-Si was also found to be significantly associated with the *Vibrio* abundance. We speculate that: On one hand, SiO_4-Si exists in the sea-water column as a sol state, which could provide attachment for the growth of *Vibrio*. On the other hand, phytoplankton and Chl-*a* are key drivers of the bacterial community. SiO_4-Si is an important component of some phytoplankton taxa such as diatom (DeLuca et al., 2020) and could thus influence the *Vibrio* abundance. However, as shown in Figure 6, the *Vibrio* abundance in the same month of the different years differed apparently based on the three-year data, suggesting that it is infeasible to estimate the *Vibrio* abundance only according to environmental factors or historical values of *Vibrio* abundance.

In recent years, some studies of model establishment and *Vibrio* prediction have been reported. Hidemasa Izumiya et al. conducted a multi-coastal study to examine relationships between environmental factors and *Vibrio* and build a linear regression model for *Vibrio* prediction (Izumiya et al., 2017). Brett Froelich et al. conducted a five-parameter mechanistic model to predict *Vibrio* abundance in the river based on environmental processes (Froelich et al., 2013). According to the previous reports, the construction of *Vibrio* predictive model is better to be improved in two points. First, environmental factors were always included in the predictive model construction as the only type of input variables in most of the previous studies. Aside from the environmental factors, *Vibrio* are also likely to respond to, or be associated with, many other aquatic bacterial species (Johnson, 2015) in some ways, such as quorum sensing. The interactions between *Vibrio* and other bacterial communities should also be included in the studies of *Vibrio* forecasting. Second, among the environmental factors, one factor usually has weak or strong dependence on others. The exclusive effect of one environmental factor on *Vibrio* abundance is hard to assess. The relationship between *Vibrio* and input variables of the predictive model is not a direct correlation but rather the relation to which many variables contribute. Multiple regression analysis is not good at the modelling with too many input variables in the construction of *Vibrio* predictive model. Therefore, an integrated model that has environmental factors and bacterial species as input variables should be established to better understand the variation of *Vibrio* abundance.

Our study improved the *Vibrio* predictive modelling by (1) including the environmental factors as well as bacterial species as input variables for more accurate prediction of *Vibrio* abundance; (2) using ANN to solve the complex mapping relationships between dozens of input variables and *Vibrio* abundance and to construct the predictive model. The accuracy was acceptable, with 95.8% of accuracy for training samples and 96.4% for testing samples. The spatial scope of model application and the accuracy will be further improved in our future studies through the inclusion of more data for model training, as the *Vibrio* prediction is better to be processed according to regional differences, rather than using a "one-size-fits-all" approach. The results of this study will contribute to the monitoring and modelling efforts of *Vibrio* abundance in the NYS for area-specific *Vibrio* forecasting and public health risk prediction.

Conclusions

The main conclusions drawn from this study are as following (Figure S2):

- The bacterial community in the shellfish aquaculture waters in this study was characterized by the enhancing ability of nitrogen removal.
- Temperature was the predominant environmental factor to drive the variation of bacterial community function and pathogenic bacteria patterns in the offshore shellfish farming waters with SCPs.
- An ANN predictive model for *Vibrio* abundance was constructed in this study for *Vibrio* forecasting, with acceptable predictive accuracy.

Data availability statement

The data presented in the study are deposited in the GenBank repository, accession number PRJNA861897.

Author contributions

LG: Methodology, Formal analysis, Writing original draft; ZY: Investigation, Sample collection; CL and NK: Sample collection; LW and LS: Writing Review & Editing, Supervision, Funding acquisition. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.997817/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Location X and location Z were set as the two sampling regions for the offshore Yesso scallop farming waters in the NYS. Horizontal distribution of mean sea surface temperature in August of 2004–2008 was showed. This figure is cited from (Lü et al., 2010).

SUPPLEMENTARY FIGURE 2
Graphical abstract of this study.

SUPPLEMENTARY TABLE 1
The prediction accuracy of ANN model for *Vibrio* abundance for both training samples and testing samples.

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