frontiers | Frontiers in Marine Science

TYPE Original Research
PUBLISHED 21 May 2025
DOI 10.3389/fmars.2025.1581190

Seasonal dynamics of microbial communities link to summer-autumn aquaculture disease outbreaks in Sanggou Bay

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RECEIVED 21 February 2025
ACCEPTED 28 April 2025
PUBLISHED 21 May 2025

CITATION
Lu L, Ni L, Ai C, Zhang D, Zheng P, Li X, Liu X and Dang H (2025) Seasonal dynamics of microbial communities link to summer-autumn aquaculture disease outbreaks in Sanggou Bay.
Front. Mar. Sci. 12:1581190.
doi: 10.3389/fmars.2025.1581190

Marine microorganisms play a vital role in aquaculture by influencing water quality and the health of cultured species. Relative to conventional mono-species aquaculture, integrated multi-trophic aquaculture is more environmentally friendly and economically sustainable. However, the temporospatial dynamics of the microbial community in different aquaculture modes and their roles in the seasonal diseases of aquacultural organisms are largely unknown. Here, the seawater bacterial communities and potential pathogens were investigated over thirteen months in three different aquaculture types in Sanggou Bay, a typical maricultural area with nearly 60 years of history. Seasonality played a primary role, while aquaculture type played a subtle role in shaping the bacterioplankton community. Diverse potential pathogens were identified, and *r*-strategist bacteria, most of which were opportunistic pathogens and typified by *Vibrio* species, increased and dominated in late summer and autumn, a period of high-risk disease outbreaks in mariculture organisms. Network analyses indicated that the increase in *r*-strategist bacteria reduced the complexity of microbial interactions, and *Vibrio halioticoli* (OTU1389), a hub species with extensive positive correlations to other *Vibrio* OTUs, likely contributed to the increase of pathogenic vibrios due to its macroalgae degradation capability. The major potential pathogenic *Vibrio* OTUs were further corroborated by genome analyses and environmental simulation experiments using pathogenic *Vibrio* isolates, including two new species. Moreover, we found seawater dissolved oxygen, temperature, and transparency correlated significantly with the bacterioplankton temporospatial dynamics and the seasonal outbreaks of bacterial pathogens. Our results emphasize the necessity of synchronically monitoring the bacterial community, its pathogens-stimulating species, such as *V. halioticoli* and other macroalgae-degrading bacteria, and critical physicochemical parameters for predicting and preventing pathogen outbreaks in mariculture.

KEYWORDS

seawater bacterial community, monthly dynamics, bacterial pathogens, seasonal diseases, *Vibrio*, marine deoxygenation, integrated multi-trophic aquaculture

1 Introduction

Aquaculture is becoming an increasingly important food source, particularly animal proteins and micronutrients (Naylor et al., 2021). Integrated multi-trophic aquaculture (IMTA) is generally designed as a co-cultivation system of different species belonging to distinct trophic levels (Nissar et al., 2023). It has been advocated as a promising solution for sustainable aquaculture, achieving economic benefits and environmental friendliness (Chopin et al., 2001; Troell et al., 2009; Buck et al., 2018; Chang et al., 2020; Knowler et al., 2020). Numerous studies have shown the benefits of IMTA systems. For instance, Yokoyama (2013) showed that integrating oysters into sea cucumber farming significantly increased the sea cucumbers' specific growth rates. Li et al. (2014) reported that polyculture of sea cucumbers, jellyfish, and shrimp improved total organic carbon utilization efficiency by 18.9% compared to monoculture of sea cucumbers. Nobre et al. (2010) found that IMTA increased the farm profits. Han et al. (2017) showed that oyster-seaweed co-culture turned the oyster farming seawater from a net CO_2 source into a net CO_2 sink. Generally, the IMTA systems enhance resource utilization and aquaculture production, improve environmental quality, reduce eutrophication, increase CO_2 sequestration, and mitigate ocean acidification (Ridler et al., 2007; Han et al., 2013; Hadley et al., 2016; Mahmood et al., 2016a). IMTA has been widely developed in many countries, such as China, Canada, Chile, Australia, the USA, and Japan (Troell et al., 2003; Granada et al., 2016; Buck et al., 2018; Wartenberg et al., 2017).

However, the persistent threat of diseases remains a considerable obstacle to aquaculture (Aly and Fathi, 2024). Microbial infectious diseases cause substantial economic losses in the aquacultural industry, amounting to billions of US dollars annually (Lafferty et al., 2015; Mohamad et al., 2019; Patil et al., 2021; Vaiyapuri et al., 2021; Abd El-Hack et al., 2022; Rowley et al., 2024). Studies have reported that some bacterial pathogens are the main causes responsible for disease outbreaks, leading to massive mortality in cultivated fish, shellfish, and shrimps (Toranzo et al., 2005; Sawabe et al., 2007; Janda, 2014; Travers et al., 2015; Yang et al., 2021). Moreover, some aquaculture-originated bacteria are also human pathogens, causing foodborne or direct-contact infections (Baker-Austin et al., 2018). Besides, due to the widespread use of antibiotics in aquaculture, the appearance of antibiotic-resistant pathogens makes disease prevention and control more difficult (Cabello et al., 2016; Preena et al., 2020; Algammal et al., 2023).

The case of Sanggou Bay, with its approximately 60-year history of aquaculture (Li et al., 2018) and an annual production of over 240,000 tons of seafood from a 100 km^2 aquaculture area, demonstrates the potential of IMTA (Fang et al., 2016; Hossain et al., 2022). Since adopting the IMTA model in the late 1980s, Sanggou Bay has not only increased its economic profits but also improved its ecosystem functions, including enhanced carbon sequestration through macroalgae co-cultivation (Fang et al., 2016; Li et al., 2016). Nevertheless, seasonal mortality of farmed organisms, typically peaking in late summer and early autumn, remains challenging (Mao et al., 2006). In semi-enclosed bays, tidal currents govern coastal hydrodynamics (Zeng et al., 2015). Aquaculture occupies nearly 90% of Sanggou Bay's water surface and extends well outside the bay (Fu et al., 2013). The high aquaculture density reduces current velocity, prolongs nutrient retention, and increases phytoplankton bloom risk and disease susceptibility in cultured species (Mao et al., 2006; Wang et al., 2018a). In 2019, the Pacific abalones (*Haliotis discus hannai* Ino) suffered mortality rates of 30%-60%, Zhikong scallops (*Chlamys farreri*) 10%-20%, and Yesso scallops (*Patinopecten yessoensis*) 10%-30%, with the highest mortality rates observed in late summer and early autumn. Additionally, diseases in cultured and wild seaweed started in May and became the most severe in September (data from local enterprises and farmers). Therefore, predicting pathogen outbreaks is particularly important for aquaculture and human health. As conventional culturing-based methods are less time-efficient or pathogen-specific, high-throughput methods are more suitable for pathogen detection.

Microbial communities have been proposed as one of the most critical indicators for microbial disease development in aquaculture systems (Bentzon-Tilia et al, 2016). Theoretically, microbial communities could depict the health status of the aquaculture environments and ecosystems, providing valuable information about the emergence of diseases (de Bruijn et al., 2018; Liu et al., 2020). Recent studies have indicated that long-term aquaculture could change the bacterial community structure (Liang et al., 2019; Zhang et al., 2019; Liu et al., 2020), and microbes could participate in some important physiological processes of cultured species in IMTA, such as influencing the immune response of fed species and regulating the metabolic and nutritional pathways (Bentzon-Tilia et al, 2016; Deng et al., 2019; Califano et al., 2020; Langlois et al., 2021; Zhang et al., 2022). However, few studies have investigated the link between pathogen population behaviors and microbial community dynamics in aquaculture (Fu et al., 2022; Zhang et al., 2022). Disease outbreaks remain a high risk in aquaculture, highlighting the necessity for a holistic understanding of the microbial community's roles in diseases and comprehensive pathogen detection methods.

Although IMTA's benefits have been reported to improve water quality, stimulate probiotics, and enhance disease control (Ying et al., 2018; Lee, 2019; Zhang et al., 2022; Stabili et al., 2023), contradictory reports have also appeared (Pietrak et al., 2012; Molloy et al., 2013; Tarnecki et al., 2025). We hypothesized that the community composition and microbial interactions therein may play important roles in determining the health status of IMTA systems, in addition to their critical roles in shaping the ecological functions and stability of the ecosystems (Nawaz et al., 2022). The current study investigated the monthly changes of bacterioplankton communities in three maricultural systems (*i.e.*, shellfish monoculture, algae monoculture, and algae-shellfish co-culture) in Sanggou Bay. It also characterized potential bacterial pathogens through a comprehensive approach, including 16S rRNA gene-based community analyses, potential bacterial pathogen screening, environmental simulation experiments, and pathogen whole-genome analyses. The value of analyzing microbial communities and interactions in mechanistically predicting bacterial pathogens' seasonal dynamics in mariculture environments was demonstrated.

2 Materials and methods

2.1 Environmental description and sampling strategy

Sanggou Bay is a shallow, semi-enclosed coastal bay in the Yellow Sea. As one of the largest aquaculture production areas in China, the environment of Sanggou Bay is influenced by land (in particular river discharges and anthropogenic pollutions), the Yellow Sea, internal processes such as pelagic-benthic exchange, and extensive aquaculture activities (Mahmood et al., 2016b). River discharges constitute the primary source of nutrient inputs in Sanggou Bay (Mahmood et al., 2016b), and *Bacillariophyta* and *Dinophyta* usually dominate the phytoplankton communities (Han et al., 2024). Tidal currents, especially their semi-diurnal constituents, dominate the Sanggou Bay hydrodynamics, contributing to water exchange with the Yellow Sea (Zeng et al., 2015). However, the water exchange rate decreases significantly in the upper water layers due to the frictional effect caused by the densely planted seaweeds and suspended aquaculture structures (shellfish cages and nets), which occupy nearly 2/3 of the area of the entire Sanggou Bay (Zeng et al., 2015). This reduction in water exchange could impact nutrient cycling, waste transport, and, consequently, potential eutrophication and phytoplankton bloom formation (Wang et al., 2018a). In addition, elevated anthropogenic activities such as agriculture and wastewater discharges further increase the ecological risks of eutrophication and algal blooms (Mahmood et al., 2016b).

Seawater samples were collected from Sanggou Bay to investigate the monthly bacterial communities and potential pathogens in different aquaculture systems (Table 1), including shellfish monoculture (Type I, density: 38 scallop/m^2 or 12 abalone/m^2), algae-shellfish co-culture (Type II, density: 38 scallop/m^2 or 12 abalone/m^2 for shellfish and 6 kelp/m^2 or 0.3–2 kg *Gracilaria*/m^2 for algae), and algae monoculture (Type III, density: 6 kelp/m^2 or 0.3–2 kg *Gracilaria*/m^2), where Type II belonged to the IMTA mode. The stocking densities were set based on local aquaculture practices. Based on the three distinct maricultural systems, seawater from four stations along a transect (from the nearshore to the offshore aquaculture sites) was sampled monthly from February 2019 to February 2020, including S1 (Type I), SA1 (Type II), A1 (Type III), and A2 (Type III). Two additional stations, AG1 (Type II) and AG2 (Type II), were sampled from July 2019 to November 2019 to provide more samples for late summer and autumn, when diseases in cultivated marine organisms were the most severe (Figure 1A; Table 1). Sampling was conducted during mid-tide periods to

TABLE 1 Detailed information for the sampling stations in Sanggou Bay.

Stations	Aquaculture type	Latitude (°N)	Longitude (°E)	Aquaculture species	Sampling month
S1	Type I	37.170	122.575	Shellfish*	Feb., 2019 - Feb., 2020
SA1	Type II	37.168	122.580	Shellfish* & algae**	Feb., 2019 - Feb., 2020
AG1	Type II	37.140	122.592	Shellfish* & algae**	Aug., 2019 - Nov., 2019
AG2	Type II	37.142	122.623	Shellfish* & algae**	Aug., 2019 - Nov., 2019
A1	Type III	37.162	122.585	Algae**	Feb., 2019 - Feb., 2020
A2	Type III	37.143	122.631	Algae**	Feb., 2019 - Feb., 2020

* According to the breeding program of Weihai Changqing Ocean Science Technology Co., Ltd., scallops were cultivated in stations S1 and SA1, and abalones were cultivated in AG1 and AG2.

** According to the breeding program of Weihai Changqing Ocean Science Technology Co., Ltd., *Gracilaria lemaneiformis* was cultivated from July to November, and kelp (*Laminaria japonica*) was cultivated from December to June of the following year.

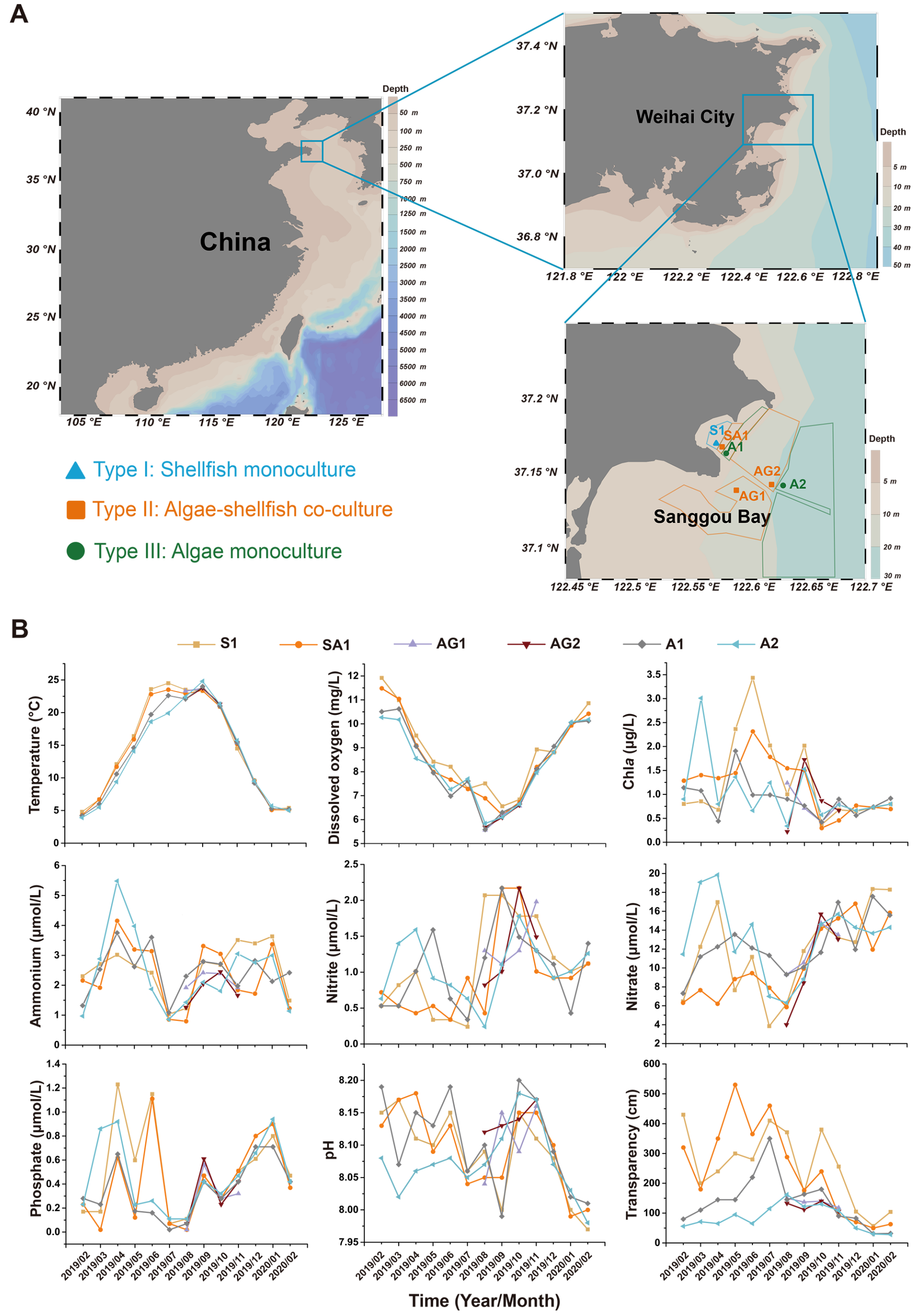

FIGURE 1
Locations and environmental conditions of the sampling stations in Sanggou Bay. **(A)** Maps showing the geographic locations of the sampling stations and cultivation areas of 3 different mariculture types. Blue: Type I (shellfish monoculture); orange: Type II (algae-shellfish co-culture); and green: Type III (algae monoculture). **(B)** Monthly changes in physicochemical parameters of the sampling stations from February 2019 to February 2020. Lines of different colors represent different sampling stations.

minimize variability caused by tidal fluctuations. The four sampling seasons were defined as spring (March, April, and May), summer (June, July, and August), autumn (September, October, and November), and winter (December, January, and February) (Han et al., 2024).

2.2 Sample collection and environmental factor measurement

Surface seawater from ~ 0.5 m depth was collected with a 2.5 L acrylic water sampler, with a total of 60 samples obtained.

Measurements of *in situ* seawater temperature, salinity, and dissolved oxygen (DO) were taken immediately onboard using a YSI-556MPS handheld multiparameter meter (YSI Incorporated, USA). Seawater transparency was assessed with a 30 cm Secchi disk, and pH was determined in the laboratory with a pH meter (Mettler-Toledo FE28, China). Environmental factors including chlorophyll *a* (Chl*a*) (Standard method: HJ897-2017), ammonium (NH_4^+) (Standard method: GB/T12763.4-2007), nitrite (NO_2^-) (Standard method: GB/T12763.4-2007), nitrate (NO_3^-) (Standard method: GB/T12763.4-2007), and phosphate (PO_4^{3-}) (Standard method: GB/T12763.4-2007) were measured following the corresponding standard methods, respectively. For microbial community analyses, seawater samples were filtered onto 47 mm diameter polycarbonate filters with a 0.22 μm pore size (Merck Millipore Ltd., USA) under low vacuum pressure. The filters were then stored at -80°C until DNA extraction.

2.3 DNA sequencing and bacterial community taxonomic analyses

Microbial community DNA was extracted using a MagPure Stool DNA LQ Kit (Magen, China) following the manufacturer's instructions. DNA quantity was measured with a Qubit 2.0 Fluorometer (Invitrogen, USA), and DNA quality was assessed by electrophoresis. The bacterial 16S rRNA gene V3-V4 hypervariable region was amplified using universal PCR primers 338F and 806R tagged with Illumina adapter, pad, and linker sequences (Salas-González et al., 2021; Dai et al., 2022). PCR was performed in triplicate with a 50 μL reaction mixture containing 30 ng template DNA. The PCR reaction conditions were: 94°C for 3 min, 30 cycles of 94°C for 30 s, 56°C for 45 s, 72°C for 45 s, and a final extension at 72°C for 10 min. PCR products were purified using Agencourt AMPure XP beads (Beckman Coulter, USA), and their quality and concentration were determined using an Agilent 2010 bioanalyzer (Agilent, USA). The PCR products were sequenced on the Illumina MiSeq PE 300 platform at BGI Genomic Co., Ltd, Wuhan, China.

Paired-end raw reads were processed using FLASH (v1.2.11) to trim and merge sequences (Magoč and Salzberg, 2011). High-quality sequences were retained after removing low-quality reads based on the following criteria: (1) sliding window size = 25 nt; (2) quality score< 20; (3) reads that contained N; (4) length< 75% of the original. Operational taxonomic units (OTUs) were identified using USEARCH (v7.0.1090) at a 3% sequence dissimilarity (Edgar, 2013) and classified with the RDP Classifier (v2.2) against the Silva database (v138.1) (accessed on 11 April 2023) (Quast et al., 2012) with an 80% confidence threshold. Chimeric sequences were removed with UCHIME (v4.2.40) (Edgar, 2016; Edgar et al., 2011), and chloroplastic and non-bacterial sequences were excluded. Sample A2_2020/01 was removed due to low sequencing quality. The raw 16S rRNA gene sequences are available in the NCBI Sequence Read Archive (SRA) under accession number PRJNA1154816.

2.4 Statistical and bioinformatic analyses

Principal component analysis (PCA) and clustering analysis were performed to differentiate sampling environments using the vegan R package (v2.5-7) (Oksanen et al., 2020). Alpha-diversity indices, principal coordinate analysis (PCoA) with Bray-Curtis dissimilarities, and analysis of community similarities (ANOSIM) (Clarke, 1993) were also conducted with vegan. Canonical correspondence analysis (CCA) was performed using Canoco5 (Microcomputer Power, USA), with collinear variables removed during forward selection. Structural equation modeling (SEM) analysis was conducted via the piecewiseSEM R package to assess the direct and indirect effects of the significant environmental factors identified in the above CCA analysis on the seawater bacterial diversity and community structure (Lefcheck, 2016). Using the stats R package (v3.6.3), Spearman correlation tests assessed correlations between bacterial taxa and environmental factors, with significance at $p< 0.05$.

High-abundance sequences (relative abundance > 0.5% across the database) were selected to construct a bacterial 16S rRNA gene phylogenetic tree using the build function of ETE 3.1.2 (Huerta-Cepas et al., 2016), with alignment performed using MAFFT v6.861b (Katoh and Kumah, 2005) and the tree constructed with FastTree v2.1.8 (Price et al., 2010) on the GenomeNet (https://www.genome.jp/tools-bin/ete).

The iCAMP software (https://github.com/DaliangNing/iCAMP1) was used to decode community assembly mechanisms, distinguishing deterministic (homogenous and heterogeneous selection) from stochastic (dispersal limitation, homogenizing dispersal, and drift) processes based on the beta Net Relatedness Index (βNRI) and Raup-Crick metric (RC) (Zhou and Ning, 2017; Ning et al., 2020). Distance-decay relationship (DDR) analyses were performed using the Geosphere R package with Bray-Curtis similarity geographic distances (Hijmans et al., 2017).

Co-occurrence networks were constructed for the bacterial communities with the random matrix theory (RMT)-based methods using the integrated Network Analysis Pipeline (iNAP) (https://inap.denglab.org.cn/) and visualized with Gephi v.0.10.1 (Bastian et al., 2009; Feng et al., 2022). Only the bacterial species at the OTU level occurring > 50% of all samples were included in network calculations. Uniform RMT threshold parameters were applied during network construction to ensure cross-group comparability.

2.5 Potential bacterial pathogens analyses

The seawater bacterial communities were screened for potential pathogens by analyzing 16S rRNA gene sequences against three pathogen databases: the multiple bacterial pathogen detection (MBPD) database (Yang et al., 2023), the Fish Pathogen Database (FPD) (Dronen et al., 2022, Dronen et al., 2023), and the human pathogen database (Chen et al., 2016; An et al., 2020). As in previous studies (Chen et al., 2016; Li et al., 2024), BLASTn analysis was used (E-value ≤ 1×10^{-10}, ≥ 99% identity).

Vibrio OTUs were further analyzed phylogenetically by comparing their sequences to the sequences of GenBank *Vibrio* type strains and isolates from the pathogen surveillance repository (PSR) of Weihai Changqing Ocean Science Technology Co. Ltd. This curated collection contains *Vibrio* strains isolated from diseased shellfish and surrounding aquaculture seawater within Sanggou Bay's aquaculture zones from 2018 to 2022. Phylogenetic reconstruction of the 16S rRNA sequences was performed with MEGA-X (version 10.2.6) using the maximum likelihood algorithm with 1000 bootstrap replicates (Kumar et al., 2018). The top-match PSR isolates were subject to further genome analyses and environmental simulation experiments.

Accordingly, six PSR *Vibrio* isolates were selected and genomically sequenced. Genomic DNA was extracted using the CTAB method (Wilson, 2001). Sequencing was performed using a PacBio Sequel II and DNBSEQ platform at Beijing Genomics Institute (BGI, Shenzhen, China). Draft genomic unitigs were assembled using Canu (v1.5) (Koren et al., 2017) and refined with GATK (https://www.broadinstitute.org/gatk/) (McKenna et al., 2010). A phylogenomic tree was constructed using the genome BLAST distance phylogeny method (GBDP) on the TYGS platform (https://tygs.dsmz.de/) (accessed on 15 July 2024) (Meier-Kolthoff and Göker, 2019). Gene prediction was performed using glimmer3 (http://www.cbcb.umd.edu/software/glimmer/) with the Hidden Markov models (Delcher et al., 1999). Virulence factors and antibiotic resistance genes were identified using VFDB (Liu et al., 2022) and ARDB (Antibiotic Resistance Genes Database) (Liu and Pop, 2009), respectively. The genome sequences are deposited in NCBI GenBank (Accession numbers SAMN43439310-SAMN43439315).

Environmental simulation experiments were conducted to assess the pathogenicity of the six selected *Vibrio* isolates. Three species of scallops, including bay scallop (*Argopecten irradians*), Zhikong scallop (*Chlamys farreri*), and Yesso scallop (*Patinopecten yessoensis*), along with Pacific abalone (*Haliotis discus hannai*), were used as the experimental animals. They were placed at 12 ± 1°C with aerated running seawater for 7 days, with daily water changes and regular feeding (microalgae for scallops and kelp for abalones). For each species, 420 individuals (Supplementary Table S1 for body size details) were divided into seven groups, including one control group and six experiment groups (three replicates per group). Test bacteria were introduced into the rearing water of the experiment group at a final concentration of 10^5 individuals/mL, while the control group received an equal volume of culture medium. The feeding rate was determined 1 h after the addition of bacterial strains.

The feeding rate of scallops was determined by calculating the clearance rate (CR, L h^{-1} ind^{-1}) based on the removal of *Nannochloropsis* particles. Optical density (OD_{750}) was measured at the start and after 1 h. The CR (Loret et al., 2000; Vaquer et al., 2000; Wildish et al., 1992) was calculated as:

$$CR = (V/nt) \times Ln(C_0/C_t)$$

Where V is the volume of the rearing water, n is the number of experimental scallops, t is the experiment time, C_0 is the concentration of *Nannochloropsis* at the beginning of adding, and C_t is the concentration of *Nannochloropsis* after 1 h.

The reduced weight of fresh kelp was used to determine the feeding rate (FR, g d^{-1} ind^{-1}) of abalones following a previous study (Li X. et al., 2022):

$$FR = (W_0 - W_t)/nt$$

Where W_0 is the weight of kelp at the beginning of adding, W_t is the weight of kelp after 1 h, n is the number of abalones, and t is the experiment time.

3 Results

3.1 Temporospatial dynamics of environmental condition in Sanggou Bay

The environmental condition of Sanggou Bay showed apparent seasonal variation, with seawater temperature and DO showing greater consistency across sampling stations (Figure 1B). Higher water temperatures and lower DO concentrations were observed from June to September, with the highest temperature appearing at station A2 (24.8°C) in August and the lowest DO appearing at sampling station AG2 (5.56 mg/L) in September. Concentrations of Chl*a* and inorganic nutrients, including ammonium, nitrite, nitrate, and phosphate, varied across stations with less pronounced seasonal patterns. Low concentrations of seawater ammonium, nitrite, nitrate, and phosphate were usually observed in July and August and Chl*a* in August. PCA and clustering analysis showed that seasonal variation outweighed spatial differences in shaping the sampling environment (Supplementary Figures S1, S2). Therefore, subsequent analyses mainly focused on seasonality-related bacterial communities and pathogens.

3.2 Bacterial community composition and diversity

After quality filtering, 1,987,548 valid bacterial 16S rRNA gene sequences were identified, representing 4069 OTUs across 59 samples. A total of 50 phyla, 107 classes, 225 orders, 314 families, and 571 genera were taxonomically assigned. Thirteen dominant bacterial classes (relative abundance of each > 0.5%) were identified, with *Alphaproteobacteria* (33.89%), *Gammaproteobacteria* (33.01%), and *Bacteroidia* (16.32%) being the most abundant (Figure 2A). Twenty-five dominant bacterial families were identified, with *Rhodobacteraceae* (28.78%), *Flavobacteriaceae* (11.63%), and *Moraxellaceae* (5.14%) being the most abundant (Figure 2A). The bacterial community in Sanggou Bay showed seasonal and aquaculture-type variations (Supplementary Figure S3).

The Shannon biodiversity of the seawater bacterial communities varied with season and aquaculture type

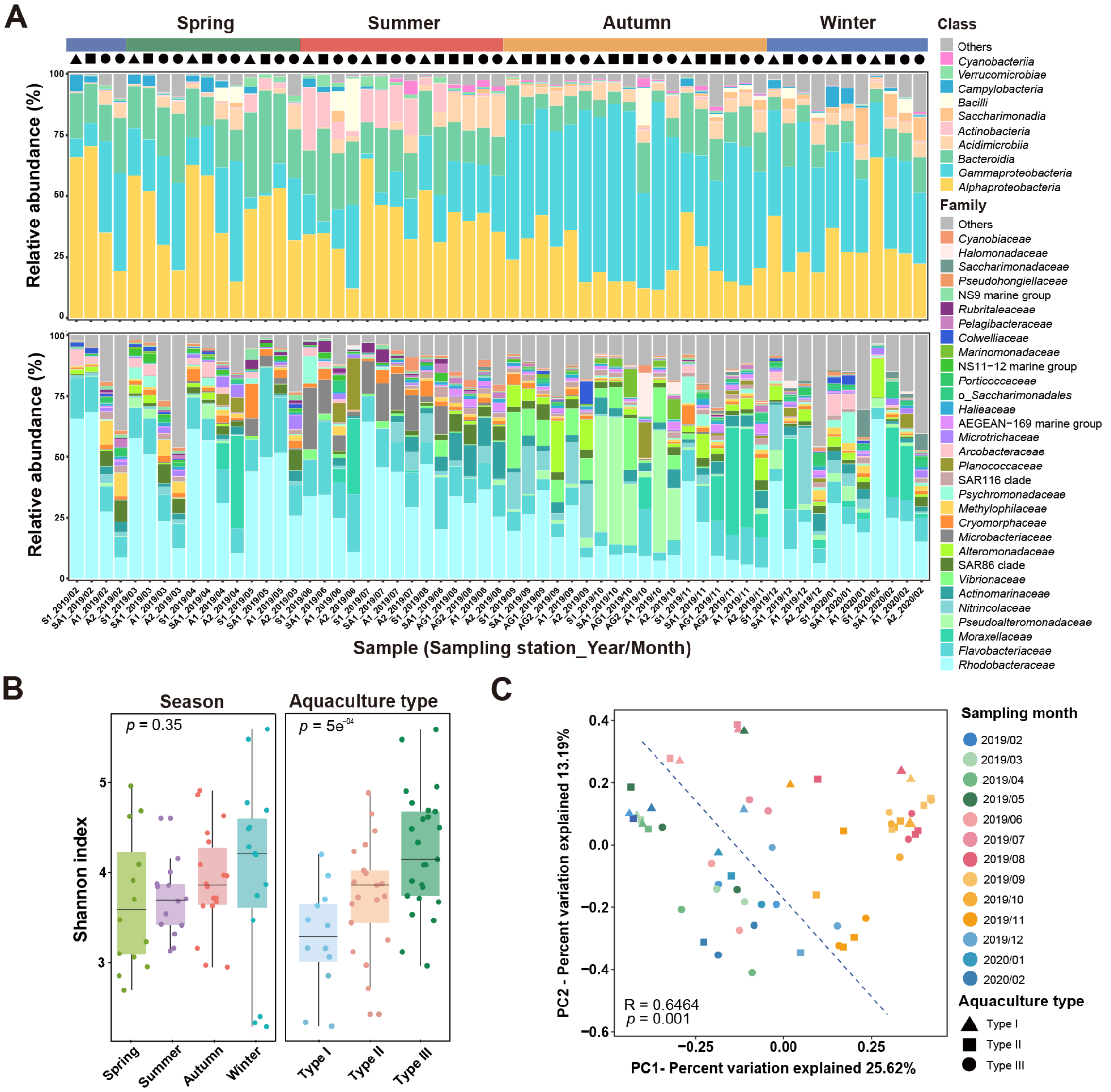

FIGURE 2
Community composition and diversity of seawater bacteria in Sanggou Bay. **(A)** Bacterial community compositions at class level and family level, respectively. Classes or families representing< 0.5% of the total community composition are classified as "others." **(B)** Comparisons of community Shannon biodiversity indices in different seasons and aquaculture types. **(C)** Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity illustrating the variation in bacterial community structure. Colors represent months, and shapes represent aquaculture types.

(Figure 2B). However, only the aquaculture type showed a significant influence (ANOVA, *p*< 0.05) on the bacterial diversity, with the highest diversity being observed in Type III and the lowest diversity being observed in Type I (Figure 2B). These suggest that cultivating algae might have increased the diversity of seawater bacteria in Sanggou Bay, likely due to the enhanced effect of photosynthesis-driven seawater quality enhancement. In contrast, the shellfish monoculture might decrease the seawater bacterial diversity, and including algae cultivation in shellfish aquaculture (*i.e.*, the IMTA mode) might enhance seawater quality and thus enhance bacterioplankton community diversity.

The PCoA result showed that seasonality might be a major factor driving the shift of seawater bacterial community structure, with similar bacterial communities being found in winter and spring and in summer and autumn, respectively (Figure 2C). ANOSIM statistical analyses showed that the bacterial community difference among different seasons or aquaculture types was highly significant (*p*< 0.01), and those between each pair of seasons or aquaculture types were generally significant (*p*< 0.05), as well, except for the pair between the algae-shellfish co-culture system (Type II) and the shellfish monoculture system (Type I) (Table 2).

3.3 Dynamics of bacterial taxa in response to seasonality and aquaculture type

A total of 41 OTUs were identified as abundant OTUs (relative abundance > 0.5%), exhibiting varying seasonal patterns (Figure 3A).

TABLE 2 Two-way crossed analysis of similarity (ANOSIM) of bacterial community structure based on Bray-Curtis dissimilarity across different seasons and aquaculture types (999 permutations).

Group	R	*p*-value*
Season		
All four seasons	0.448	**0.001**
Spring *vs.* Summer	0.307	**0.001**
Spring *vs.* Autumn	0.794	**0.001**
Spring *vs.* Winter	0.096	**0.048**
Summer *vs.* Autumn	0.355	**0.001**
Summer *vs.* Winter	0.421	**0.001**
Autumn *vs.* Winter	0.627	**0.001**
Aquaculture type		
All three aquaculture types	0.145	**0.001**
Type I *vs.* Type II	0.068	0.114
Type I *vs.* Type III	0.346	**0.001**
Type II *vs.* Type III	0.067	**0.045**

* Bold: significant correlation ($p < 0.05$)

The five most dominant OTUs, ranked by abundance, were Otu1 (8.46%), Otu6 (5.31%), Otu16 (4.31%), Otu4 (3.71%), and Otu3 (3.08%). Of these, the relative abundance of Otu1 (*Sulfitobacter* sp.) was higher in winter and spring, Otu6 (*Rhodobacteraceae* HIMB11) in summer, Otu16 (*Planktomarina* sp.) in spring and summer, Otu4 (*Psychrobacter* sp.) in autumn and winter, and Otu3 (*Pseudoalteromonas* sp.) in autumn (Figures 3A,B). In addition to seasonality, the bacterial community composition of the abundant OTUs also varied in response to the different aquaculture types (Figure 3B). For the five most abundant OTUs, Otu1 had the highest relative abundance in Type I, Otu6 in Type II, Otu16 in Type I and Type III, Otu4 in Type II and Type III, and Otu3 in Type I and Type II (Figure 3B).

Forty-eight OTUs exhibited increased relative abundance during late summer and early autumn, a period of high disease risks, including common marine bacteria, such as those affiliated with *Rhodobacteraceae*, *Pseudoalteromonadaceae*, *Actinomarinaceae*, *Vibrionaceae*, *Flavobacteriaceae*, and *Alteromonadaceae* (Figure 3C).

3.4 Drivers of bacterial composition and community structure

Spearman non-parametric correlation analysis revealed significant correlations ($p < 0.05$) between several dominant bacterial OTUs and seawater parameters, including DO, temperature, transparency, NO_3^-, NO_2^-, TN, PO_4^-, and Chl*a* (Figure 4A). In addition, differences in the interrelationships between aquaculture types and high-abundance bacterial taxa were found. Shellfish monoculture had significant positive correlations ($p < 0.05$) with the abundances of certain OTUs affiliated with *Rhodobacteraceae* and *Flavobacteriaceae* (2.97% of the total community) and significant negative correlations ($p < 0.05$) with certain OTUs affiliated with *Actinomarinaceae*, *Microtrichaceae*, *Methylophilaceae*, *Nitrincolaceae*, *Rhodobacteraceae*, SAR86 clade, *Pelagibactereae*, SAR116 clade, and *Planococcaceae* (12.24%). Algae monoculture had significant positive correlations with the abundances of certain OTUs affiliated with SAR86 clade, SAR116 clade, *Pelagibacterceae*, *Actinomarinaceae*, *Methylophilaceae*, *Planococcaceae*, and AEGEAN-169 marine group (9.48%) and significant negative correlations with certain OTUs affiliated with *Rhodobacteraceae*, *Arcobacteraceae*, and *Flavobacteriaceae* (5.92%). Algae-shellfish co-culture only negatively correlated with the abundance of one OTU affiliated with *Microtrichaceae* (0.53%).

The CCA result identified seven significant environmental factors ($p < 0.05$) mainly contributing to the variation of the bacterial communities, including seawater DO, transparency, temperature, NO_2^-, Chl*a*, NO_3^-, and algae cultivation (Figure 4B). Seawater DO made the highest contribution (8.5%) among these factors. The SEM analysis further confirmed seawater DO, along with seawater transparency, as the most significant environmental factor ($p < 0.05$) directly affecting (negatively) the seawater bacterial community variation (Figure 4C). In contrast, seawater temperature exerted an indirect effect, through the effect of seawater DO, on the bacterial community variation (Figure 4C). The SEM result also revealed that the seawater bacterial diversity was directly affected by seawater DO, transparency, Chl*a*, NO_3^-, and NO_2^- ($p < 0.05$) and indirectly affected by seawater temperature through its effects on seawater DO, NO_3^-, and NO_2^- ($p < 0.05$) (Figure 4C). The SEM result provides a more insightful explanation than the CCA result by revealing additional information about the interactions among the key environmental factors in driving the variation of the seawater bacterial communities.

The CCA results provided a limited explanation (< 20%) for the total variation of the bacterial communities, indicating the presence of other contributing factors. Indeed, the iCAMP analysis results showed that the stochastic processes, especially dispersal limitation and drift, were the primary bacterial community assembly mechanisms (Figure 5A). Among the deterministic processes, homogenous selection contributed the most to the bacterial community assembly (Figure 5A). Results of the DDR analyses statistically showed a significant but weak geographic distance decay ($p < 0.001$, $r^2 = 0.002$) of the bacterial community similarity, further confirming the role of dispersal limitation in the assembly of the seawater bacterial communities in Sanggou Bay (Figure 5B).

The iCAMP analysis results also showed the seasonal variation in the different bacterial community assembly mechanisms, with autumn exhibiting the highest contribution by homogenous selection and the lowest contribution by dispersal limitation (Figure 5A). A further analysis of the bacterial community assembly mechanisms was conducted across different aquaculture types. The stochastic processes exhibited the highest contribution in Type III (80.51%), followed by Type II (73.66%) and Type I (65.18%). Conversely, the deterministic processes, predominantly homogenous selection, exhibited a higher contribution in Type I

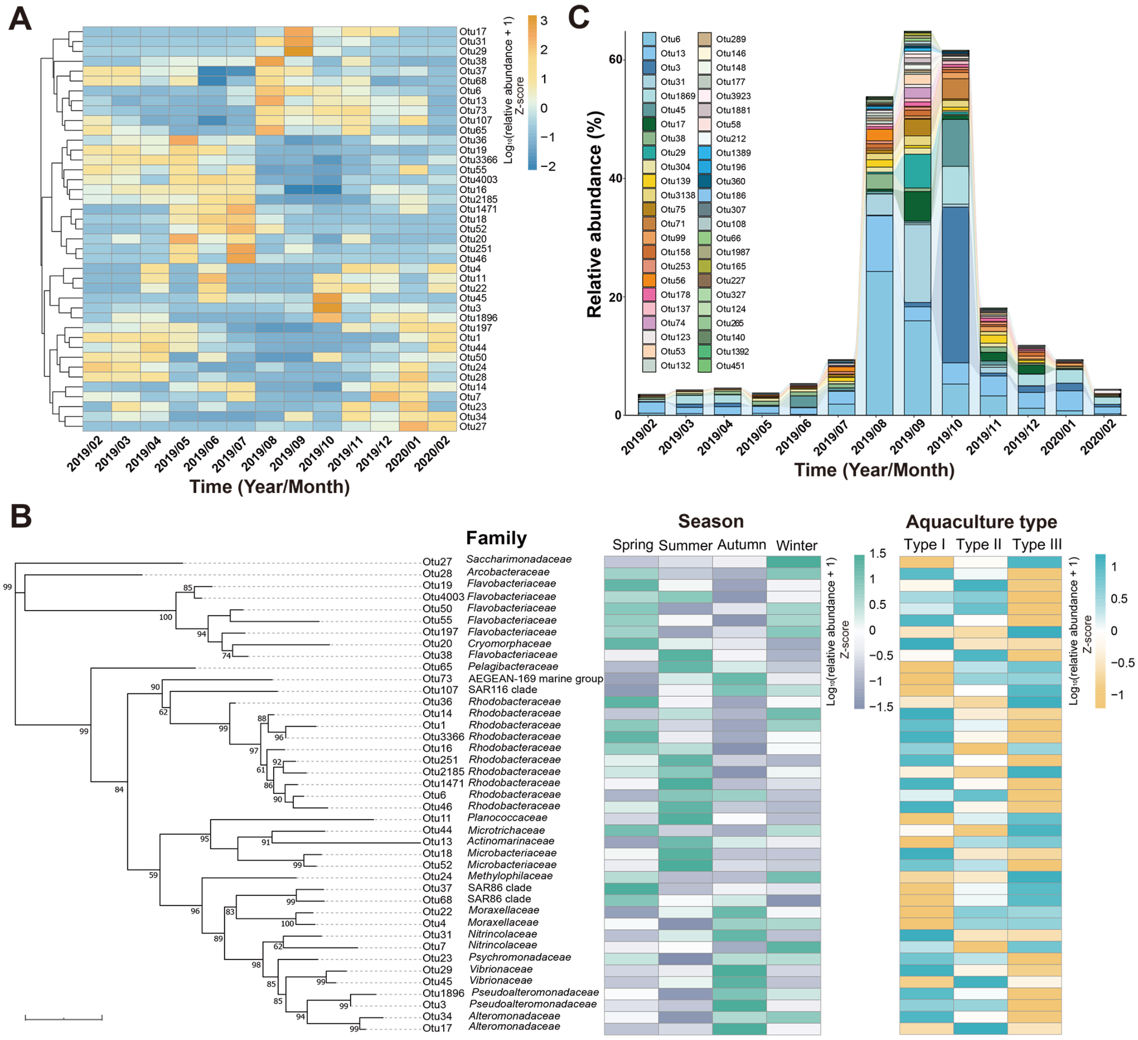

FIGURE 3

Distribution patterns of the abundant OTUs and OTUs with an increased relative abundance in late summer and early autumn. **(A)** Heatmap of abundant OTUs showing their monthly variations. The relative abundances were shown in the z-score scale of the log-transformed values for easy visibility of the temporal variation patterns. **(B)** Phylogenetic tree of the 16S rRNA gene sequences showing the taxonomies of the abundant OTUs and their distributional variations related to seasons and aquaculture types. Bootstrap values greater than 50% were shown. The heatmaps on the right show the relative abundance of each OTU in different seasons and aquaculture types. The relative abundances were shown in the z-score scale of the log-transformed values for easy visibility of the variation patterns. **(C)** Monthly dynamics of the OTUs that showed increased relative abundance in later summer and early autumn.

(32.92%) than in the other two aquaculture types (Type II: 24.61%, Type III: 17.92%) (Figure 5A).

3.5 Dynamics of putative interactions in the bacterial communities

Ecological network analyses were conducted to examine potential microbial interactions within the bacterial communities in different seasons and aquaculture types, respectively (Figure 6). The topological properties of each network are listed in Supplementary Table S2. Positive interactions predominated over negative interactions in all networks (Supplementary Table S2). Seasonal comparisons revealed a substantial network structural variation. The autumn network exhibited markedly reduced complexity, containing merely 81 nodes (OTUs) and 97 links, approximately 2.28 to 4.06-fold fewer nodes, and 4.51 to 14.25-fold fewer edges than the spring network (329 nodes, 1382 links), the summer network (185 nodes, 437 links), and the winter network (240 nodes, 687 links) (Figures 6A, B; Supplementary Table S2). Consistent with this pattern, network connectivity metrics showed autumn had the lowest average degrees (avgK = 2.395), much lower than spring (8.401), summer (4.724), and winter (5.725) (Supplementary Table S2). The nodes with the maximum degrees also varied seasonally, with Otu138 (affiliated with SAR116 clade) in spring, Otu139 (*Flavobacteriaceae*) in summer, Otu1389 (*Vibrionaceae*) and Otu148 (*Nitrincolaceae*) in autumn, and Otu154 (*Woeseiaceae*) in winter (Supplementary Table S2). These

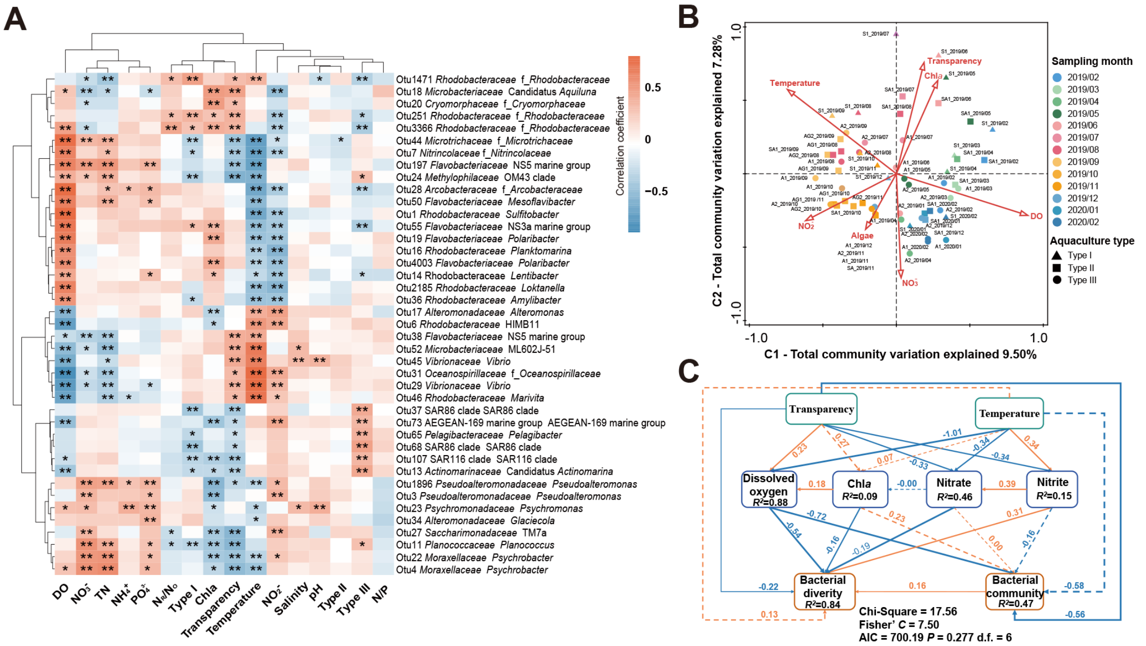

FIGURE 4

Relationships between environmental conditions and the seawater bacterial communities. **(A)** Heatmap plot showing the relationship between the abundant OTUs and environmental factors. The plot was produced at OTU, family, and genus taxonomic ranks. The color bar indicates the *r* values. * indicates $0.01 \le p < 0.05$. ** indicates $p < 0.01$. **(B)** Canonical correspondence analysis (CCA) ordination plot for the first two dimensions of the relationships between the environmental factors and the seawater bacterial communities. **(C)** Structural equation modeling (SEM) result showing the effects of environmental factors on bacterial Shannon diversity and community structure. Orange and blue arrows indicate positive and negative relationships, respectively. Solid and dashed lines indicate significant ($p < 0.05$) and nonsignificant relationships. Numbers near pathway arrows indicate the standard path coefficients. R^2 represents the proportion of variance explained for each dependent variable.

findings indicate the seasonality of the microbial interactions and network complexity, presenting autumn as a particularly unique situation.

The network topological properties also varied significantly among different aquaculture types, with the highest number of nodes (190) and links (368) in Type III, followed by Type I (152 nodes, 274 links) and Type II (132 nodes, 221 links) (Figures 6C, D; Supplementary Table S2). In addition, the highest network degrees were observed in Type III (3.874), followed by Type I (3.605) and Type II (3.348) (Supplementary Table S2). The nodes with the maximum degrees were Otu1655 (*Rhodobacteraceae*) and Otu356 (*Psychromonadaceae*) in Type I, Otu6 (*Rhodobacteraceae*) in Type II, and Otu154 (*Woeseiaceae*) in Type III, respectively (Supplementary Table S2).

3.6 Seasonal dynamics of potential pathogenic bacteria

Forty-two potential pathogenic OTUs spanning six phyla and 35 genera were identified, including 24 genera of animal pathogens, eight genera of zoonotic pathogens, two genera of plant pathogens, and one genus of fungus pathogens (Supplementary Table S3). Plant and fungus pathogens were excluded in subsequent analyses due to their limited ecological relevance to the Sanggou Bay aquaculture species. Bacteria in the *Vibrio* genus emerged as the predominant potential pathogens, accounting for 1.57% of total bacterial 16S rRNA gene sequences, followed by *Mycobacterium* (0.02%), *Arthrobacter* (0.01%), and *Prevotella* (0.01%). All other potential pathogenic genera exhibited relative abundances< 0.01%. Monthly distribution showed that the abundances of putative *Vibrio* pathogens progressively increased from May, peaking in October (Figure 7A; Supplementary Figure S4). Sampling-station-specific distribution showed that the *Vibrio* abundances were high across all sampling stations in September and October, with Otu45, Otu75, and Otu685 representing putative pathogens (Figure 7B).

A subnetwork was extracted from the autumn network (Figures 6A, B) to explore the microbial interactions, focusing on the *Vibrio* OTUs (Figure 7C). Notably, Otu1389 (annotated as *Vibrio halioticoli*) showed positive correlations with six other *Vibrio* OTUs, including two putative pathogens (Otu75 and Otu685). Otu1389 was detected in 39 of 59 samples and exhibited a high relative abundance in autumn, especially in September (0.56% of the bacterial community). Spearman correlation analysis further found significant and positive correlations between Otu1389 and other 14 *Vibrio* OTUs (Figure 7D). Its hub positioning in the network and extensive associations with other *Vibrio* OTUs suggested a pivotal role of the Otu1389-represented bacterium in supporting the growth of other *Vibrio* species in autumn (see the Discussion section for further reasoning).

Through 16S rRNA gene sequence phylogenetic analysis, three putative pathogenic *Vibrio* OTUs identified in the seawater

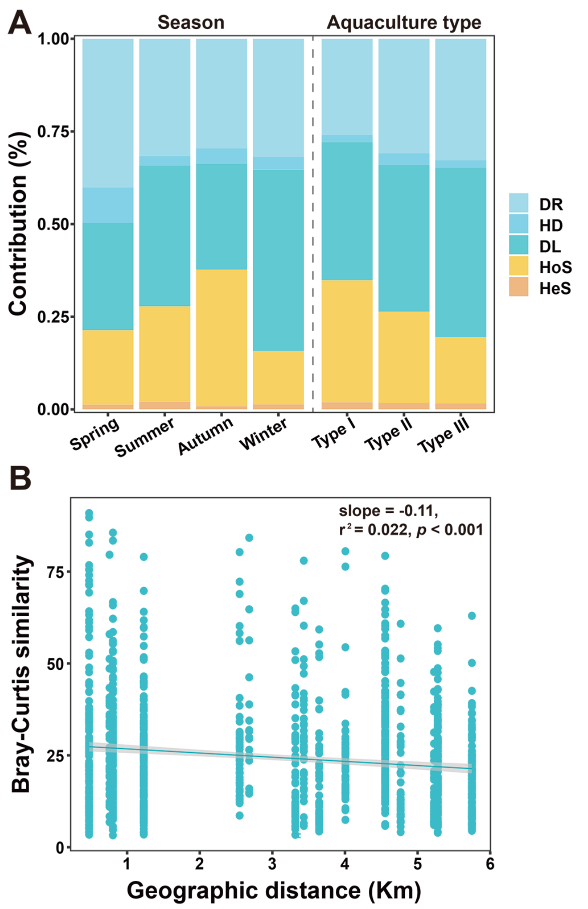

FIGURE 5
(A) The contributions of different mechanisms to the assembly of the seawater bacterial communities in Sanggou Bay analyzed using iCAMP. Percentage values indicate the specific contributions of deterministic and stochastic processes in different seasons and aquaculture types. Deterministic processes include homogenous (HoS) and heterogeneous (HeS) selection, and stochastic processes include dispersal limitation (DL), homogenizing dispersal (HD), and drift (DR). **(B)** Distance-decay relationship (DDR) analysis result showing the bacterial community Bray-Curtis similarity against geographic distances in Sanggou Bay.

bacterial communities were found to match pathogenic *Vibrio* strains from the previously established PSR (Supplementary Figure S5), providing further supporting evidence that these OTUs may represent authentic *Vibrio* pathogens. Precisely, Otu45 (0.32%-7.92%, 2.90% on average from August to October) and Otu75 (0.24%-2.81%, 1.21% on average from August to October), two of the most dominant *Vibrio* OTUs, particularly in high-disease-risk late summer and autumn, matched pathogenic *Vibrio* strains ScY-2108 and ScY-2109, and ScY-2106 and WaG-2229, respectively, while less-abundant Otu685 matched pathogenic *Vibrio* strains AbY-1905 and AbY-2104. These six pathogenic strains were thus selected for further whole genome sequencing and environmental simulation experiments. Phylogenomic analysis showed that strains ScY-2106 and WaG-2229 belonged to *V. alginolyticus*, strains AbY-1905 and AbY-2104 belonged to *V. mediterranei*, and strains ScY-2108 and ScY-2109 might represent two new species of *Vibrio*, tentatively named *V. sanggoullaii* and *V. sanggoullbii*, respectively (Supplementary Figure S6). The six pathogenic *Vibrio* strains harbored diverse virulence factors, such as those involved in adherence (OmpU, tcpI, and Type IV pili), antimicrobial activity/competitive advantage (AcrAB), biofilm formation (PlcR-PapR quorum sensing and lateral flagella), effector delivery (HIS, *P. syringae* TTSS effectors, and T3SS1), exoenzyme production (NanH/VCNA, HAP, and streptococcal enolase), exotoxin production (haemolysin, cytolysin, phytotoxin phaseolotoxin, TLH, Ymt, and PlaB), immune modulation (Capsular polysaccharide, LOS, and LPS), motility (flagella), invasion (K1 capsule), nutrient uptake (iron uptake, siderophore biosynthesis, vibriobactin/vulnibactin, and vibrioferrin), post-translational modification (Mip), regulation (Fur), and stress survival (urease and ClpP) (Supplementary Tables S4–S9). Antibiotic resistance genes were found in the genomes of all six strains (Supplementary Table S10). Further antibiotic susceptibility tests showed all strains were resistant to 60.0%-83.3% of the tested antibiotics (Supplementary Tables S11–S16).

The survival and feeding/clearance rates were measured in the environmental simulation experiments to assess the impact of these six *Vibrio* pathogens on farmed shellfish (Figure 8). Although no significant mortality was observed (The survival rates ranged from 87.50% to 100%, details not shown), all *Vibrio* strains reduced the feeding/clearance rates (0.05%-98.72%, 24.15% on average), with *Argopecten irradians* and *Chlamys farreri* showing to be the most pronouncedly affected (Figure 8). *Argopecten irradians* demonstrated a significant decrease in clearance rate on the first day following the challenge with all six pathogenic *Vibrio* strains. This rate remained notably lower than that of the control group throughout the five-day experiments. A similar pattern was observed for *Chlamys farreri*, except for strains AbY-1905 and ScY-2108 on the first day. The tested pathogens had less effect on the clearance/feeding rate of *Patinopecten yessoensis* and *Haliotic discus hannai* (Figure 8). *Patinopecten yessoensis* exhibited a decrease in clearance rate on the third day following bacterial challenge. In contrast, *Haliotic discus hannai* exhibited heightened sensitivity to strains AbY-2104, WaG-2229, and ScY-2109, resulting in a conspicuous decline in feeding rate on the first day of pathogen challenging, with sustained reduction in comparison to the control groups throughout the experimental duration. These findings highlight the potential negative impacts of *Vibrio* pathogens on the shellfish's physiology.

4 Discussion

4.1 Seasonal dynamics of bacterial communities in mariculture environments

Certain microbial taxa maintained stable across seasonal and aquaculture-type gradients. The surface seawater bacterial communities exhibited high diversities yet maintained persistent dominance of three classes: *Alphaproteobacteria* (mainly *Rhodobacteraceae*), *Gammaproteobacteria* (taxa varied among different samples), and *Bacteroidia* (mainly *Flavobacteriaceae*)

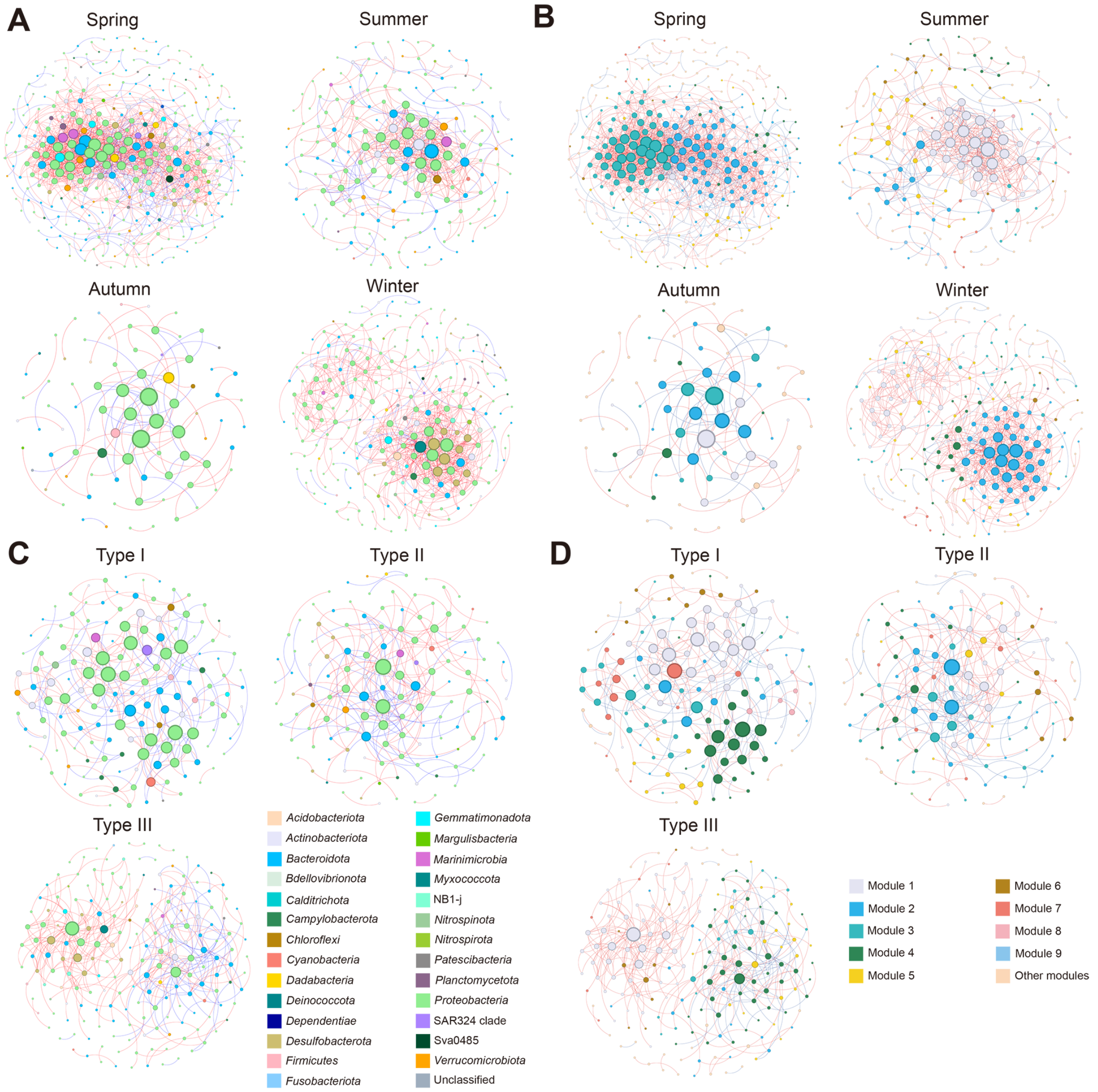

FIGURE 6
Results of ecological interaction network analyses of the seawater bacterial communities. **(A)** Ecological networks constructed for different seasons, with bacterial taxa distinguished by colors according to their affiliated phyla. **(B)** Ecological networks constructed for different seasons, with bacterial taxa distinguished by colors according to network modules. **(C)** Ecological networks constructed for different aquaculture types, with bacterial taxa distinguished by colors according to their affiliated phyla. **(D)** Ecological networks constructed for different aquaculture types, with bacterial taxa distinguished by colors according to network modules. Each node represents an OTU (*i.e.*, a species), and its size represents the degree level, with larger nodes indicating greater degrees. The edge between each two nodes represents a positive (red) or negative (blue) interaction. "Other modules" include the network modules with less than five nodes.

(Figure 2A; Supplementary Figure S3). These results are consistent with published studies in other aquaculture environments, such as the Laoshan Bay (Fang et al., 2021), shrimp culture ponds (Hu et al., 2022), Yantai intensive mariculture systems (Wang et al., 2018b), and Dongying intensive mariculture systems (Zhao et al., 2017). *Rhodobacteraceae* bacteria act as metabolic generalists through organoheterotrophy, photoheterotrophy, and non-obligate chemolithotrophy (Luo and Moran, 2014), enabling the utilization of various labile and recalcitrant organic substrates (Dang and Lovell, 2016). In addition, *Rhodobacteraceae* are usually associated with algae, fecal pellets, other marine particles, and submerged surfaces (Wagner-Döbler and Biebl, 2006; Mayali et al., 2008; Dang and Lovell, 2016). Moreover, specific *Rhodobacteraceae* bacteria could inhibit and kill bacterial pathogens (Bruhn et al., 2005; Zhao et al., 2019), correlating with maintaining the health of farmed animals at higher relative abundances (Xue et al., 2017; Hu et al., 2022). *Flavobacteriaceae* specialize in macromolecule degradation (Dang and Lovell, 2016; Enke et al., 2019; Gavriilidou et al., 2020). Studies showed that *Flavobacteriaceae* were often associated with the surface of algae, marine invertebrates, fish, and detrital particles (Dang and Lovell, 2016; Gavriilidou et al., 2020). Bacteria in the *Rhodobacteraceae* and

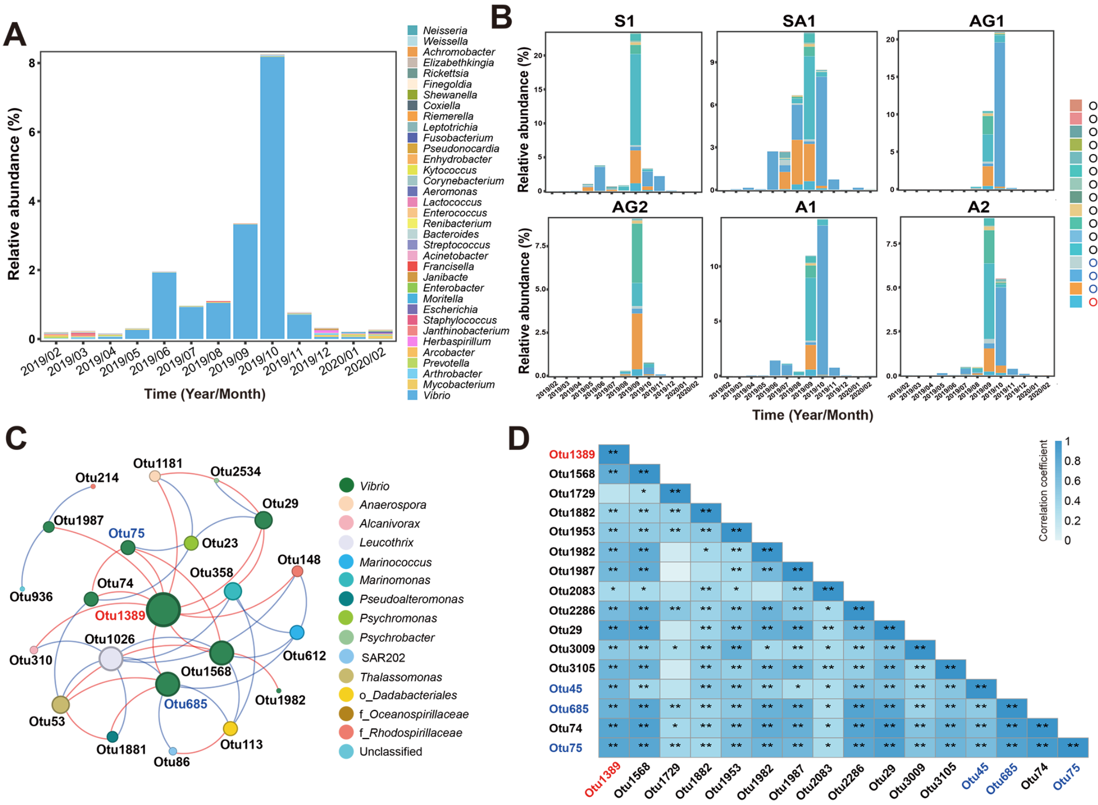

FIGURE 7
Analytical results of potential bacterial pathogens in the seawater bacterial communities of Sanggou Bay. **(A)** Monthly variation of potential pathogenic bacteria at the genus level. **(B)** Monthly variations of OTUs annotated as *Vibrio* in each sampling station. OTUs identified as pathogenic *Vibrio* are labeled in blue. **(C)** A partial ecological network of the autumn bacterial communities specifically showing the *Vibrio* OTUs' interactions with each other and with other bacteria. The node colors indicate different bacterial genera or families if the OTUs cannot be annotated to the genus level. Each node represents an OTU (*i.e.*, a species), and its size represents the degree level, with larger nodes indicating greater degrees. The edge between each two nodes represents a positive (red) or negative (blue) interaction. Otu1389 is labeled in red, and putative pathogenic *Vibrio* OTUs are labeled in blue. **(D)** A heatmap of Spearman correlation between OTUs assigned to *Vibrio*. Otu1389 is labeled in red. OTUs identified as pathogenic *Vibrio* are labeled in blue. * indicates $0.01 \leq p < 0.05$. ** indicates $p < 0.01$.

Flavobacteriaceae families may play an essential role in particulate matter degradation, nutrient recycling, organic waste scavenging, and farmed animals' health.

Bacteria can be classified into *r*-strategists (fast-growing, small body size, opportunistic strategy) or *K*-strategists (slow-growing, large body size, conservative strategy) (Reznick et al., 2002). The *r*/*K* selection theory explains seasonal pathogen proliferation. In the current study, specific bacterial taxa exhibited an obvious seasonal pattern, among which the relative abundance of *Vibrionaceae*, *Pseudoalteromonadaceae*, and *Alteromonadaceae* increased significantly in late summer and autumn. These bacteria are classified as *r*-strategists, while *Rhodobacteraceae* and *Flavobacteriaceae* that were consistently dominant in aquaculture seawater in our study, are classified as *K*-strategists (Lauro et al., 2009; Vadstein et al., 2018; Pettersen et al., 2021; Wietz et al., 2022). A recent study suggests that the rise in *r*-strategist bacteria increases homogeneous selection pressure (Liu and Salles, 2024), which aligns with our results. Homogeneous selection contributed the most to the bacterial community assembly in autumn, accompanied by increased *r*-strategist bacteria in Sanggou Bay mariculture seawater (Figure 5A).

The rise of *r*-strategist bacteria may reduce microbial interactions. Bacterial pathogens are usually *r*-strategists, with *Vibrio* species serving as typical representatives (Andrews and Harris, 1986; Vine et al., 2004). It has been shown that some health-indicator bacteria, such as those affiliated with *Psychromonadaceae* and *Thiotrichaceae*, appear significantly reduced in marine organisms' intestines or surrounding seawater during pathogenic bacteria infection (Baliga et al., 2021; Reyes et al., 2024). Network analyses in our current study (Figure 7C) identified negative correlations between pathogenic *Vibrionaceae* (Otu75, Otu685) and health-indicator bacteria (*Psychromonadaceae*, Otu23; *Thiotrichaceae*, Otu1026). Ecological network analyses also revealed a significant reduction in bacterial interactions and network complexity in autumn (Figures 6A, B). These results suggest that pathogenic *Vibrio* species may inhibit the growth of health-indicator bacteria. Mechanistically, *Vibrio* bacteria often employ type VI secretion systems and/or toxin-antitoxin systems for competition (Kostiuk et al., 2017; Song et al., 2022). Therefore, elevated *r*-strategist pathogens may reduce the bacterial diversity and interaction complexity in the mariculture ecosystems. In contrast, *K*-strategist bacteria could protect farmed species from

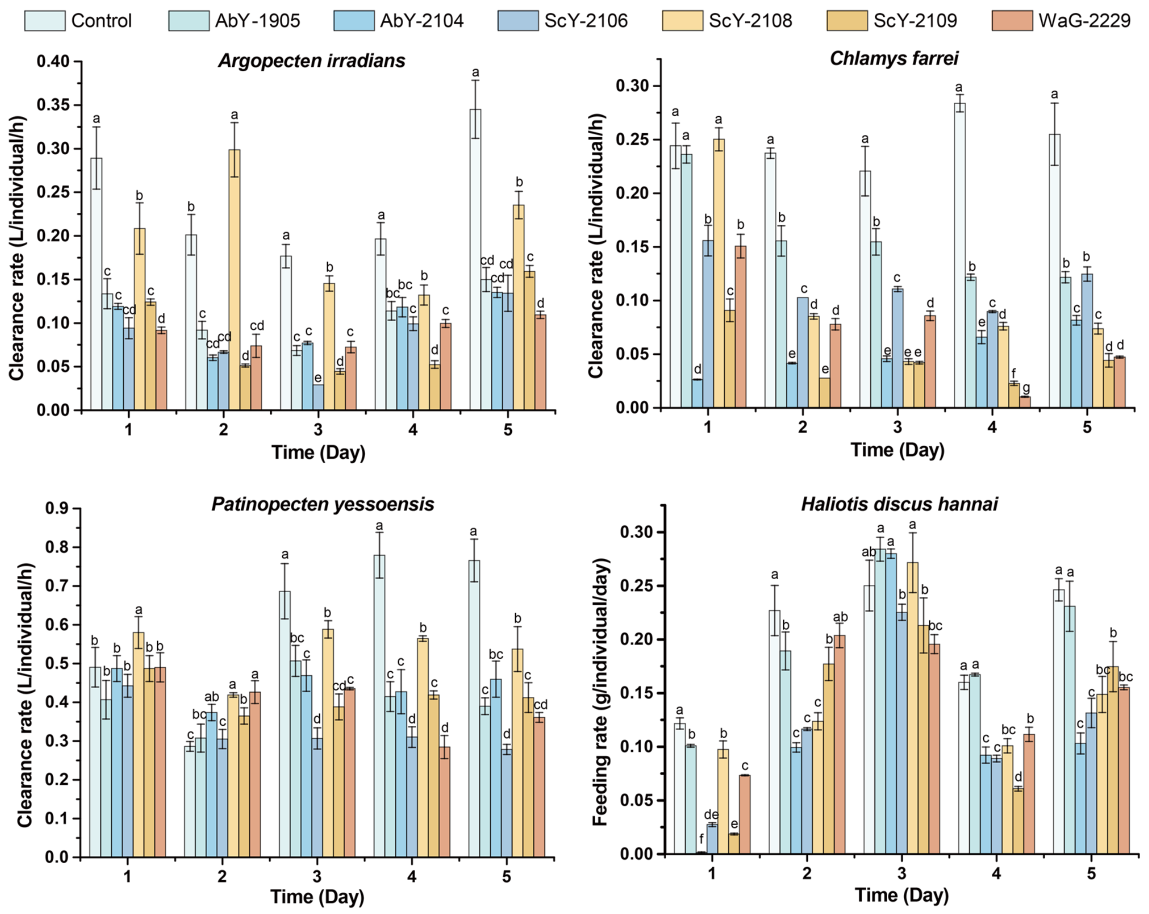

FIGURE 8
Feeding/clearance rate dynamics of farmed shellfish. Significant differences (ANOVA test, $p < 0.05$) among different groups at each time point are presented by different letters. Error bars represent standard deviation.

pathogens, improving survival, growth, and stress robustness (D'Alvise et al., 2013; Vadstein et al., 2018; Pettersen et al., 2021). Therefore, maintaining a high abundance of *K*-strategist bacteria and monitoring the dynamics of *r*-strategist bacteria could help prevent bacterial disease outbreaks in mariculture.

4.2 Bacterial diversity and community structure in different aquaculture types

Macroalgae-based aquaculture harbors the highest bacterial diversity. The bacterial Shannon diversity was the highest in type III (algae monoculture) and the lowest in type I (shellfish monoculture) (Figure 2B). Previous studies have shown that intensive monoculture of marine animals reduces bacterial diversity in coastal seawaters compared to non-culture ecosystems (Wang et al., 2018b), whereas kelp cultivation can enhance bacterial biodiversity (Wang et al., 2020; Sun et al., 2023). Macroalgae cultivation plays an increasingly important role in modern aquaculture, which is not only seen as the potential to improve seawater quality by assimilating excess inorganic nutrients but also as a possible "carbon sink" for CO_2 sequestration, let alone providing an important source of food and natural products (Gross, 2003; Xiao et al., 2017; Duarte et al., 2022; Yong et al., 2022). Moreover, algae could secrete diverse and abundant dissolved organic matter, leading to complex algae-bacteria interactions and increased microbial community diversity and functionality (Singh and Reddy, 2014; Li H. et al., 2022; Weigel et al., 2022; Sun et al., 2023).

The dominant bacterial taxa exhibited ecosystem-specific functional traits. ANOSIM revealed a significant structural divergence among bacterial communities (Table 2), with each aquaculture type harboring unique OTUs (61 in type I, 151 in type II, and 828 in type III). In addition, although many (273) bacterial families were common among different aquaculture types, the relative abundances of these bacterial families varied in distinct aquaculture types. For example, the bacterial families *Rhodobacteraceae*, *Microbacteriaceae*, and *Cryomorphaceae* were more abundant in type I, whereas *Methylophilaceae*, *Microtrichaceae*, and *Woeseiaceae* dominated type III (Supplementary Figure S3). *Rhodobacteraceae*, known for their versatile carbon, nitrogen, and sulfur metabolic capabilities, may help detoxify metabolic wastes from farmed marine animals (Hu et al., 2022; Ahmed and Campbell, 2025). *Microbacteriaceae* play a crucial role in degrading and remineralizing polycyclic aromatic hydrocarbon compounds, which is important for detoxifying chemical contaminants and farmed organisms' health (Jacques et al., 2008; Tonon et al., 2014; Wang et al., 2019; Hu et al., 2022). *Methylophilaceae* are reported to produce plant hormones such as cytokinins to promote the growth of terrestrial plants (Ivanova et al., 2000). Although the effect of *Methylophilaceae* on macroalgae is unclear, high abundances of these bacteria have often been found in algae cultures and aquatic angiosperm studies (Crump and Koch, 2008; Zhang et al., 2022). *Microtrichaceae* were reported to be one of the core phycosphere families in the macroalgae microbiomes (Lu et al., 2023). A recent study on coastal microbial populations showed that *Woeseiaceae* carried polysaccharide utilization loci predicted to target laminarin, alginate, and α-glucan (Viver et al., 2024). In our current study, *Woeseiaceae* (Otu154) was found to be the module hub with the maximum degrees in the type III (algae monoculture) bacterial network (Supplementary Table S2), which may be due to its ability to degrade algal polysaccharides. Farmed organisms may alter seawater's chemical and nutritional conditions, selecting specific bacteria that adapt to the changed environment and contribute to inorganic nutrient transformation and organic waste scavenging (Dang and Lovell, 2016; Enke et al., 2019; Gavriilidou et al., 2020). These data suggest that bacterial communities play an essential role in the health status of the aquaculture ecosystems (Deng et al., 2021; Ebeling et al., 2006; Hu et al., 2022).

4.3 Environmental drivers of the mariculture bacterial communities

Seawater bacterial communities' temporospatial dynamics were closely related to certain environmental factors, including seawater DO, transparency, temperature, NO_2^-, NO_3^-, Chl*a*, and algae culture (Figure 4B). Previous studies also indicated that DO, temperature, and Chl*a* were closely correlated with bacterial communities in mariculture systems, especially for surface waters (Alfiansah et al., 2018; Guan et al., 2020; Wang et al., 2021). Seawater DO is the most significant environmental factor affecting the bacterioplankton communities in the present study (Figure 4B). The highest DO concentrations were observed in late winter (February) (10.27-11.92 mg/L), while the lowest values were observed in late summer or early autumn (August or September) (5.56-7.51 mg/L) (Figure 1B). Our results are consistent with previous studies on surface waters of certain coastal seas and mariculture ecosystems (Li et al., 2022; Mahmood et al., 2016b; Zhou et al., 2020). Possible reasons for the observed seasonal DO dynamics include higher metabolic rates (particularly respiration) of marine organisms (including both macro- and microorganisms) and lower oxygen solubility in warmer seasons than in colder seasons in temperate marine waters (Dang, 2020; Dang and Jiao, 2014). Oxygen is essential for aerobic bacterial respiration and growth. Seawater deoxygenation could lead to a decreased oxygen utilization rate of bacteria (Lee et al., 2002). Our current study observed a relatively higher Shannon diversity in winter (Figure 2B). Long-term analyses showed that elevated DO could increase microbial diversity (Riding et al., 2019). Moreover, a reduction in DO concentration may increase facultative anaerobes, including pathogens like vibrios (Johnson et al., 2012; Guo et al., 2022), which partially explains the increased abundance of vibrios in autumn in Sanggou Bay (Figure 7A). The finding highlights the potential deoxygenation risk of mariculture for both farmed marine animals and coastal ecosystems, particularly in warmer seasons.

In the current study, a significant difference in seawater temperature was observed among different seasons, with the high temperatures observed from July to September (23.1 ± 1.6°C) and the low temperatures observed from January to March (5.3 ± 0.8°C) (Figure 1B). Temperature changes strongly influence bacterial community structure and the population dynamics of many OTUs (Figures 4A, B), consistent with previous studies (Pomeroy and Wiebe, 2001). The temperature effect is usually based on its influence on bacterial growth and production rates (White et al., 1991). In addition, elevated temperatures reduce the microbial interactions (Rajeev et al., 2021). A study by Zhou et al. (2021) also found that seawater warming could reduce prokaryotic network complexity, which aligns with our finding that microbial network nodes and links were significantly lower in summer (nodes: 185, links: 437) and autumn (nodes: 81, links: 97), compared to winter (nodes: 240, links: 687) and spring (nodes: 329, links: 1382) (Figures 6A, B; Supplementary Table S2). Moreover, the SEM result further revealed that the effects of temperature on bacterial community structure and diversity were indirect (Figure 4C), emphasizing the multiplex importance of temperature and its complex interactions with other environmental factors in driving the dynamics of bacterial communities.

Seawater transparency is another important environmental factor in aquaculture, particularly for shellfish production. The growth of phytoplankton, which is the natural feed for bivalves, is affected by seawater transparency (Tilzer et al., 1994). The current study identified a significant relationship (Spearman correlation, $p < 0.05$) between seawater transparency and Chl*a*. In addition, CCA and SEM analyses both identified seawater transparency as a key environmental factor influencing the bacterial communities (Figures 4B,C). Low transparency is typically linked to high seawater turbidity and elevated particulate material concentrations, which increase (micro)niche diversity and complexity in the otherwise seemingly homogenous seawater environment (Dang and Lovell, 2016). This provides a rational explanation for the observed importance of seawater transparency in driving the variation of bacterioplankton community structure and diversity in the studied mariculture ecosystems.

4.4 Seasonal dynamics and putative driving factors of pathogenic bacteria

Seasonal changes in bacterial communities are key to understanding disease outbreaks. Disease outbreaks of aquatic organisms are usually associated with an increased abundance of pathogens (de Bruijn et al., 2018). Diseases and mortality in high-temperature seasons are common in cultivated shellfish, including abalones, scallops, and oysters (Xiao et al., 2005; Ashton et al., 2020; Bansemer et al., 2023). Pathogenic diseases also occur in some cultivated macroalgae in these seasons (Eggert et al., 2010), as high temperatures promote bacterial pathogen proliferation and pathogenicity (Colwell, 1996; Yang et al., 2021; Wang et al., 2024). In September, the highest seawater temperature was observed, coinciding with the peak mortality of the farmed animals in Sanggou Bay in 2019, which increased from late August and peaked in September, reaching an estimated ~30%-60% mortality (survey results from Weihai Changqing Ocean Science Technology Co., Ltd., data not shown). This mortality pattern largely corresponded to the monthly pattern of potential bacterial pathogens, with the bacterial genus *Vibrio* as a typical and the most dominant member (Figures 7A, B).

Six pathogenic *Vibrio* strains were found to match certain *Vibrio* OTUs in the seawater bacterial communities (Supplementary Figure S5), and the genomes of these strains carried a variety of virulence factors, which could lead to the massive mortality of marine organisms (Frans et al., 2011; Darshanee Ruwandeepika et al., 2012) (Supplementary Tables S4-Supplementary Tables S9). Eight exotoxin-encoding genes were identified, including hemolysin III (hlyIII) and thermolabile hemolysin (TLH). Among the various hemolysins, hlyIII was first found in *V. vulnificus* (Chen et al., 2004), and TLH was found in *V. parahaemolyticus* (Taniguchi et al., 1985). As the most widely distributed bacterial toxins in vibrios, hemolysins exert diverse effects during infection (Shinoda, 1999). Hemolysins can act on erythrocyte membranes and cause rupture of blood cells in infected animals (Zhang and Austin, 2005). Hemolysins can also cause tissue necrosis, leading to massive mortality in cultivated marine organisms (Jia et al., 2010; Wong et al., 2012; Paria et al., 2021). One-component proteins and secreted effectors of Type III secretion system (T3SS), widely implicated in *Vibrio* pathogenesis, were also predicted in the genomes of ScY-2106 and WaG-2229. T3SS is usually regarded as a pathogenic island that can inject a variety of effector proteins into host cells. T3SS effectors exert their virulence by manipulating the modification of host protein functions or signaling pathways (Calder et al., 2014; Portaliou et al., 2016; Li et al., 2019). The genomes of *Vibrio* isolates provide supporting evidence for the potential pathogen screening results of the bacterial communities. Further evidence was provided by the environmental simulation experiment, which showed that all six pathogenic *Vibrio* isolates could reduce the feeding/clearance rate of the tested shellfish (Figure 8), demonstrating that bacterial pathogens at near-natural densities (10^5 individuals/mL) in seawater could reduce the physiological activities of shellfish.

Vibrio bacteria pose a grave threat to public health as they naturally inhabit estuarine and coastal environments, with some species being human pathogens closely associated with seafood animals (Sepala Dahanayake et al., 2023; Brauge et al., 2024). Unraveling the temporospatial dynamics of the mariculture microbiomes and the pathogenic members therein, especially in warm seasons, is paramount in human and farmed animals' health. *Vibrio* typically increases with rising water temperatures (Maugeri et al., 2004; Turner et al., 2009), and a similar trend was observed in the present study (Figure 7B; Supplementary Figure S4). This trend is further exacerbated by anthropogenic stressors such as global warming and intensified aquacultural activities, leading to a surge in the abundance of pathogenic and harmful (*e.g.*, antibiotic-resistant) vibrios and the incidence of *Vibrio* diseases (Vezzulli et al., 2013; Ina-Salwany et al., 2019; Sanches-Fernandes et al., 2022).

Along with high temperatures, seawater deoxygenation also increases pathogen abundance, infection, and marine animal mortality (Mikulski et al., 2000; Phippen and Oliver, 2017). In Sanggou Bay, the highest abundances of bacterial pathogens, such as *Vibrio* species, coincided with the lowest seawater DO levels (Figure 4A), showing that seasonal deoxygenation stimulated the rise of pathogenic bacteria, especially *Vibrio* (Guo et al., 2022). Moreover, low-oxygen conditions can upregulate bacterial virulence gene expression in marine animals' intestines and hypoxic seawater (Liu et al., 2011; El-Malah et al., 2014; Fan et al., 2014), mechanistically explaining the observed ecological phenomenon. In addition, hypoxia adversely impacts the survival, growth, metabolism, behavior, and immunity of marine animals (McCormick and Levin, 2017; Song et al., 2024; Waller et al., 2024), amplifying the deoxygenation effects on the losses of mariculture industries, fisheries, and environmental health. Future seawater oxygen reduction, driven by global warming and anthropogenic eutrophication, could further exacerbate the pathogenic threat (Guo et al., 2022). Our results indicate the importance of monitoring seawater DO in predicting the health status of the farmed shellfish and maricultural ecosystems.

The proliferation of algal degraders may act as a stimulator for pathogen outbreaks in shellfish mariculture. This study identified *V. halioticoli* (Otu1389) (Supplementary Figure S5) as a key biotic factor driving seasonal *Vibrio* dynamics in Sanggou Bay. This OTU emerged as a hub node with the highest degrees in the autumn bacterial network (Figures 6A, B, 7C) and showed significant positive correlations with almost all the other *Vibrio* OTUs (including all the pathogenic *Vibrio* species identified) (Figure 7D). *V. halioticoli* is commonly found in aquaculture seawater and the guts of herbivorous invertebrates, particularly abalones, known for its alginate lyase activities (Sawabe et al., 1998; Sugimura et al., 2000). This bacterium can form biofilms and has been detected on seaweed surfaces (Tanaka et al., 2002; Dash et al., 2009). The degradation of macroalgal alginate by *V. halioticoli* releases simple sugars and short-chain organic acids (Sawabe et al., 2003), promoting the growth of other heterotrophic bacteria, including pathogens. Analyses of the genomes of two *V. halioticoli* strains ASM49669 (GenBank accession number: GCA_000496695.1) and IAM14596 (GCA_003568965.1) through CAZy database annotation (https://www.cazy.org/Home.html) (Drula et al., 2022) revealed an extensive algal polysaccharide-degrading repertoire, including numerous algal polysaccharides-related lyases and hydrolases (Supplementary Figure 9). Moreover, genomic virulence factor analyses via the Virulence Factor Database (VFDB) identified numerous virulence determinants in *Vibrio halioticoli*, likely involved in *Vibrio*-algae interactions

(Supplementary Table 17). Alginate degradation may cause the disruption of macroalgal cell walls, resulting in algal rotting and death (Zhu et al., 2016; Costa et al., 2021), consistent with the observation that diseases in cultivated *Gracilaria* and wild kelp became the most severe in September (data from Weihai Changqing Ocean Science Technology Co., Ltd.). The degraded macroalgae release cellular contents in the form of dissolved and particulate organic matter into the surrounding seawater, further stimulating the growth of opportunistic bacteria (*i.e.*, the *r*-strategist bacteria, including opportunistic pathogens). This hypothesized scenario is supported by the observed low seawater DO and transparency in autumn (Figure 1B). The degraded macroalgal materials stimulated microbial community respiration and increased seawater turbidity. These findings suggest that the bacterial degradation of macroalgae in the IMTA systems may be an important biotic factor leading to the outbreak of shellfish pathogenic bacteria. Simultaneously monitoring algae-degrading bacteria and the health status of mass-cultivated macroalgae should be a prerequisite for preventing pathogenic diseases in mariculture.

5 Conclusions

In the present study, temporospatial bacterial community diversities and structures were investigated, and potential bacterial pathogens and their dynamics were also explored in three distinct aquaculture systems in Sanggou Bay. Seawater bacterial communities showed obvious season- and aquaculture-type-related dynamics. Environmental factors, such as seawater DO, transparency, temperature, NO_2^-, NO_3^-, Chl*a*, and algae culture, may significantly influence the bacterial communities in Sanggou Bay. By performing a combined analysis of bacterial communities and pathogenic strains as well as environmental simulation experiments, it was found that the outbreaks of pathogenic bacteria are closely related to the seasonal changes in bacterial communities and seawater DO, temperature, and transparency. Furthermore, macroalgae-degrading bacteria, such as *V. halioticoli*, were found for the first time as a putative biotic factor stimulating the growth of pathogenic bacteria in high-temperature seasons via their active degradation and transformation of macroalgal biomass, thus providing enriched carbon and energy sources to the pathogens. For future aquaculture practices, some optimizing strategies are proposed: (1) synchronically monitoring the bacterial communities and critical physicochemical parameters, including seawater dissolved oxygen, temperature, and transparency to provide valuable information for the prediction of pathogenic bacteria in the marine aquaculture systems; (2) monitoring the health status of cultivated macroalgae (e.g., relative growth rate and tissue necrosis index) and the temporospatial dynamics of macroalgae-degrading bacteria, especially during high-temperature seasons; and (3) optimizing the balance between shellfish and macroalgae cultivations and carefully managing harvest timing. These practical strategies may help mitigate the outbreaks of seasonal pathogenic diseases for farmed marine animals in the IMTA systems.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

LL: Conceptualization, Investigation, Project administration, Validation, Writing – original draft, Funding acquisition. LN: Formal Analysis, Writing – review & editing. CA: Writing – review & editing. DZ: Funding acquisition, Writing – review & editing. PZ: Formal Analysis, Writing – review & editing. XJL: Data curation, Formal Analysis, Investigation, Software, Visualization, Writing – original draft, Writing – review & editing. XL: Formal Analysis, Funding acquisition, Methodology, Resources, Writing – review & editing. HD: Funding acquisition, Supervision, Writing – review & editing.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This work was supported by grants from the National Key Research and Development Program of China (2020YFA0608302), the National Natural Science Foundation of China (42076111, 42141003, 42188102, and 42376084), the Natural Science Foundation of Shandong Province (ZR2021QC220), the Beijing Natural Science Foundation (8222047), and the Zhejiang Provincial Natural Science Foundation of China (LZ24D060003).

Conflict of interest

Author LL was employed by the company Weihai Changqing Ocean Science Technology CO., Ltd.

The remaining 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.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1581190/full#supplementary-material

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