

WINDLY WATER

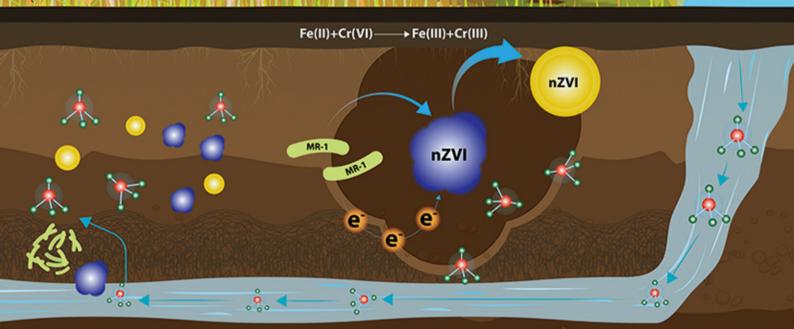
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ENVIRONMENTAL SCIENCE

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电活性微生物激活生物质炭/零价铁协同钝化Cr(VI)及机制

廖聪坚,赵晓蕾,刘凯,钟松雄,李芳柏,方利平,叶挺进,石虎砚



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#### Environmental Science

# 输水情景下白洋淀好氧反硝化菌群落对溶解性有机物 的响应

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摘要:溶解性有机物(DOM)是影响微生物群落演变的重要因素,而生态输水是白洋淀的一个重要特征,为了探究输水情境下DOM 对好氧反硝化菌的影响,本文结合水体 DOM 的组分解析和好氧反硝化高通量测序技术,进行了水体好氧反硝化菌对DOM 的响应研究.结果显示,白洋淀水体 DOM 的相对浓度存在显著差异,河口区要低于内部区; DOM 呈现出较强自生源特征,河口区具有更高的分子量和更强的腐殖化; 平行因子法解析出 3 种类蛋白组分和 1 种类腐殖质组分,类蛋白组分占比达到 35.64%~96.38%,与荧光区域积分得到类蛋白占主体的结果相一致.与此同时,该时期水体好氧反硝化菌主要属于变形菌门(Protebacterice),主要包括 Cupriavidus、Aeromonas、Thauera、Shewanella 和 Pseudomonas,与随机森林筛选出的指示物种相一致;网络分析得到 35 个网络关键节点,主要隶属于 Thauera、Cupriavidus 以及 Unclassified\_bacteria; 冗余分析(RDA)显示类腐殖质物质是影响水体整体好氧反硝化菌群落组成的因子,类蛋白物质是影响指示物种群落和关键节点群落结构分布的重要因素.综上可知,水体溶解性有机物中类蛋白组分可以作为筛选适于生态输水期水体特征的耐低温高效好氧反硝化菌的碳源选择. 关键词:白洋淀;溶解性有机物(DOM);平行因子分析(PARAFAC);好氧反硝化;生物信息分析;网络分析中图分类号: X172 文献标识码:A 文章编号: 0250-3301(2021)09-4319-13 DOI: 10.13227/j. hjkx. 202101290

# Structure of Aerobic Denitrification Bacterial Community in Response to Dissolved Organic Matter in Baiyangdian Lake During the Water Delivery Period

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Abstract: Dissolved organic matter (DOM) plays an important role in the evolution of microbial communities. Meanwhile, ecological water delivery is an important feature of Baiyangdian Lake. To explore how the structure of the aerobic denitrification bacteria community responds to DOM during the water delivery period, the DOM components of water were examined and high-throughput sequencing of aerobic denitrification bacteria was performed. The results showed significant differences in DOM concentration in Baiyangdian Lake, with the estuary area exhibiting lower DOM concentrations. The water exhibited strong autogenous source, while DOM in the estuary area had a higher molecular weight and degree of humification. Three protein-like substances (C1, C2, and C4) and one humic-like substance (C3) were identified through PARAFAC. The protein-like substances accounted for the major proportion of DOM, which was consistent with the results of fluorescence regional integration (FRI). The genera of the water body were mainly in the Protebacterice phylum, including *Cupriavidus*, *Aeromonas*, *Thauera*, *Shewanella*, and *Pseudomonas*. Meanwhile, *Cupriavidus*, *Thauera*, *Shewanella*, *Agrobacterium*, and *Pseudomonas* were the main indicator species, according to random forest (RF) analysis. Through network analysis, 35 key nodes of the network were obtained, belonging to *Thauera*, *Cupriavidus*, and Unclassified\_bacteria, respectively. Redundancy analysis (RDA) showed that a humic-like substance was the main environmental factor regulating the whole structure of the aerobic denitrification bacterial community, while protein-like substances played important roles in changes to the indicator species and key nodes of the community. Overall, protein-like substances could provide an important reference for selecting carbon sources during the screening of efficient and cold resistance aerobic denitrification bacteria that are adapted to actual water bodies.

**Key words:** Baiyangdian Lake; dissolved organic matter (DOM); parallel factor analysis (PARAFAC); aerobic denitrification; bioinformatics analysis; network analysis

好氧反硝化不仅可以在同一系统中完成硝化和 反硝化的过程,同时还能利用反硝化过程产生的碱 中和硝化过程产生的酸. 因此,好氧反硝化逐渐成为 生物脱氮的研究热点<sup>[1]</sup>. 近年来,研究者从不同的 环境中分离出大量的高效好氧反硝化菌. 比如,人工 湿地系统中的 Alcaligenes faecalis strain WT14<sup>[2]</sup>和

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Paracoccus thiophilus strain LSL 251<sup>[3]</sup>; 水产养殖废水处理系统中的 Pseudomonas sp. DM02<sup>[4]</sup>、Achromobacter sp. JL9<sup>[5]</sup> 和 Arthrobacter sp. HHEP5<sup>[6]</sup>;海底淤泥中的 Paracoccus versutus LYM<sup>[7]</sup>;污水处理厂中的 Pseudomonas mendocina X49<sup>[8]</sup>和 Thauera sp. strain SND5<sup>[9]</sup>;水库沉积物中的 Pseudomonas sp. HXF1<sup>[10]</sup>;河流沉积物中的 Pseudomonas stutzeri ADP- 19<sup>[11]</sup>;松花江中的 Janthinobacterium sp. M-11<sup>[12]</sup>;工业园区沉积物中的 Achromobacter sp. L3<sup>[13]</sup>.众多分离的高效好氧反硝化菌还具有异养硝化、聚磷、耐低温、耐重金属以及降解抗生素的特性<sup>[14,15]</sup>.

然而,目前关于好氧反硝化菌的分析大多集中 于分离鉴定和实验室的脱氮特性分析[14,15]. 虽然, 在自然环境中关于好氧反硝化有所研究[16,17]. 但 是,涉及应用好氧反硝化菌进行实际天然水体环境 脱氮的研究却鲜见报道. 仅有如下研究涉及实际水 体的应用, Guo 等[18] 将好氧反硝化菌 Pseudomonas stutzeri strain T1 投加到太湖水体试验系统中实现总 氮水质从 V 类到 Ⅱ 类水体的转变; Tang 等[19] 应用 好氧反硝化菌剂修复城市河流,实现沉积物中 14.7%的总氮的去除; 文献[20,21]通过原位混合 充氧强化了水库土著好氧反硝化菌,使水体氮素得 到高效去除. 适于实际天然水体的高效好氧反硝化 菌难于获取很重要的原因,可能是实验室采用的培 养基与实际水体中碳源组成差异太大,使筛选出来 的高效好氧反硝化菌株无法在实际水体中发挥作 用. 然而, 涉及天然环境中好氧反硝化菌群分布与环 境中溶解性有机物的相关分析却相对较少.目前,有 学者研究了不同分子量的天然有机物[22]以及水库 沉积物中有机物[23]对好氧反硝化细菌脱氮的影响: 有学者研究了白洋淀冬季好氧反硝化菌群落空间分 布特征及驱动因素[24,25]. 考虑到自然环境下好氧反 硝化菌群分布与溶解性有机物存在耦合作用,有机 碳源的种类直接影响高效好氧反硝化菌筛选的成功 与否. 因此,开展天然环境中好氧反硝化菌群落对溶 解性有机物的响应研究变得十分必要.

白洋淀作为雄安新区的核心水体,是新区建设的重要生态屏障.为恢复白洋淀的生态功能,河北省统筹调度了黄河水、南水北调水、上游水库水以及再生水等多种水源对白洋淀进行了生态输水.本文选取冬季输水期白洋淀典型区域的水体样品,通过研究该时期水体好氧反硝化菌群落分布特征和关键物种;并结合溶解性有机物组分的分析,来研究输水情景下好氧反硝化菌群落对溶解性有机物的响应,以期为将来制定适应白洋淀冬季输水期水体特征的

耐低温好氧反硝化菌筛选的碳源选择提供必要的技术支持.

#### 1 材料与方法

#### 1.1 研究区域与样品采集

结合研究者的文献资料和白洋淀的历史承载功能<sup>[26]</sup>,白洋淀划分为5个典型区域,分别为河口区、自然区、旅游区、养殖区以及生活区<sup>[24]</sup>(图1).

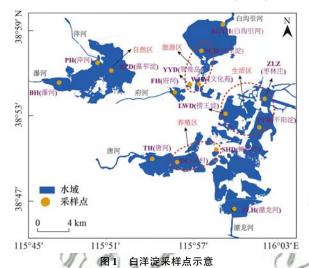


Fig. 1 Locations of the sampling sites in Baiyangdian Lake

其中,河口区承接上游入淀河流的来水,主要包 括白沟引河(BGYH, 水库水)、萍河(PH, 水库水)、 瀑河(BH, 南水北调水)、府河(FH, 保定再生水)、 唐河(TH, 南水北调和水库水)和潴龙河(ZLH, 黄 河水);自然区包括藻苲淀(ZZD);旅游区为白洋 淀主要观赏景点、承接游客的区域,主要包括文化苑 (WHY)、鸳鸯岛(YYD)和烧车淀(SCD);养殖区主 要包括端村(DC)和鲥鯸淀(SHD); 生活区主要包 括捞王淀(LWD)、平阳淀(PYD)和枣林庄(ZLZ). 同时依据河流输水的影响程度,将白洋淀分为河口 区和内部区(自然区、旅游区、养殖区和生活区).本 研究于2020年1月(生态输水期)对白洋淀进行取 样,用纯水清洗过的聚乙烯瓶采集各采样点5 L 中 层水样,冷藏避光运回实验室,用于分析水体好氧反 硝化菌群落分布和溶解性有机物特征.其中,水样用 0.45 μm 醋酸纤维滤膜过滤后进行光谱测定, 3 d 内测定完成.

#### 1.2 DNA 提取与 PCR 扩增

本文利用  $0.22~\mu m$  醋酸纤维滤膜过滤水样,将滤膜送至测序公司进行水体总 DNA 样本的提取. 通过引物 F:5'-TGGACVATGGGYTTYAAYC- 3' 和 R:5'-ACYTCRCGHGCVGTRCCRCA- 3' 对水体的 napA 基因进行 PCR 扩增,完成好氧反硝化菌高通量测序 [27](上海派森诺生物科技股份有限公司).  $25~\mu L$ 

PCR 反应体系为:  $5 \times$  reaction buffer  $5 \mu L$ ,  $5 \times$  GC buffer  $5 \mu L$ ,  $2.5 \text{ mmol} \cdot \text{L}^{-1} \text{ dNTP } 2 \mu L$ , forward primer (  $10 \mu \text{mol} \cdot \text{L}^{-1}$ )  $1 \mu L$ , reverse primer (  $10 \mu \text{mol} \cdot \text{L}^{-1}$ )  $1 \mu L$ , Q5 DNA polymerase  $0.25 \mu L$ , DNA Template  $2 \mu L$ ,  $ddH_2O$   $8.75 \mu L$ . 扩增条件为: 预变性温度  $98 \, ^{\circ} \text{C} 2 \text{ min}$ ;  $98 \, ^{\circ} \text{C}$  变性 15 s,  $55 \, ^{\circ} \text{C}$  退火 30 s,  $72 \, ^{\circ} \text{C}$  延伸 10 min.

#### 1.3 溶解性有机物测定及分析

利用紫外-可见分光光度计(DR6000,美国)和 荧光分光光度计(F-7000,日本)测量过滤水样的紫

外-可见吸收光谱和三维荧光光谱,具体测定参数设定参见文献 [28,29] 执行. 采用  $a_{254}$ 、 $a_{355}$ 和  $a_{440}$ 来表征溶解性有机物相对浓度 [29]. 采用三维荧光平行因子法 [28] 和荧光区域积分法 [30] 对三维荧光光谱的组分进行解析. 与此同时,选用了一系列紫外可见光谱以及三维荧光光谱的光谱指数来表征 DOM 的特征,包括 E2/E3、E3/E4、 $S_R$ 、荧光指数 (FI)、腐殖化指数 (HIX)、生物源指数 (BIX)以及新鲜度指数 ( $\beta$ :  $\alpha$ )等 (表 1). 三维荧光光谱的荧光强度进行拉曼(单位 R. U)的标准化处理,具体操作详见文献 [38].

表 1 荧光区域积分组分以及光谱特征指数

Components of fluorescence region integration and spectra indices 项目 具体指标 环境意义 文献 第 I 区域(P1) 酪氨酸类蛋白质含量 第Ⅱ区域(P2) 色氨酸类蛋白质含量 荧光区域积分 第Ⅲ区域(P3) 类富里酸含量 微生物代谢产物含量 第Ⅳ区域(P4) 第 V 区域(P5) 类腐殖酸含量 表征 DOM 分子量的大小 E2/E3 [31] 衡量 DOM 腐殖质腐殖化程度 E3/E4 [31]  $S_{\mathrm{R}}$ 反映 DOM 来源信息 [32] 荧光指数(FI) 评估 DOM 的来源 [33] 评估 DOM 的腐殖化程度 光谱特征指数 腐殖化指数(HIX) [34] 生物源指数(BIX) 反映内源 DOM 的贡献程度 [35] 新鲜度指数( $\beta$ :  $\alpha$ ) 反映新生 DOM 的所占比例 [36] Fn280 反映 DOM 中类蛋白相对丰度 [37] 反映 DOM 中类腐殖质相对丰度 Fn355 [37]

Table 1 Community of Community in the state of the state

#### 1.4 生物信息分析

利用R进行好氧反硝化菌的生物信息学分析 (http://www.r-project.org/). 具体分析如下,通过 Chao1 指数来表征好氧反硝化菌的丰度[39],通过香 农指数、辛普森指数来反映好氧反硝化菌的多样 性[39],通过覆盖度指数评估好氧反硝化菌的测序深 度<sup>[39]</sup>;通过主坐标分析(principal co-ordinates analysis, PCoA)来研究不同区域好氧反硝化菌的差 异: 基于随机森林分析(random forest, RF)来筛选 输水期好氧反硝化菌群落的指示物种[40,41];依据 Spearman 的相关分析,选取相关性 |r| > 0.7,显著 性 P < 0.05 的物种进行网络分析; 研究好氧反硝化 菌群落中各个物种的相互关系[42],并基于对节点的 类型分析研究网络中关键物种<sup>[43]</sup>;通过冗余分析 (redundancy analysis, RDA)得到溶解性有机物各组 分与好氧反硝化菌的相关性<sup>[44]</sup>. 本文中绘图由 R 和 Gephi 完成,数据统计分析中 P 值 < 0.05, 0.001 < P值 < 0.01 以及 P值 < 0.001 表示统计学不同水平 上存在显著差异.

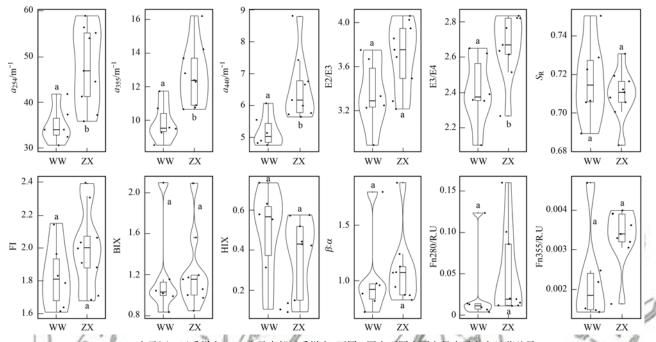
#### 2 结果与讨论

#### 2.1 水体溶解性有机物分析

从  $a_{254}$ 、 $a_{355}$  和  $a_{440}$  的数据可知(图2),河口区的  $a_{254}$ 、 $a_{355}$ 和  $a_{440}$ 达到(35.05 ± 3.98)、(9.88 ± 1.15) 和(5.21 ±0.51) m<sup>-1</sup>,白洋淀内部区的  $a_{254}$ 、 $a_{355}$ 和  $a_{440}$ 达到(47.81 ± 8.64)、(12.66 ± 1.85)和(6.55 ± 1.02) m<sup>-1</sup>:河口区的溶解性有机物的相对浓度显著 低于内部区(P<0.05). 从统计学上看,河口区和内 部区的 E2/E3 不存在显著差异,但是白洋淀内部区 的 E2/E3 达到 3.70 ± 0.31 高于河口区的 3.35 ± 0.32;数据表明河口区的水体溶解性有机物的分子 量要高于内部区,与入淀河流输水携带大分子量溶解 性有机物有关. 河口区的 E3/E4 达到 2.41 ±0.20,要 小于内部区的 2.66 ± 0.18,表明河口区水体溶解性有 机物的腐殖化程度要高于内部区.  $S_{\rm R}$  值呈现出河口 区 $(0.72 \pm 0.02)$ 高于内部区 $(0.71 \pm 0.01)$ ,也显示出 河口区溶解性有机物呈现出更高的分子量和腐殖化 特征. 白洋淀内部区 FI 达到 2.00 ±0.24,高于河口区

的 1.83 ± 0.20; 内部区 FI 大于 1.9,河口区的小于 1.9,表明内部区水体溶解性有机物的自生源特征要强于河口区.河口区和内部区的 BIX 达到 1.19 ± 0.46 和 1.23 ± 0.38,都大于 1.0,表明都呈现较强的自生源特征,其中内部区的自生源更强一些.两个区域的 HIX 都小于 4,与 FI 和 BIX 呈现的结果相一致,该时

期水体的溶解性有机物腐殖化程度较低. 内部区和河口区的 $\beta$ :  $\alpha$  达到1.  $10 \pm 0$ . 32 和 1.  $02 \pm 0$ . 39,结果表明内部区的新生 DOM 占比要高于河口区. Fn280 和Fn355 指数显示,河口区和内部区在统计学上不存在显著差异;但是相比于河口区而言,内部区具有更高的类蛋白丰度.



WW 表示河口区采样点; ZX 表示内部区采样点,下同; 图中不同小写字母表示存在显著差异 图 2 白洋淀溶解性有机物相对浓度和光谱特征指数

Fig. 2 Concentration of DOM and spectral characteristics of the sampling sites in Baiyangdian Lake

通过平行因子分析得出4种荧光组分(图3): 组分  $C1(E_x/E_m = 275 \text{ nm}/340 \text{ nm})$  为长波类酪氨酸 物质,多源于微生物降解和生活污水[45];组分 C2  $(E_x/E_m = 230 \text{ nm}/340 \text{ nm})$  为类色氨酸物质,属于类 蛋白组分,多源于微生物降解和生活污水[46];组分  $C3(E_x/E_m = 240 \text{ nm}/400 \text{ nm})$  为富里酸物质,属于腐 殖质类,较难降解<sup>[47]</sup>;组分 C4( $E_x/E_m = 220 \text{ nm/}$ 325 nm) 为短波类酪氨酸物质,属于类蛋白组分,多 源于微生物降解和生活污水[48]. C1 组分相对丰度 的变化范围为 5.92%~52.04%, 最大值为养殖区的 SHD 采样点,最小值为河口区的 PH 采样点; C2 组 分相对丰度的变化范围为 3.71%~40.00%,最大值 为 TH 采样点,最小值为 PH 采样点; C3 组分相对 丰度的变化范围为 3.62%~64.36%, 最大值为 PH 采样点,最小值为 DC 采样点; C4 组分相对丰度的 变化范围为 5.70%~26.01%,最大值为 PH 采样点, 最小值为 FH 采样点; 类蛋白类物质(C1 + C2 + C4) 变化范围为 35.64%~96.38%, 最大值为 SHD 采样点,最小值为 PH 采样点.基于河口区和内部区 进行分类,平行因子解析的各组分荧光强度和相对 丰度在统计学上不存在显著差异,但是类蛋白类组 分 C1、C2 和 C4 都呈现出内部区高于河口区的特点,类腐殖质物质 C3 呈现出河口区高于内部区的特点(图 3),与入淀河流输送腐殖质的情况有关.

荧光区域积分解析的 5 种组分的分布情况如图 4 所示,河口区和内部区的各个组分同样在统计学上都不存在显著差异. 其中类蛋白物质(P1、P2 和 P4)都呈现出内部区占比高于河口区的特征,类腐殖质物质(P3 和 P5)呈现出河口区高的特征. 荧光区域积分的结果与平行因子解析出荧光组分的情况相一致.

与此同时,分布对紫外可见光谱[图 4(f)]、平行因子分析组分[图 4(g)]和荧光区域积分组分[图 4(h)]进行了 PCoA 分析. 基于紫外可见光谱的 PCoA 分析显示,前两轴共解释了总体变化的 88.94%,河口区与内部区呈现显著差异(Adonis, R²=0.49, P < 0.01);基于平行因子分析组分的 PCoA 分析显示,前两轴共解释了总体变化的 75.85%;基于荧光区域积分组分的 PCoA 分析显示,前两轴共解释了总体变化的 82.15%;平行因子和荧光区域积分组分并未存在统计学上的显著差异.平行因子解析的荧光组分与紫外可见光谱和荧

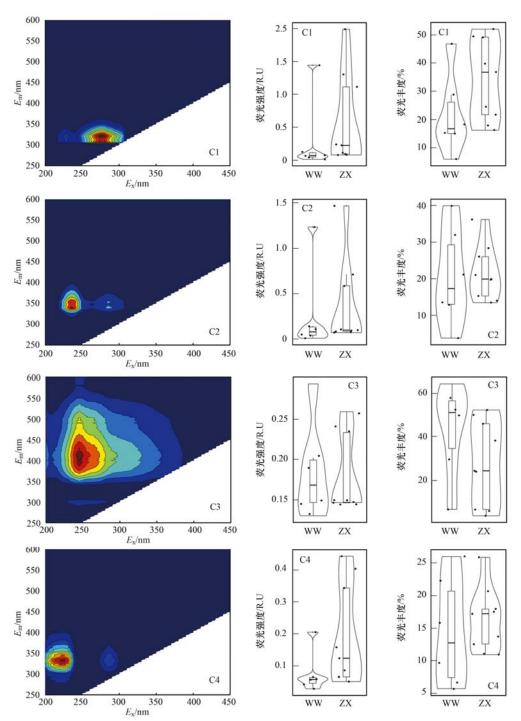


图 3 基于平行因子法解析出的白洋淀水体 CDOM 的荧光组分及分布特征

Fig. 3 Distribution and fluorescence components of CDOM identified using the PARAFAC model in Baiyangdian Lake

光区域积分组分的相关性分析如图 5 所示,荧光组分 C1 与 C2 和 C4 呈现显著正相关(P < 0.001), C2 与 C4 呈现显著正相关(P < 0.001), C1、C2 和 C4 与 Fn280 呈现显著正相关(P < 0.001), 表明 C1、C2 和 C4 存在相似的来源,与 3 个组分为类蛋白物质相一致. 类蛋白类物质(C1、C2 和 C4)与 E2/E3 呈现显著正相关(P < 0.05),表明分子量越小类蛋白物质 越 多. 类 蛋白类物质(C1、C2、C4 和 Fn280)与荧光区域积分的类蛋白组分 P2 和 P4 呈现显著正相关(P < 0.01),与类腐殖质组分 P3 和

P5 呈现显著负相关(*P* < 0.001). 综上可知,平行因子法解析的组分和荧光区域积分划分的组分呈现较高的一致性.

#### 2.2 微生物 α 多样性分析

如表 2 所示,依据历史功能划分来看,自然区的 Chao1 指数最高,其次为旅游区和生活区,最后为河口区和养殖区,表明自然区的好氧反硝化菌微生物 群落的丰富度最高;依据河口区和内部区划分,内部区的 Chao1 指数(2 184. 37 ± 323. 35)高于河口区 (1 815. 93 ± 260. 70). 各个采样点的 Simpson 和

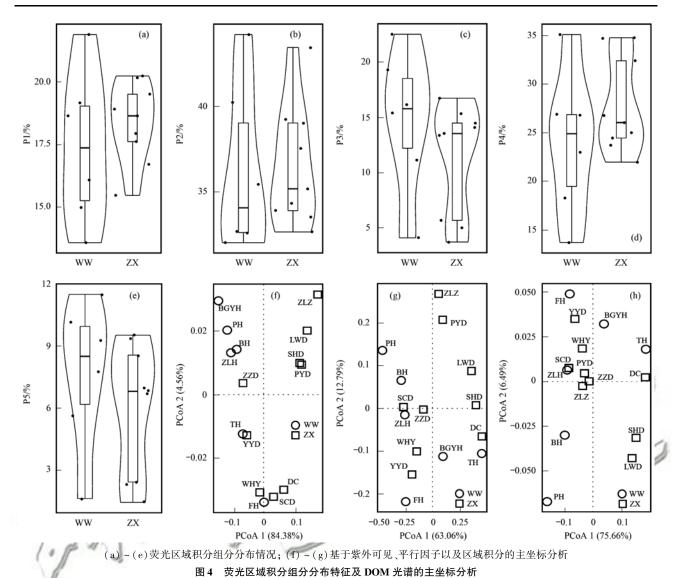


Fig. 4 Distribution characteristics of components identified using the FRI model and PCoA of the DOM spectrum

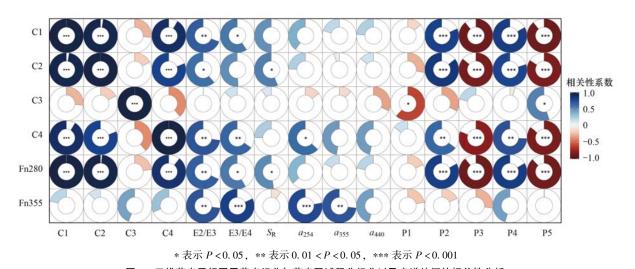


图 5 三维荧光平行因子荧光组分与荧光区域积分组分以及光谱特征的相关性分析 Fig. 5 Correlation analysis of PARAFAC components and FRI components/spectral characteristics

Shannon 指数中,养殖区和河口区较高,自然区最 样本测序深度能够很好地覆盖物

Shannon 指数甲, 养殖区和河口区较高, 目然区最低; 内部区的 Simpson 和 Shannon 指数要低于河口区. 各个采样点间覆盖度指数大于 0.99, 显示出各

样本测序深度能够很好地覆盖物种信息. 综上, 白洋 淀河口区与内部区的好氧反硝化菌群落丰富度和多 样性存在一定差异.

表 2	白洋淀好氧反硝化菌微生物多样性指数
1X 4	口什此为 乳及阴化图似土物 夕什压归奴

区域	样本	Chaol 指数	Simpson 指数	Shannon 指数	覆盖度指数
河口区	6	1 815. 93 ± 260. 70	0. 97 ± 0. 01	6. 51 ± 0. 18	0. 99 ± 0. 00
自然区	1	$2716.91 \pm 0.00$	$0.95 \pm 0.00$	$6.22 \pm 0.00$	$0.99 \pm 0.00$
旅游区	3	$2\ 285.\ 76\pm170.\ 19$	$0.96 \pm 0.00$	$6.46 \pm 0.06$	$0.99 \pm 0.00$
养殖区	2	$1.781.08 \pm 72.08$	$0.97 \pm 0.00$	$6.65 \pm 0.11$	$0.99 \pm 0.00$
生活区	3	$2\ 174.\ 33\pm258.\ 18$	$0.96 \pm 0.01$	$6.40 \pm 0.34$	$0.99 \pm 0.00$
河口区	6	1 815. 93 ± 260. 70	$0.97 \pm 0.01$	6. 51 ± 0. 18	0.99 ± 0.00
内部区	9	$2\ 184.\ 37\pm 323.\ 35$	$0.96 \pm 0.01$	$6.46 \pm 0.22$	$0.99 \pm 0.00$

#### 2.3 好氧反硝化菌群落组成

该时期各个采样点的好氧反硝化菌主要属于变 形菌门 (Protebacterice) 和未分类 (Unclassified\_ bacteria),其中变形菌门为第一大门类,占比为 39.34%~57.92%;未分类菌达到41.93%~ 60.54%. 变形菌门中, β-Proteobacteria 为第一大纲, 占比达到 15.46% ~ 32.11%; γ-Proteobacteria 是第 二大纲,占比达到 4.14% ~ 12.95%; α-Proteobacteria 是为第三大纲,占比为 3.05% ~ 8.03%. 在属水平上(图 6), Cupriavidus 是第一大 属,占比范围为 2.05%~14.91%,自然区 ZZD 最多, 河口区 BH 最少. Cupriavidus 作为重要的好氧反硝 化菌属被广泛报道,包括具有耐重金属性能的高效 异养硝化-好氧反硝化菌 Cupriavidus sp. S1[49],能在 好氧条件下同时去除硝酸盐、磷和镉的高效菌株 Cupriavidus sp. H29<sup>[50]</sup>以及兼具修复地下水硝酸盐 和锰污染的混合营养的反硝化菌 Cupriavidus sp. HY129<sup>[51]</sup>. Aeromonas 是第二大属,占比为 2.22%~ 4.08%,在 DC 和 ZLZ 的占比最大;与此同时,有研 究不仅发现 Aeromonas 是水源水库好氧反硝化脱氮 过程中主要的菌属[37],而且还发现好氧反硝化菌 Aeromonas sp. VNT<sup>[52]</sup>和 Aeromonas sp. HN-02<sup>[53]</sup>都

具有耐低温的特性. Thauera 占比为 2.06% ~ 3.83%, 在TH和PH占比较多:有研究发现Thauera sp. strain SND5 是 1 株高效且同时具有脱氮和聚磷 功能的菌株[9],而且还有以好氧反硝化菌 Thauera 为主的微生物燃料电池实现脱氮和发电的报 道<sup>[54,55]</sup>. Shewanella 占比 0.05%~7.83%,有研究发 现 Shewanella baltica OS678 具有好氧反硝化特 性[56],而且 Shewanella oneidensis MR-1 还可以通过 影响电子竞争和分布提高反硝化性能[57] Pseudomonas 作为典型好氧反硝化菌被广泛地研究, 包括:能在高溶解氧环境下实现氨氮、硝氮和亚硝氮 高效去除的 Pseudomonas sp. DM02<sup>[4]</sup>,能同时去除 地下水中氮素和氟的 Pseudomonas sp. HXF1[10],具 有脱氮和聚磷的 Pseudomonas stutzeri ADP-19[11] 有 耐 低 温 的 Pseudomonas sp. Magnetospirillum 菌在府河的占比最大,达到 0.91%. Janthinobacterium sp. M-11 是 1 株分离于松 花江的耐低温高效异养硝化-好氧反硝化菌[12]. 异 养硝化-好氧反硝化菌 Agrobacterium sp. LAD9 能实 现氮素以" $NH_4^+ \rightarrow NH_2OH \rightarrow NO_2^- \rightarrow N_2O \rightarrow N_2$ "的 方式高效去除[58]. Azoarcus 菌是低盐度硝化反硝化 系统中的优势菌<sup>[59]</sup>. Serratia marcescens W5 是 1 株

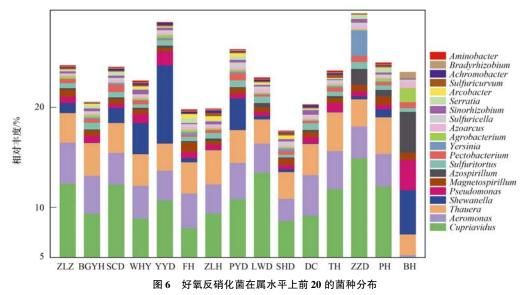


Fig. 6 Distribution characteristics of top 20 aerobic denitrification bacteria at genus level

高效的异养脱氮菌<sup>[60]</sup>. Achromobacter sp. JL9 是能同时降解抗生素和氮素的高效菌株<sup>[61]</sup>. Bradyrhizobium 也是具有脱氮功能的反硝化菌<sup>[62]</sup>. 综上分析,白洋淀冬季输水期解析的好氧反硝化菌与已报道的典型高效好氧反硝化菌相吻合.

基于属水平对该时期的好氧反硝化菌进行了PCoA分析[图7(a)],结果显示,PCoA1和PCoA2分别解释了总体变化的53.65%和18.1%,其中PCoA1起主要作用.在河口区和内部区的划分角度来看,不存在统计学上的显著差异;ZLH、BGYH和FH采样点的差异较小,PH和TH间物种组成差异较小,DC、WHY和SHD采样点的差异较小,SCD、YYD、PYD、LWD和ZLZ间的差异较小.与此同时,对该时期的好

氧反硝化菌进行随机森林分析,筛选出重要性前 20 的重要物种[图 7(b)]. 其中属于丰度前 10 的主要有 Thauera(2.06% ~ 3.83%)、Shewanella(0.05% ~ 7.83%)、Agrobacterium (0.07% ~ 1.42%)、Pseudomonas (0.39% ~ 3.03%)、Bradyrhizobium (0.03% ~ 0.66%)、Aeromonas(2.24% ~ 4.08%)、Cupriavidus (2.05% ~ 14.91%)、Sinorhizobium (0.07% ~ 0.47%)、Magnetospirillum (0.35% ~ 0.91%)和 Achromobacter(0.01% ~ 0.26%);其他为相对低丰度菌,包括 Dechloromonas、Ferrimonas、Pasteurella、 Janthinobacterium、 Campylobacter、Moraxella、Cutibacterium、Photobacterium、Escherichia 和 Sulfuritalea.

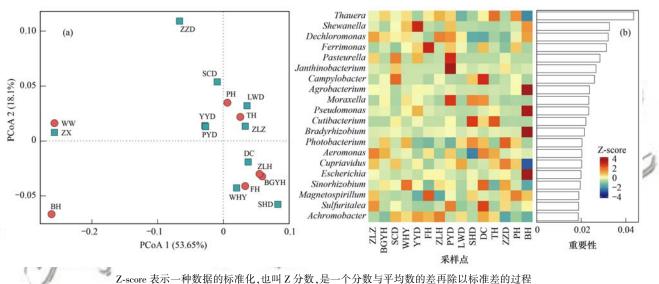


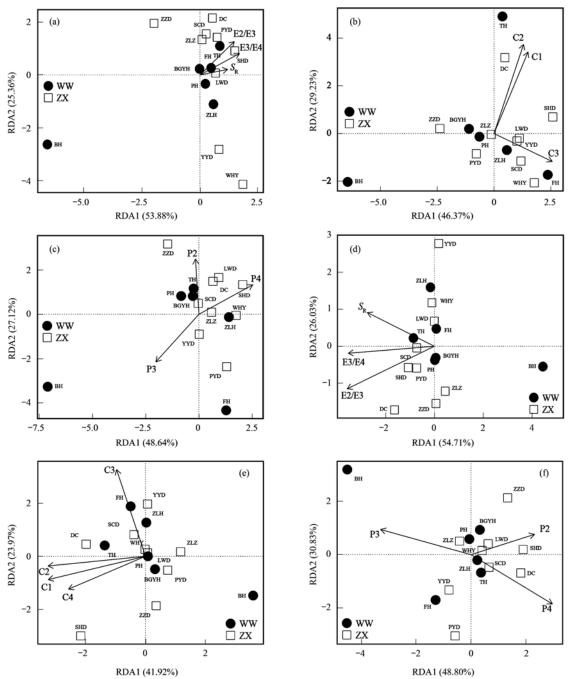
图 7 白洋淀好氧反硝化菌的主坐标分析和随机森林分析 Fig. 7 PCoA and random forest analysis of aerobic denitrification bacteria in Baiyangdian Lake

与此同时,本文通过 RDA 分析研究该时期水体 好氧反硝化菌与溶解性有机物的关系(图8).基于 紫外可见光谱的 RDA 分析结果显示, RDA1 和 RDA2 共同解释了总体变化的 79.24%, E2/E3、 E3/E4 和  $S_R$  主要影响其分布[图 8(a)]; 基于随机 森林筛选出的指示物种群落的 RDA 结果显示[图 8 (d)], RDA1 和 RDA2 共同解释了总体变化的 80.74%, E2/E3、E3/E4 和 S<sub>R</sub> 主要影响其分布,河 口区与 E2/E3、E3/E4 和  $S_R$  呈现反向变化,表明分 子量大的腐殖化较强的有机物与入淀河口好氧反硝 化菌群落分布关系密切. 基于平行因子解析的结果 进行 RDA 分析,对于整体好氧反硝化菌群落来说 [图8(b)], RDA1 和 RDA2 共同解释了总体变化的 75.6%,组分 C3 是其主要影响因子,与 RDA1 的相 关性系数达到 0.64; 对于随机森林筛选出的指示物 种群落而言[图 8(e)], RDA1 和 RDA2 共同解释了 总体变化的65.89%,组分C1、C2和C4是其主要影

响因子,与 RDA1 的相关性系数达到 - 0.81、 -0.81和 -0.64.基于荧光区域积分解析的结果进行 RDA分析,对于整体好氧反硝化菌群落来说[图8(c)], RDA1 和 RDA2 共同解释了总体变化的75.76%,组分 P3 和 P4 是其主要影响因子,与 RDA1的相关性系数达到 -0.51和 0.63;对于随机森林筛选出的指示物种群落而言[图8(f)], RDA1和 RDA2共同解释了总体变化的79.63%,组分 P2、P3和 P4 是其主要影响因子,与 RDA1的相关性系数达到0.58、-0.82和0.74.综合平行因子分析和荧光区域积分分析的结果,类腐殖质物质主要影响整体好氧反硝化菌群落分布,而类蛋白物质主要影响指示物种群落的分布.

#### 2.4 微生物网络分析

OTU 分类水平的微生物网络如图 9 所示,其中节点大小与网络节点度成正比,节点间连线的宽度与相关系数 | r | 成正比; 节点间的连线颜色表示节



(a) ~ (c) 基于整体好氧反硝化菌群落和紫外可见光谱/平行因子分析/荧光区域积分的 RDA, (d) ~ (f) 基于指示物种群落和紫外可见光谱/平行因子分析/荧光区域积分的 RDA

图 8 白洋淀好氧反硝化菌与环境因子的冗余分析

Fig. 8 RDA of aerobic denitrification bacteria and environmental factors in Baiyangdian Lake

点间的相关关系,红色表示正相关,绿色表示负相关.微生物网络分析共得到252个节点1323个相关关系,有1293个正向相关关系,30个负向相关关系(图9).本研究得到的经验网络平均度为20.69,网络直径为6.03,平均路径长度为2.98,模块性为0.36;随机网络的相关参数:网络平均度为11.47±0.07、网络直径为4.2±0.42、平均路径长度为2.6±0.01、模块性为0.27±0.01.与同等节点数据以及相关关系数据的随机网络相比,本研究的经验网络具有明显的模块结构.本研究的微生物网络共得

到 35 个模块,本文将其划分成 9 个模块,其中模块 9 为占比较小模块的汇总,具体比例情况见图 9 (a). 有关节点的物种分类如图 9 (b) 所示,该网络分为 5 个模块,其中 Unclassified\_bacteria 比例达到 63. 10%、 $\beta$ -Proteobacteria 比例达到 23. 91%、 $\gamma$ -Proteobacteria 比例达到 6. 35%、 $\alpha$ -Proteobacteria 比例达到 5. 95%、 $\varepsilon$ -Proteobacteria 比例达到 0. 79%. 结合模块分析,模块 1 和模块 3 中主要为未分类菌,模块 2 主要为 $\beta$ -Proteobacteria.

基于网络中节点的分类标准[43],本文共得到

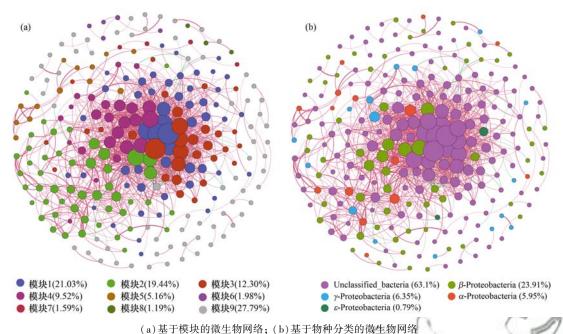
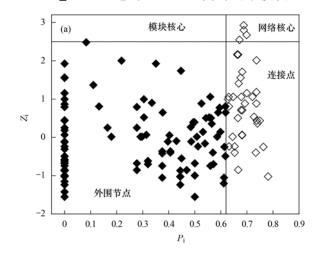


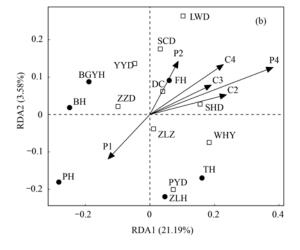
图 9 白洋淀好氧反硝化菌微生物网络

Fig. 9 Network of aerobic denitrification bacteria in Baiyangdian Lake

35 个关键节点,具体包括 4 个网络核心节点  $(Z_i \ge 2.5, P_i > 0.62)$  和 31 个连接点  $(Z_i < 2.5, P_i > 0.62)$  [图 10 (a)]. 其中 4 个网络核心节点为OTU6、OTU11、OTU17 和 OTU18,都属于Unclassified\_bacteria. 31 个连接点OTU 主要隶属于Thauera、Cupriavidus 以及 Unclassified\_bacteria,其中13 个 OTU 位于前 50 丰度的菌属. 与此同时,35 个关键节点的度都大于5,中介中心值都小于1 000,也同时满足关键物种的判别标准[24]. 本网络中的 35 个关键节点,隶属于 α-Proteobacteria 的节点达到2.7%、β-Proteobacteria 的节点达到21.62% 和Unclassified bacteria 达到75.68%. 同时属于模块5

的节点占比为 29.73%,属于模块 6 的节点占比为 13.51%,属于模块 9 的节点占比为 56.76%.与此同时,基于微生物网络的关键节点和溶解性有机物组成进行了 RDA 分析[图 10(b)],结果显示 RDA1 和 RDA2 分别解释了关键节点菌群分布总体变化的 21.19% 和 3.58%,其中 RDA1 对菌群的分布起主要作用.基于膨胀因子分析(VIF)得到组分 C2(VIF = 12.82)、C3(VIF = 3.59)、C4(VIF = 11.43)、P1(VIF = 6.72)、P2(VIF = 6.55)和 P4(VIF = 4.28)是影响关键菌群分布的重要环境因子,同时与RDA1 的相关性系数达到 0.86、0.77、0.70、-0.60、0.48 和 0.81. RDA 结果显示影响关键节点





(a) 微生物网络节点 Z-P; (b) 关键节点群落与环境因子的 RDA 分析

图 10 白洋淀好氧反硝化菌生态网络节点分布以及关键物种与环境因子的冗余分析

Fig. 10 Distribution of nodes in the molecular ecological network and RDA of key aerobic denitrification bacteria and environmental factors in Baiyangdian Lake

菌群分布的主要是类蛋白物质,与前文关于随机森林分析筛选的指示物种的影响因素相一致.因此,为了得到适应于实际水体环境的好氧反硝化菌,在将来的耐低温高效好氧反硝化菌株驯化过程中需要加入类蛋白物质的碳源进行富集驯化.

#### 3 结论

- (1)冬季输水期水体溶解性有机物的相对浓度 在白洋淀河口区和内部区间呈现显著差异,水体溶 解性有机物呈现出较强自生源、低腐殖化特征,河 口区相对于内部区呈现出高分子量和强腐殖化 特征.
- (2)基于平行因子法解析出3种类蛋白组分和1种类腐殖质组分,其中类蛋白类物质占主体,达到35.64%~96.38%;荧光区域积分组分显示类蛋白类物质(P1、P2和P4)也占主体,达到68.22%~94.85%;两种解析方法得到的类蛋白物质分布都是内部区要高于河口区,并且两种方法划分的组分呈现出显著相关,得到的物质组成结果相一致.
- (3)水体好氧反硝化菌主要为未分类菌和变形菌,主要包括 Cupriavidus、Thauera、Shewanella、Pseudomonas 以及 Aeromonas; 类腐殖质物质主要影响白洋淀整体好氧反硝化菌群分布,而类蛋白物质主要影响好氧反硝化菌指示物种群落和关键节点群落的分布.

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