南京农业大学学报 2026,49(4):742-751
Journal of Nanjing Agricultural University
http://nauxb.njau.edu.cn
DOI:10.7685/jnau.202502019

李智,孙卜文,吴卓晗,等.凡纳滨对虾养殖系统中生物絮团的形成机制及外源微生物调控作用研究进展[J]. 南京农业大学学报,2026,49(4):742-751.

Li Z,Sun B W,Wu Z H,et al. Research progress in forming mechanism of biofloc in Pacific white shrimp(*Litopenaeus vannamei*)culture systems and regulatory effects of exogenous microorganisms[J]. Journal of Nanjing Agricultural University,2026,49(4):742-751.

凡纳滨对虾养殖系统中生物絮团的形成机制及外源微生物调控作用研究进展

李智[1],孙卜文[1],吴卓晗[1],刘海燕[1],肖娜思[2],李清扬[1*]

(1.河北师范大学生命科学学院,河北 石家庄 050024;2.中海万弘(唐山)水产科技有限公司,河北 唐山 063306)

摘要:凡纳滨对虾(*Litopenaeus vannamei*)是我国水产养殖业的支柱物种,随着市场需求持续增长和养殖技术不断进步,其养殖模式正向超高密度方向发展。生物絮团(biofloc)技术在提升水产养殖效益、改善水质、防控病害等方面发挥着关键作用,已成为凡纳滨对虾超高密度养殖体系中不可或缺的核心技术。然而,关于生物絮团通过哪些特定微生物类群改善生长性能和水体质量,以及通过何种途径调控水生动物的免疫功能这两个关键机制问题仍存在不小的争议。并且外界影响因素复杂多样,难以稳定培养出良性的生物絮团系统,严重制约其推广应用。近年的研究证实,微生物群落是调控生物絮团系统的根本要素,与调节碳氮比和添加碳源等经典的调控策略相比,添加益生菌和微藻能够更稳定、有效地改善生物絮团系统,该方向研究已成为生物絮团领域的热点方向。本文综合分析了有关生物絮团作用机制的多种观点,梳理和评估了影响其稳定性的关键因素;在此基础上,重点探讨了外源微生物的种类和添加量对凡纳滨对虾生长性能、免疫状态、养殖水质以及生物絮团群落结构的综合影响,并对未来研究方向进行了展望,以期为提高生物絮团养殖系统的稳定输出、实现凡纳滨对虾的绿色、健康养殖提供科学依据。

关键词:凡纳滨对虾;生物絮团;高密度养殖;外源微生物

中图分类号:S852.6 **文献标志码**:A **文章编号**:1000-2030(2026)04-0742-10

Research progress in forming mechanism of biofloc in Pacific white shrimp (*Litopenaeus vannamei*) culture systems and regulatory effects of exogenous microorganisms

LI Zhi[1],SUN Buwen[1],WU Zhuohan[1],LIU Haiyan[1],XIAO Nasi[2],LI Qingyang[1*]

(1.College of Life Sciences,Hebei Normal University,Shijiazhuang 050024,China;
2.AquaOne Tangshan Aqua-tech Co.,Ltd.,Tangshan 063306,China)

Abstract:Pacific white shrimp(*Litopenaeus vannamei*),as a pillar species of China's aquaculture industry,has seen its farming model evolve towards super-intensive density due to the continuous growth in market demand and advancements in aquacultural technology. Biofloc technology plays a critical role in enhancing farming efficiency,improving water quality,and preventing diseases,making it an indispensably corable technology in the super-intensive farming systems of *L. vannamei*. There is still controversy about which specific microbial groups in bioflocs contribute to improving growth performance and water quality,as well as the mechanisms through which they regulate the immune functions of aquatic animals. Additionally,the complexity and diversity of external influencing factors also make it difficult to stably cultivate beneficial biofloc systems,hindering their broader applications. Recent studies have demonstrated microorganisms are the fundamental element in regulating biofloc systems. Compared to traditional strategies such as adjusting the carbon-to-nitrogen ratio and carbon sources,the exogenous addition of probIotics and microalgae has proven to be a more stable and effective approach for optimizing biofloc systems,thereby becoming a hotspot in biofloc research. This review comprehensively analyzes various perspectives on the mechanisms of biofloc,systematically identifies and evaluates the key factors affecting its stability,and focuses on the impact of different types and dosages of exogenous microorganisms on the growth performance,immune status,water quality,and biofloc community structure in *L. vannamei* farming. Additionally,future research

收稿日期:2025-02-15

基金项目:国家重点研发计划项目(2022YFD1600401);河北省农业科技成果转化项目(南美白对虾工厂化养殖用水预处理技术示范与应用);河北省自然科学青年基金项目(C2022205042)

作者简介:李智,博士,副教授,主要从事水生动物生理生态研究,E-mail:lizhi93@hebtu.edu.cn。* 通信作者:李清扬,博士,副教授,主要从事微生物学研究,E-mail:qingyangli@hebtu.edu.cn。

directions are proposed. This study aims to provide a scientific basis for stabilizing the output of biofloc farming systems and achieving sustainable and healthy farming of *L. vannamei*.

Keywords: *Litopenaeus vannamei*; biofloc; super-intensive culture; exogenous microorganism

凡纳滨对虾(*Litopenaeus vannamei*)又称南美白对虾,是全球最大的水产养殖物种,年产量超 680 万吨[1-2]。我国凡纳滨对虾的全球产量最大,相关养殖业及上下游配套产业在我国水产行业具有重要地位[3]。随着市场需求的不断增加以及捕捞资源的枯竭,超高密度养殖(super-intensive)已成为凡纳滨对虾的主流养殖模式[1]。在该模式下,每平方米养殖量大于 150 只,年产出量至少为 3 批次,在室内条件下每立方米水体年产量可达 4.5 kg 以上[4]。得益于养殖技术的持续进步,实际生产中的养殖密度通常远高于推荐水平[5-6]。随着优良品种的推广和精准饲喂的实施,养殖的密度有望进一步提高[7-9]。

凡纳滨对虾超高密度养殖模式虽然能够有效提高生产效益,但容易引起水质恶化,导致流行性疫病暴发,在短期内造成重大经济损失。此外,超高密度养殖用水量大、对饲料成本高度敏感,因此迫切需要一种能够净化水质、抑制病原菌滋生、提高饲料利用率、成本低廉且稳定可靠的养殖技术[7,10]。生物絮团(biofloc)是一种由细菌、真菌、藻类和原生动物等微生物以及悬浮固体和有机物质等在糖胺聚糖胞外聚合物的作用下形成的絮状体[11]。在理想状况下,生物絮团的摄入量占到对虾总摄入量的 3 成左右,可提高饲料转化率、降低养殖成本[12],还具有改善水质[13]、防控病害[14]、增强免疫[15]的作用。这些特点与凡纳滨对虾超高密度养殖模式的需求高度契合,并已广泛应用于实际生产[11-12]。然而,目前的生物絮团养殖系统较为脆弱,甚至会引起水体中以弧菌为代表的病原菌快速增殖[10,16-19]。因此,如何提高生物絮团系统的稳定性并提升作用效果,已成为当前亟待解决的关键问题[20]。

因此,亟须从机制出发对相关影响因素进行系统梳理和深入分析,以为未来的研究提供明确的方向和依据[21]。最新研究发现,添加外源微生物是提高生物絮团稳定性的重要因素,也为突破生物絮团技术的应用瓶颈提供了新思路[22-23]。本文将归纳和分析生物絮团的形成与作用机制,分析影响凡纳滨对虾生物絮团养殖系统的主要因素,系统比较和探讨添加外源微生物的实际效果,为凡纳滨对虾的超高密度养殖和生物絮团技术开发提供一定理论支持。

1　生物絮团的形成原理与作用机制

微生物是决定生物絮团各类功能的根本性因素,在水体和肠道中均发挥着十分复杂且多样的作用[24]。生物絮团的形成是一个复杂且快速的动态过程,主要包括初始吸附、絮团发育和形成稳定的絮团结构三阶段[23,25]。在初始微团形成阶段,水体中的微生物通过表面特异性受体识别并吸附可溶性小分子有机物,这些小分子有机物反过来刺激微生物合成并分泌以多糖为主的胞外聚合物(extracellular polymeric substances, EPS)[26]。EPS 不仅增大了微生物群落的比表面积,还通过自身网络结构以及静电和氢键等作用,促进微生物细胞间的黏附和聚集、固定水体中的大分子有机物(如蛋白质、多糖等)和悬浮固体(如饲料残渣、粪便颗粒等),形成了生物絮团微聚体。

在发育阶段,絮团吸附的有机物开始被异养细菌降解[27],其中大分子有机物在胞外酶的作用下被水解为小分子物质,同时伴随着氨化和硝化过程,产生铵盐、亚硝酸盐和硝酸盐等含氮无机物[28]。这些含氮化合物一部分经反硝化作用转化为氮气逸出,另一部分则被自养微生物(如硝化细菌、光合细菌等)转化为生物量。随着微生物群落的代谢活动持续进行,絮团的粒径不断增大,蛋白质、脂类等营养物质和维生素等有机活性物质含量也逐渐上升[10,29-31]。最终,细菌、真菌、微藻和原生动物的比例趋于固定,形成了稳定且具有良好耐受性的生物絮团系统[32]。

随着对生物絮团形成机制的深入了解,仍存在 2 个亟待明确的关键问题。首先,生物絮团主要通过哪些特定微生物类群改善生长性能和水体质量,这直接决定着如何高效快速地培养生物絮团养殖系统,以适应养殖环境和对象。鉴于生物絮团主要通过推动含氮类营养物质的循环利用来提高饲料转化效率、改善养殖水质已成为基本共识,主流观点认为兼具硝化和反硝化功能的异养硝化细菌在生物絮团养殖系统中起到首要作用[33-34]。鉴于已有研究发现光照对其作用效果的影响,推测自养型光合细菌如红杆菌科以及微藻在光照条件下可能与异养硝化细菌协同,从而进一步提高硝化和反硝化的效率[35-37]。凡纳滨对虾养殖试验已证实,添加异养硝化细菌能够改善对虾的生长性能和水体环境,且水体中硝化细菌的含量亦有所提高[38]。

其次,生物絮团通过何种途径调控水生动物的免疫功能。已有大量研究揭示生物絮团的免疫增强作用及其相关信号通路[12,24],但生物絮团通过何种机制实现这一功能尚缺乏系统性的研究。一方面,生物絮团可能作为益生菌的供体,通过调控肠道微生物群落,借助肠道微生物与宿主的互作效应提高免疫性能[19,39]。有研究表明,定殖在肠道中的红细菌可以通过 Toll 样受体通路提高宿主的免疫水平[40-41]。另一方面,关于生物絮团是否可以作为益生菌的直接供体尚有较大争议,这一观点认为生物絮团难以对肠道微生物群落产生影响,水生动物的肠道微生物群落主要受饲料日粮的影响[42]。因此,生物絮团也可能通过自身合成的多糖和羟基丁酸等物质改善宿主免疫水平,或通过这些代谢产物间接调控肠道菌群干预免疫水平。

2 影响生物絮团功能的主要因素

影响生物絮团功能的因素可以分为营养调控、水质调控、养殖管理调控、微生物调控及其他调控共 5 大类,分别是碳氮比、碳源种类、饲喂策略、盐度、温度、pH 值、碱度、光照、曝气强度、养殖密度、培养时间、外源添加微生物的种类、微生物添加方式、微生物配伍和絮体粒径等,在凡纳滨对虾养殖中也主要通过干预这些因素以培养生物絮团(表 1)。研究者在过去近 20 年中开展了深入且富有成效的研究,但由于影响因素众多且受限于养殖试验的规模和条件,即使同一主题下的不同研究得到的结果也难以避免地存在较大差异,严重阻碍了生物絮团技术的发展和推广。此外,在凡纳滨对虾高密度、工厂化养殖的大背景下,影响因素可根据调控难易度分为“刚性因子”与“柔性因子”两大类别。其中,曝气量、pH 值、养殖密度等“刚性因子”受限于基础设施和养殖规范,调整空间有限;而碳氮比、碳源种类及外源微生物添加等“柔性因子”则因其可调控性强、成本效益比显著,已成为当前研究与生产实践的焦点。

碳氮比作为便于在生产中调控的指标长期以来均是研究的热点[43-44]。传统观点认为,将养殖系统的碳氮比提高到 15∶1,可以增加异养菌的比例,提高水体有机物处理和转化效率,从而改善水质、促进凡纳滨对虾的健康生长。因此,诸多生物絮团研究均通过添加糖蜜、红糖等碳源将养殖系统碳氮比调整到 15∶1[45-47]。Xu 等[39]在养殖试验中,通过添加糖蜜将碳氮比分别设置为 9∶1、12∶1、15∶1 和 18∶1,比较了凡纳滨对虾的生长状况和存活率,结果表明,尽管不同处理组的水体和肠道微生物群落的多样性存在差异,且部分微生物的丰度还随时间发生变化,但各组在生长速率、饵料系数和存活率等关键指标上没有显著差异。Li 等[23]对碳氮比、养殖时间和外源益生菌等因素进行了 meta 回归分析,发现调控碳氮比不会影响凡纳滨对虾的生长速度、饲料利用效率和健康状况,仅外源添加益生菌能够起到改善作用。因此,尽管调控碳氮比可以干预微生物的多样性和组成,但对生产性能和存活率等直接影响养殖收益的关键指标未表现出明显作用。在实际生产中,是否继续添加额外碳源需进一步研究以明确其效益。

适合添加的碳源种类是凡纳滨对虾生物絮团研究的另一个热点。即使将碳氮比固定为 15∶1,不同研究之间仍存在较大争议。有研究发现,添加麸皮或甘蔗渣等富含纤维素的碳源会降低生物絮团系统的产出,因此提出在养殖系统中添加富含纤维素等难以降解的碳源会减少异养细菌可获取的能量,从而抑制其生长和有机物的合成,最终降低对虾的生产性能[48-49]。然而,也有研究指出,与经典的碳源糖蜜相比,添加麸皮、小米粉等富含纤维素的碳源不会影响生物絮团系统的产出[50-51]。

表 1 影响凡纳滨对虾生物絮团养殖体系的因素

Table 1 Influential factors of the biofloc system of *Litopenaeus vannamei*

类别 Category	影响因素 Influencing factor	参考文献 References	类别 Category	影响因素 Influencing factor	参考文献 References
营养调控 Nutrient regulation	碳氮比 C/N ratio	[10,25,39,47,52-54]	养殖管理调控 Management control	对虾密度 Stocking density	[58,73-75]
	碳源种类 Type of carbon source	[48,50-51,55-57]		培养时间 Culture duration	[76-77]
	饲喂策略 Feeding strategy	[58-59]	微生物调控 Microbial regulation	外源添加微生物 Exogenous microbes	[38,78-85]
水质调控 Water quality control	盐度 Salinity	[10,60-62]	其他调控 Other factors	微生物配伍 Microbial compatibility	[14,79,83]
	温度 Temperature	[63-64]		微生物添加方式 Microbial application method	[82]
	光照 Light	[65-66]		絮体粒径 Floc particle size	[21,81]
	曝气强度 Aeration intensity	[67-69]			
	pH 值(碱度) pH value(alkalinity)	[70-72]			

这些案例证明,影响生物絮团功能的因素相互间可能存在复杂的作用关系,即使在同一主题下的研究也难以完全控制所有变量,导致研究成果难以提供具有实践指导价值的信息。考虑到养殖试验规模的局限,未来研究应注重发掘和调控影响生物絮团功能的关键因素进行全面、系统地分析论证,以实现对生物絮团养殖系统的有效干预。

基于这一现实困境,近年来的研究逐渐将重点放在添加外源微生物上。这种方法能够直接地干预絮团微生物群落,优化生物絮团系统的性能和效益[86-87]。添加外源微生物不仅可以快速建立和维持高效的微生物群落,还能针对特定的水质问题进行定向调控,从而提升养殖环境的稳定性和对虾的健康水平。相关研究也进一步发现添加不同微生物的效果存在明显的差异[23,38]。因此,有必要开展更加全面、系统的探究,筛选出最佳的微生物及其组合,以满足对虾高密度养殖的实际需求。

3　外源微生物在凡纳滨对虾生物絮团体系中的应用

在凡纳滨对虾生物絮团养殖体系中,添加外源微生物是优化系统性能的重要手段[38]。已报道的外源微生物主要为细菌和微藻两类[38,80],前者包括芽胞杆菌(*Bacillus*)、光合细菌和异养硝化细菌,后者包括硅藻、绿藻、黄藻和裂壶藻等。也有研究通过添加菌-菌、菌-藻混合微生物以实现协同效应[14]。这些微生物培养的凡纳滨对虾生物絮团养殖系统在水质、生长性能、免疫水平和存活率等方面存在明显差异。总的来看,当添加外源细菌时,添加的频率要高于微藻,且添加的剂量和方式与换水量密切相关[81-82]。当换水量较少时,可以在养殖初期阶段加入较大剂量的细菌或微藻培养液,以便快速形成稳定的生物絮团体系(表 2)。

表 2　凡纳滨对虾生物絮团养殖体系中外源微生物添加情况

Table 2　Addition of exogenous microorganisms on the biofloc system of *L. vannamei*

外源微生物类别 Exogenous microorganism	添加剂量 Dosage	添加频率及换水量 Addition frequency and water exchange	参考文献 References
高地芽胞杆菌、矮小芽胞杆菌、蜡样芽胞杆菌* *Bacillus altitudinis*, *B. pumilus*, and *B. cereus*	10^6 CFU·mL^{-1}	仅开始时添加,不换水 Initially only, no water exchange	[81]
枯草芽胞杆菌 *B. subtilis*	10^6 CFU·mL^{-1}	每 3 d 1 次 Once every 3 days	[82]
龙舌兰芽胞杆菌 *B. tequilensis*	10^6 CFU·mL^{-1}	连续添加 6 d 后每 2 d 1 次,3 d 换水 1 次 Every 2 days after 6 days, once exchange per 3 days	[78]
芽胞杆菌混合菌剂 *Bacillus*	10^3 CFU·mL^{-1}	每 7 d 添加 1 次,每天换水 40% Once per 7 days, 40% daily exchange	[80]
枯草芽胞杆菌、红螺菌、雷特氏普罗威登斯菌* *B. subtilis*, *Rhodospirillum rubrum*, and *Providencia rettgeri*	10^3 CFU·mL^{-1}	每 2 d 1 次,每天换水 5% Once per 2 days, 5% daily exchange	[38]
斜生栅藻 *Scenedesmus obliquus*	5 mg·L^{-1}	每 3.5 d 1 次,循环水养殖 Once every 3.5 days, recirculating system	[88]
赫氏扁藻,普通小球藻,穆勒角毛藻* *Platymonas helgolandica*, *Chlorella vulgaris*, and *Chaetoceros mulleri*	Chl-a, 0.02 mg·L^{-1}	仅开始时添加,不换水 Initially only, no water exchange	[14]
眼点小球藻、伪微小海链藻* *Nannochloropsis oculata*, and *Thalassiosira pseudonana*	10^2 cells·mL^{-1}	仅开始时添加,不换水 Initially only, no water exchange	[56]
芽胞杆菌菌剂 BCM、BME* *Bacillus* BCE, BME 钙化角毛藻 *Chaetoceros calcitrans* 硝化细菌 *Nitrifying bacteria*	5 g·L^{-1} 3×10^{-5} 12 g·L^{-1}	异位培养,仅开始时添加,不换水 Off-site culture, initially only, no water exchange	[79]
裂壶藻 *Schizochytrium* 植物乳杆菌混合 *Lactobacillus plantarum*	10^2 cells·mL^{-1}, 10^5 CFU·mL^{-1}	仅开始时添加,不换水 Initially only, no water exchange	[14]

注:* 各菌添加剂量相同 The dosage of each bacterial additive is the same.

3.1　细菌在生物絮团体系中的应用

添加外源细菌的研究主要集中于经典的水产益生菌芽胞杆菌。其中,*B. altitudinis*、*B. pumilus*、*B. cereus*、*B. subtilis*、*B. licheniformes*、*B. tequilensis* AP BFT3、*Bacillus* BCE 和 BME 菌株等在凡纳滨对虾生物絮团体系中均有应用,部分已作为商业菌剂推向市场。Wu 等[80]研究发现,*B. altitudinis*、*B. pumilus* 和 *B. cereus* 均能够加快絮团形成,改善絮团的尺寸分布,提高氨氮去除率和对虾的生长性能,不同菌株构建的絮团系统在产出上存在差异。He 等[81]添加 *B. subtilis* 培养生物絮团后对虾的生长性能并未出现差异,但培养液与饲料混合后添加的效果优于直接泼洒。Panigrahi 等[85]研究表明,*B. tequilensis* 能够提高对虾

的生长性能、免疫力和存活率,同时增加絮团中异养细菌和具有外泌消化酶功能的细菌含量。*Hostins* 等[82]和 Waiho 等[79]也证实了芽胞杆菌商用菌剂对凡纳滨对虾养殖系统的改善作用。总体来看,添加芽胞杆菌能够促进以异养细菌为主导的生物絮团的形成,这些絮团能够抑制弧菌繁殖,提高对虾的存活率和生长性能,同时降低总氨氮含量,但在作用效果上存在种间差异。

生物絮团中硝化细菌的含量直接影响氨氮和亚硝酸盐浓度,已逐渐成为凡纳滨对虾生物絮团研究的热点[86,89]。根据能量来源,硝化细菌可分为自养型和异养型。通过调控光照等因素,分别定向培育以自养和异养硝化细菌为主的生物絮团,均可以改善对虾的生长性能并提高存活率[65]。与自养型硝化细菌相比,异养型能够同时催化硝化和反硝化反应,催化效率大幅提高,环境适应性也更好,因此是生物絮团体系中去除氨氮和亚硝态氮的主要细菌[33-34,79]。然而目前关于异养硝化细菌在凡纳滨对虾生物絮团领域的研究较少。Li 等[38]系统比较了添加枯草芽胞杆菌、异养硝化细菌和光合细菌培养生物絮团对凡纳滨对虾生长、免疫和水质的影响,证明前两者均通过提供蛋白改善生长性能,同时具有水质净化的功效。异养硝化细菌还能激活前酚氧化酶通路和提高热休克蛋白 70 的表达水平,增强对虾的免疫力和抗应激能力。此外,肠道和絮团菌群分析结果显示,枯草芽胞杆菌和异养硝化细菌可能通过提高红杆菌科的含量,间接改善对虾的肠道健康,抑制弧菌的滋生。这些发现进一步证实了多种细菌在生物絮团体系中的协同作用。

3.2 微藻在生物絮团体系中的应用

微藻具有良好的环境适应能力,常在不换水生物絮团体系中作为外源微生物添加。微藻能够提供丰富的蛋白质和二十碳五烯酸(eicosapentaenoic acid,EPA)、二十二碳六烯酸(docosahexaenoic acid,DHA)等凡纳滨对虾必需的不饱和脂肪酸,还能与细菌协同作用,形成稳定的微藻-细菌生物絮团体系,从而有效降低水体中的氨氮和亚硝态氮含量[90-91]。根据能量来源,微藻也分为自养型和异养型。自养型微藻通过光合作用获取能量,利用二氧化碳和光能进行生长;而异养型微藻则依赖有机物质作为能量来源。微藻生产成本低廉,且本身就是对虾的日常食物,其繁殖形成的生物絮团系统尤其适合虾类的生长和繁殖,因此,藻类在凡纳滨对虾生物絮团系统中的应用前景更加广阔[92-94]。

目前,硅藻、绿藻和黄藻等多种微藻已被应用于凡纳滨对虾生物絮团研究。Silva 等[88]在生物絮团体系中添加了斜生栅藻(*S. obliquus*),提高虾的存活率,但虾生长性能和水体质量没有变化。Ge 等[83]则比较了赫氏扁藻(*P. helgolandica*)、普通小球藻(*C. vulgaris*)和穆勒角毛藻(*C. mulleri*)在不换水系统中的作用,发现这些微藻均能有效净化水质,抑制弧菌滋生,并改善对虾的生长性能。Huang 等[84]的研究进一步证实,眼点小球藻(*N. oculata*)和伪微小海链藻(*T. pseudonana*)能够改善水质,并提升对虾的生长性能。此外,微藻的添加剂量和添加频率均低于益生菌,能够有效减少工作量并简化养殖流程。

3.3 细菌、微藻在生物絮团体系中的联合应用

关于同时添加细菌和微藻培养生物絮团的研究尚处于起步阶段,对其作用效果和机制的研究较少。不同细菌和微藻的联合应用对凡纳滨对虾养殖系统的影响迥异[78]。Situmorang 等[78]研究发现,微藻和有益菌同时添加效果更加明显,说明“藻-菌”体系在凡纳滨对虾生物絮团养殖中具有重要作用。微藻在生物絮团体系中的应用不仅有助于改善水质和提高水产动物的生长性能,还能通过与细菌的协同作用,形成稳定、高效的生物絮团养殖系统。Pacheco-Vega 等[14]同时添加裂壶藻和植物乳杆菌,结果显示除了弧菌数量降低外,凡纳滨对虾的生长性能和存活率均无变化。这些结果揭示了利用细菌和微藻联合培养生物絮团的潜在优势,但也表明不同细菌和微藻的组合效果差异较大,可能存在协同或拮抗效应,影响“菌-藻”生物絮团体系的产出效果。鉴于不同类型微藻的代谢产物和合成效率差异较大,可以从菌、藻优势互补的角度进行合理组合。例如,选用具有高效油脂合成能力的微藻与具备优异蛋白质合成能力的细菌共同培养生物絮团,以实现生物絮团养殖体系的精准化建设。

4 结论与展望

在凡纳滨对虾生物絮团养殖体系中,添加细菌和微藻等均能够改善对虾的生长性能、存活率以及水体质量,还能够提高对虾的免疫水平。微生物是生物絮团发挥功能的核心要素,相较于其他因素,添加微生物能够更加直接地干预生物絮团的群落组成,调控形成速度,实现生物絮团体系的稳定和高效输出[95-96]。这种方法不仅能够保障工厂化超高密度养殖的顺利进行,还可以为絮团结构更加不稳定的露天养殖应用提供技术支持。为进一步优化和推广凡纳滨对虾生物絮团体系中外源微生物调控技术,后续对以下 3 个

方面开展深入研究。

第一,全面、系统探究微生物在凡纳滨对虾生物絮团养殖体系中的作用。外源微生物在凡纳滨对虾生物絮团养殖中的研究仍处于起步阶段,相关研究主要集中于芽胞杆菌等菌株,对于在生物絮团体系中发挥重要作用的微生物如光合细菌[65,97]和硝化细菌[33-34]的研究数量极少且缺乏系统性。此外,目前应用的微生物主要为野生型,缺少在生物絮团中添加经定向改造的工程菌[98]和工程藻[99-100]的相关报道。因此,未来有必要通过生长性能、免疫水平、存活率和水体质量这些关键指标,系统研究工程菌、工程藻等微生物对凡纳滨对虾生物絮团养殖系统的影响,并在此基础上,结合换水量探究合适的添加频率和剂量,进一步探讨碳氮比和碳源种类等因素。

第二,探讨“菌-菌”和“菌-藻”之间的协同效应,优化微生物组合。不仅细菌之间存在复杂的相互作用,微藻和细菌之间也有一定的营养互补关系。微藻可以在光合作用下,将细菌分解产生的无机物重新合成能够被对虾吸收的有机物,提高养殖系统的生产力[94]。某些细菌还可以分泌促进微藻生长的大分子有机物[101-102]。两者还可能通过分泌抑制物质来影响彼此的生长,进而改变微生物群落,促进自身的增殖[103-104]。因此,有必要在了解单株微生物添加效果的基础上进行组合运用,找寻“菌-藻”体系的最佳配比。

第三,深度解析生物絮团在改善系统提高水产养殖产出方面的作用机制。将生物絮团技术广泛应用于水产养殖,不仅需要了解其表观作用,还需深度解析其增强免疫的作用机制,特别是明确生物絮团对肠道菌群的影响。未来的研究应结合多种先进技术方法,从微生物群落结构、代谢功能、营养物质循环和免疫调节等方面,全面系统地探讨生物絮团的作用机制,从而推动生物絮团技术的进一步优化和应用。

参考文献 References:

[1] FAO. The State of World Fisheries and Aquaculture 2024[M]. FAO,2024.

[2] 农业农村部渔业渔政管理局,全国水产技术推广总站,中国水产学会. 中国渔业统计年鉴 2024[M]. 北京:中国农业出版社,2024.
Fishery and Fishery Administration Bureau of the Ministry of Agriculture and Rural Affairs,National Aquaculture Technology Promotion Station,Chinese Fisheries Society. China Fisheries Statistical Yearbook 2024[M]. Beijing:China Agriculture Press,2024(in Chinese).

[3] Villarreal H,Juarez L. Super-intensive shrimp culture:analysis and future challenges[J]. Journal of the World Aquaculture Society,2022,53(5):928-932.

[4] da Silveira L G P,Krummenauer D,Poersch L H,et al. Hyperintensive stocking densities for *Litopenaeus vannamei* grow-out in biofloc technology culture system[J]. Journal of the World Aquaculture Society,2020,51(6):1290-1300.

[5] de Almeida M S,Gimenes R M T,Furtado P S,et al. Economic analysis of intensive and super-intensive *Litopenaeus vannamei* shrimp production in a biofloc technology system[J]. Boletim do Instituto de Pesca,2022,48:e692.

[6] Emerenciano M G C,Rombenso A N,Vieira F D N,et al. Intensification of penaeid shrimp culture:an applied review of advances in production systems,nutrition and breeding[J]. Animals,2022,12(3):236.

[7] Fões G,Krummenauer D,Lara G,et al. Long term storage and the compensatory growth of white shrimp *Litopenaeus vannamei* in aquaculture ponds[J]. Latin American Journal of Aquatic Research,2017,44(3):588-594.

[8] Samocha T M,Prangnell D I,Hanson T R,et al. Design and operation of high-density,biofloc-dominated production systems of Pacific white shrimp,*Penaeus vannamei*[M]//Vannamei Shrimp Farming. Boca Raton:CRC Press,2020:14-36.

[9] Ciji A,Akhtar M S. Stress management in aquaculture:a review of dietary interventions[J]. Reviews in Aquaculture,2021,13(4):2190-2247.

[10] Khanjani M H,Alizadeh M,Sharifinia M. Rearing of the Pacific white shrimp,*Litopenaeus vannamei* in a biofloc system:the effects of different food sources and salinity levels[J]. Aquaculture Nutrition,2020,26(2):328-337.

[11] Yu Y B,Lee J H,Choi J H,et al. The application and future of biofloc technology(BFT) in aquaculture industry:a review[J]. Journal of Environmental Management,2023,342:118237.

[12] Ramasubburayan R,Prakash S,Immanuel G,et al. The transformative role of prebiotics,probiotics,and microbiomes in biofloc systems for sustainable aquaculture:a comprehensive review[J]. Reviews in Aquaculture,2025,17(1):e13000.

[13] Sun Y,Hou H C,Dong D P,et al. Comparative life cycle assessment of whiteleg shrimp(*Penaeus vannamei*) cultured in recirculating aquaculture systems(RAS),biofloc technology(BFT) and higher-place ponds(HPP) farming systems in China[J]. Aquaculture,2023,574:739625.

[14] Pacheco-Vega J M,Cadena-Roa M A,Leyva-Flores J A,et al. Effect of isolated bacteria and microalgae on the biofloc characteristics in the Pacific white shrimp culture[J]. Aquaculture Reports,2018,11:24-30.

[15] Ghosh A K,Hasanuzzaman A F M,Sarower M G,et al. Unveiling the biofloc culture potential:harnessing immune functions for resilience of shrimp and resistance against AHPND:causing *Vibrio parahaemolyticus* infection[J]. Fish & Shellfish Immunology,2024,151:109710.

[16] Rego M A S,Sabbag O J,Soares R,et al. Risk analysis of the insertion of biofloc technology in a marine shrimp *Litopenaeus vannamei* production in a farm in Pernambuco,Brazil:a case study[J]. Aquaculture,2017,469:67-71.

[17] Gutiérrez S M,Dosta M,Partida A H,et al. Effect of two carbon sources in microbial abundance in a Biofloc culture system with *Oreochromis*

niloticus(Linnaeus,1758)[J]. International Journal of Fisheries and Aquatic Studies,2016,4(3):421-427.

[18] Kasan N A,Ghazali N A,Ikhwanuddin M,et al. Isolation of potential bacteria as inoculum for biofloc formation in Pacific whiteleg shrimp,*Litopenaeus vannamei* culture ponds[J]. Pakistan Journal of Biological Sciences,2017,20(6):306-313.

[19] Tepaamorndech S,Nookaew I,Higdon S M,et al. Metagenomics in bioflocs and their effects on gut microbiome and immune responses in Pacific white shrimp[J]. Fish & Shellfish Immunology,2020,106:733-741.

[20] El-Sayed A M. Use of biofloc technology in shrimp aquaculture:a comprehensive review,with emphasis on the last decade[J]. Reviews in Aquaculture,2021,13(1):676-705.

[21] Ríos L D M,Monteagudo E B,Barrios Y C,et al. Biofloc technology and immune response of penaeid shrimp:a meta-analysis and meta-regression[J]. Fish & Shellfish Immunology,2023,138:108805.

[22] 周航先,赵建华,徐奇友.基于文献计量学的生物絮团技术在水产中的研究热点分析[J]. 水生态学杂志,2025,46(3):193-204.
Zhou H X,Zhao J H,Xu Q Y. Research hotspot analysis of bioflocs technology in aquaculture based on bibliometrics[J]. Journal of Hydroecology,2025,46(3):193-204(in Chinese with English abstract).

[23] Li Z,Ju C W,Jiao T Y,et al. Effects of biofloc on growth performance and survival of Pacific white shrimp(*Litopenaeus vannamei*)through C/N ratio manipulation,probiotic supplementation,and cocultivation time:a meta-analysis[J]. Aquaculture,2024,587:740837.

[24] Liu G,Verdegem M,Ye Z Y,et al. Advancing aquaculture sustainability:a comprehensive review of biofloc technology trends,innovative research approaches,and future prospects[J]. Reviews in Aquaculture,2025,17(1):e12970.

[25] Guo H P,Huang L,Hu S T,et al. Effects of carbon/nitrogen ratio on growth,intestinal microbiota and metabolome of shrimp(*Litopenaeus vannamei*)[J]. Frontiers in Microbiology,2020,11:652.

[26] Yang S F,Li X Y. Influences of extracellular polymeric substances(EPS)on the characteristics of activated sludge under non-steady-state conditions[J]. Process Biochemistry,2009,44(1):91-96.

[27] Wilén B M,Lumley D,Mattsson A,et al. Dynamics in flocculation and settling properties studied at a full-scale activated sludge plant[J]. Water Environment Research,2010,82(2):155-168.

[28] Schmidt I,Sliekers O,Schmid M,et al. New concepts of microbial treatment processes for the nitrogen removal in wastewater[J]. FEMS Microbiology Reviews,2003,27(4):481-492.

[29] Czepiel P,Crill P,Harriss R. Nitrous oxide emissions from municipal wastewater treatment[J]. Environmental Science & Technology,1995,29(9):2352-2356.

[30] Ahmed Alkhamis Y,Sultana A,Tareq Arafat S,et al. The impact of biofloc technology on water quality in aquaculture:a systematic meta-analysis[J]. Aquaculture Nutrition,2023,2023(1):9915874.

[31] Kumar V,Roy S,Behera B K,et al. Biofloc microbiome with bioremediation and health benefits[J]. Frontiers in Microbiology,2021,12:741164.

[32] Weber S D,Wanner G,Ludwig W,et al. Microbial composition and structure of aerobic granular sewage biofilms[J]. Applied and Environmental Microbiology,2008,74(1):343.

[33] Duan S P,Zhang Y Y,Zheng S K. Heterotrophic nitrifying bacteria in wastewater biological nitrogen removal systems:a review[J]. Critical Reviews in Environmental Science and Technology,2022,52(13):2302-2338.

[34] Shi S H,He X J,He L,et al. Overlooked pathways of endogenous simultaneous nitrification and denitrification in anaerobic/aerobic/anoxic sequencing batch reactors with organic supplementation[J]. Water Research,2023,230:119493.

[35] Li C W,Li J W,Liu G,et al. Performance and microbial community analysis of combined denitrification and biofloc technology(CDBFT)system treating nitrogen-rich aquaculture wastewater[J]. Bioresource Technology,2019,288:121582.

[36] Liu H J,Guo J B,Qu J H,et al. Catalyzing denitrification of *Paracoccus versutus* by immobilized 1,5-dichloroanthraquinone[J]. Biodegradation,2012,23(3):399-405.

[37] Raza B,Zheng Z M,Zhu J Y,et al. A review:microbes and their effect on growth performance of *Litopenaeus vannamei*(white leg shrimps)during culture in biofloc technology system[J]. Microorganisms,2024,12(5):1013.

[38] Li Z,Du Q Y,Jiao T Y,et al. Effects of probiotic supplementary bioflocs(*Rhodospirillum rubrum*,*Bacillus subtilis*,*Providencia rettgeri*)on growth,immunity,and water quality in cultures of Pacific white shrimp(*Litopenaeus vannamei*)[J]. Aquaculture,2024,591:741141.

[39] Xu W J,Wen G L,Su H C,et al. Effect of input C/N ratio on bacterial community of water biofloc and shrimp gut in a commercial zero-exchange system with intensive production of *Penaeus vannamei*[J]. Microorganisms,2022,10(5):1060.

[40] Cao H P,Zhang S M,An J,et al. *Rhodobacter azotoformans* supplementation improves defense ability of Chinese mitten crab *Eriocheir sinensis* against citrobacteriosis[J]. Fish & Shellfish Immunology,2022,131:991-998.

[41] Murakami K,Kamimura D,Hasebe R,et al. *Rhodobacter azotoformans* LPS(RAP99-LPS)is a TLR4 agonist that inhibits lung metastasis and enhances TLR3-mediated chemokine expression[J]. Frontiers in Immunology,2021,12:675909.

[42] de Souza Valente C,Rodiles A,Freire Marques M R,et al. White spot syndrome virus(WSSV)disturbs the intestinal microbiota of shrimp(*Penaeus vannamei*)reared in biofloc and clear seawater[J]. Applied Microbiology and Biotechnology,2020,104(18):8007-8023.

[43] Ebeling J M,Timmons M B,Bisogni J J. Engineering analysis of the stoichiometry of photoautotrophic,autotrophic,and heterotrophic removal of ammonia-nitrogen in aquaculture systems[J]. Aquaculture,2006,257(1/2/3/4):346-358.

[44] Hargreaves J A. Photosynthetic suspended-growth systems in aquaculture[J]. Aquacultural Engineering,2006,34(3):344-363.

[45] Avnimelech Y. Carbon/nitrogen ratio as a control element in aquaculture systems[J]. Aquaculture,1999,176(3/4):227-235.

[46] Minaz M,Kubilay A. Operating parameters affecting biofloc technology:carbon source,carbon/nitrogen ratio,feeding regime,stocking density,salinity,aeration,and microbial community manipulation[J]. Aquaculture International,2021,29(3):1121-1140.

[47] Xu W J,Morris T C,Samocha T M. Effects of C/N ratio on biofloc development,water quality,and performance of *Litopenaeus vannamei* juveniles in a biofloc-based,high-density,zero-exchange,outdoor tank system[J]. Aquaculture,2016,453:169-175.

[48] Zhao D H,Pan L Q,Huang F,et al. Effects of different carbon sources on bioactive compound production of biofloc,immune response,antioxidant level,and growth performance of *Litopenaeus vannamei* in zero-water exchange culture tanks[J]. Journal of the World Aquaculture Society,2016,47(4):566-576.

[49] Mansour A T,Ashry O A,Ashour M,et al. The optimization of dietary protein level and carbon sources on biofloc nutritive values,bacterial abundance,and growth performances of whiteleg shrimp(*Litopenaeus vannamei*)juveniles[J]. Life,2022,12(6):888.

[50] Ekasari J,Hanif Azhar M,Surawidjaja E H,et al. Immune response and disease resistance of shrimp fed biofloc grown on different carbon sources[J]. Fish & Shellfish Immunology,2014,41(2):332-339.

[51] Panigrahi A,Sundaram M,Saranya C,et al. Carbohydrate sources deferentially influence growth performances,microbial dynamics and immunomodulation in Pacific white shrimp(*Litopenaeus vannamei*)under biofloc system[J]. Fish & Shellfish Immunology,2019,86:1207-1216.

[52] Panigrahi A,Saranya C,Sundaram M,et al. Carbon:nitrogen(C:N)ratio level variation influences microbial community of the system and growth as well as immunity of shrimp(*Litopenaeus vannamei*)in biofloc based culture system[J]. Fish & Shellfish Immunology,2018,81:329-337.

[53] Chakrapani S,Panigrahi A,Sundaresan J,et al. Three different C:N ratios for Pacific white shrimp,*Penaeus vannamei* under practical conditions:evaluation of growth performance,immune and metabolic pathways[J]. Aquaculture Research,2021,52(3):1255-1266.

[54] Asaduzzaman M,Rahman M M,Azim M E,et al. Effects of C/N ratio and substrate addition on natural food communities in freshwater prawn monoculture ponds[J]. Aquaculture,2010,306(1/2/3/4):127-136.

[55] Xue Y M,Wei F Y,Jiang Y L,et al. Transcriptome signatures of the Pacific white shrimp *Litopenaeus vannamei* hepatopancreas in response to stress in biofloc culture systems[J]. Fish & Shellfish Immunology,2019,91:369-375.

[56] Huang H H,Liao H M,Lei Y J,et al. Effects of different carbon sources on growth performance of *Litopenaeus vannamei* and water quality in the biofloc system in low salinity[J]. Aquaculture,2022,546:737239.

[57] 鲍方剑,黄雷,陈伟,等.蔗糖输入对凡纳滨对虾养殖系统真核微生物群落的影响[J]. 水生生物学报,2021,45(1):172-181.
Bao F J,Huang L,Chen W,et al. The effects of sucrose on microeukaryotic community in the shrimp aquaculture system[J]. Acta Hydrobiologica Sinica,2021,45(1):172-181(in Chinese with English abstract).

[58] Rego M A S,Sabbag O J,Soares R B,et al. Technical efficiency analysis of marine shrimp farming(*Litopenaeus vannamei*)in biofloc and conventional systems:a case study in northeastern Brazil[J]. Anais da Academia Brasileira de Ciencias,2018,90(4):3705-3716.

[59] 曲寅,章晓栋,任岗,等.间歇性饥饿对南美白对虾生物絮团养殖系统中微生物群落结构、水质和生长的影响[J]. 农业生物技术学报,2024,32(2):417-426.
Qu Y,Zhang X D,Ren G,et al. Effects of intermittent fasting on microbial community structure,water quality and growth of *Litopenaeus vannamei* in a biofloc system[J]. Journal of Agricultural Biotechnology,2024,32(2):417-426(in Chinese with English abstract).

[60] Esparza-Leal H M,Ponce-Palafox J T,Álvarez-Ruiz P,et al. Effect of stocking density and water exchange on performance and stress tolerance to low and high salinity by *Litopenaeus vannamei* postlarvae reared with biofloc in intensive nursery phase[J]. Aquaculture International,2020,28(4):1473-1483.

[61] Ray A J,Lotz J M. Comparing salinities of 10,20,and 30‰ in intensive,commercial-scale biofloc shrimp(*Litopenaeus vannamei*)production systems[J]. Aquaculture,2017,476:29-36.

[62] van Hoa N,Tao C T,Terahara T,et al. Influence of salinity on nursery-phase whiteleg shrimp(*Litopenaeus vannamei*)reared in a biofloc system[J]. Journal of Applied Aquaculture,2022,34(4):907-921.

[63] de Souza D M,Martins Á C,Jensen L,et al. Effect of temperature on antioxidant enzymatic activity in the Pacific white shrimp *Litopenaeus vannamei* in a BFT(Biofloc technology)system[J]. Marine and Freshwater Behaviour and Physiology,2014,47(1):1-10.

[64] de Souza D M,Borges V D,Furtado P,et al. Antioxidant enzyme activities and immunological system analysis of *Litopenaeus vannamei* reared in biofloc technology(BFT)at different water temperatures[J]. Aquaculture,2016,451:436-443.

[65] Becerra-Dórame M J,Martínez-Porchas M,Martínez-Córdova L R,et al. Production response and digestive enzymatic activity of the Pacific white shrimp *Litopenaeus vannamei*(Boone,1931)intensively pregrown in microbial heterotrophic and autotrophic-based systems[J]. The Scientific World Journal,2012,2012:723654.

[66] Baloi M,Arantes R,Schveitzer R,et al. Performance of Pacific white shrimp *Litopenaeus vannamei* raised in biofloc systems with varying levels of light exposure[J]. Aquacultural Engineering,2013,52:39-44.

[67] Lara G,Krummenauer D,Abreu P C,et al. The use of different aerators on *Litopenaeus vannamei* biofloc culture system:effects on water quality,shrimp growth and biofloc composition[J]. Aquaculture International,2017,25(1):147-162.

[68] Lim Y S,Ganesan P,Varman M,et al. Effects of microbubble aeration on water quality and growth performance of *Litopenaeus vannamei* in biofloc system[J]. Aquacultural Engineering,2021,93:102159.

[69] de Morais A P M,Abreu P C,Wasielesky W,et al. Effect of aeration intensity on the biofilm nitrification process during the production of the white shrimp *Litopenaeus vannamei*(Boone,1931)in biofloc and clear water systems[J]. Aquaculture,2020,514:734516.

[70] Piérri V, Valter-Severino D, Goulart-de-Oliveira K, et al. Cultivation of marine shrimp in biofloc technology (BFT) system under different water alkalinities[J]. Revista Brasleira de Biologia, 2015, 75(3): 558-564.

[71] Furtado P S, Poersch L H, Wasielesky W. The effect of different alkalinity levels on *Litopenaeus vannamei* reared with biofloc technology (BFT)[J]. Aquaculture International, 2015, 23(1): 345-358.

[72] de Moura P S, Wasielesky W, da Paz Serra F, et al. Partial seawater inclusion to improve *Litopenaeus vannamei* performance in low salinity biofloc systems[J]. Aquaculture, 2021, 531: 735905.

[73] Deng Y L, Xu X Y, Yin X W, et al. Effect of stock density on the microbial community in biofloc water and Pacific white shrimp (*Litopenaeus vannamei*) gut microbiota[J]. Applied Microbiology and Biotechnology, 2019, 103(10): 4241-4252.

[74] Liu G, Zhu S M, Liu D Z, et al. Effects of stocking density of the white shrimp *Litopenaeus vannamei* (Boone) on immunities, antioxidant status, and resistance against *Vibrio harveyi* in a biofloc system[J]. Fish & Shellfish Immunology, 2017, 67: 19-26.

[75] Said M M, El-barbary Y A, Ahmed O M. Assessment of performance, microbial community, bacterial food quality, and gene expression of whiteleg shrimp (*Litopenaeus vannamei*) reared under different density biofloc systems[J]. Aquaculture Nutrition, 2022, 2022(1): 3499061.

[76] Iunes R S, Branco P C, Pressinotti L N, et al. Does the heterotrophic system influence the cellular immune response of *Litopenaeus vannamei* shrimp? *in vitro* phagocytosis indices and superoxide anion production comparisons[J]. Fish and Shellfish Immunology Reports, 2021, 2: 100009.

[77] Kim S K, Song J, Rajeev M, et al. Exploring bacterioplankton communities and their temporal dynamics in the rearing water of a biofloc-based shrimp (*Litopenaeus vannamei*) aquaculture system[J]. Frontiers in Microbiology, 2022, 13: 995699.

[78] Situmorang M L, Uawisetwathana U, Arayamethakorn S, et al. Supplementation of *ex situ* produced bioflocs improves immune response against AHPND in Pacific whiteleg shrimp (*Litopenaeus vannamei*) postlarvae[J]. Applied Microbiology and Biotechnology, 2022, 106(9): 3751-3764.

[79] Waiho K, Abd Razak M S, Abdul Rahman M Z, et al. A metagenomic comparison of clearwater, probiotic, and rapid BFT™ on Pacific whiteleg shrimp, *Litopenaeus vannamei* cultures[J]. PeerJ, 2023, 11: e15758.

[80] Wu J P, Chen Y F, Xu X N, et al. Screening of bioflocculant and cellulase-producing bacteria strains for biofloc culture systems with fiber-rich carbon source[J]. Frontiers in Microbiology, 2022, 13: 969664.

[81] He X, Abakari G, Tan H X, et al. Effects of different probiotics (*Bacillus subtilis*) addition strategies on a culture of *Litopenaeus vannamei* in biofloc technology (BFT) aquaculture system[J]. Aquaculture, 2023, 566: 739216.

[82] Hostins B, Wasielesky W, Decamp O, et al. Managing input C/N ratio to reduce the risk of acute hepatopancreatic necrosis disease (AHPND) outbreaks in biofloc systems: a laboratory study[J]. Aquaculture, 2019, 508: 60-65.

[83] Ge H X, Li J, Chang Z Q, et al. Effect of microalgae with semicontinuous harvesting on water quality and zootechnical performance of white shrimp reared in the zero water exchange system[J]. Aquacultural Engineering, 2016, 72: 70-76.

[84] Huang C, Luo Y Y, Zeng G Q, et al. Effect of adding microalgae to whiteleg shrimp culture on water quality, shrimp development and yield[J]. Aquaculture Reports, 2022, 22: 100916.

[85] Panigrahi A, Esakkiraj P, Saranya C, et al. A biofloc-based aquaculture system bio-augmented with probiotic bacteria *Bacillus tequilensis* AP BFT3 improves culture environment, production performances, and proteomic changes in *Penaeus vannamei*[J]. Probiotics and Antimicrobial Proteins, 2022, 14(2): 277-287.

[86] 高远, 李甍, 董登攀, 等. 凡纳滨对虾养殖系统中异养和自养型生物絮团的微生物特性及其与养殖水环境的关系[J]. 中国水产科学, 2022, 29(6): 864-873.
Gao Y, Li M, Dong D P, et al. Microbial characteristics of heterotrophic and autotrophic biofloc in *Litopenaeus vannamei* culturing systems and their relationship with water quality[J]. Journal of Fishery Sciences of China, 2022, 29(6): 864-873(in Chinese with English abstract).

[87] McCusker S, Warberg M B, Davies S J, et al. Biofloc technology as part of a sustainable aquaculture system: a review on the status and innovations for its expansion[J]. Aquaculture, Fish and Fisheries, 2023, 3(4): 331-352.

[88] Silva V F, Pereira P K M, Martins M A, et al. Effects of microalgae addition and fish feed supplementation in the integrated rearing of Pacific white shrimp and Nile *Tilapia* using biofloc technology[J]. Animals, 2022, 12(12): 1527.

[89] 陈睿, 陈晓颖, 刘智明, 等. 生物絮团技术在水产养殖业中的研究进展[J]. 工业微生物, 2023, 53(1): 51-54.
Chen R, Chen X Y, Liu Z M, et al. On the research progress of biofloc technology in aquaculture industry[J]. Industrial Microbiology, 2023, 53(1): 51-54(in Chinese with English abstract).

[90] Nie X F, Mubashar M, Zhang S, et al. Current progress, challenges and perspectives in microalgae-based nutrient removal for aquaculture waste: a comprehensive review[J]. Journal of Cleaner Production, 2020, 277: 124209.

[91] Ma M Y, Hu Q. Microalgae as feed sources and feed additives for sustainable aquaculture: prospects and challenges[J]. Reviews in Aquaculture, 2024, 16(2): 818-835.

[92] Wan Mahari W A, Waiho K, Fazhan H, et al. Emerging paradigms in sustainable shellfish aquaculture: microalgae and biofloc technologies for wastewater treatment[J]. Aquaculture, 2024, 587: 740835.

[93] Wang H, Qi B F, Jiang X M, et al. Microalgal interstrains differences in algal-bacterial biofloc formation during liquid digestate treatment[J]. Bioresource Technology, 2019, 289: 121741.

[94] Ramanan R, Kim B H, Cho D H, et al. Algae-bacteria interactions: evolution, ecology and emerging applications[J]. Biotechnology Advances,

2016,34(1):14-29.

[95] Abakari G,Wu X,He X,et al. Bacteria in biofloc technology aquaculture systems:roles and mediating factors[J]. Reviews in Aquaculture,2022,14(3):1260-1284.

[96] Mugwanya M,Dawood M A O,Kimera F,et al. Biofloc systems for sustainable production of economically important aquatic species:a review[J]. Sustainability,2021,13(13):7255.

[97] Khoa T N D,Tao C T,van Khanh L,et al. Super-intensive culture of white leg shrimp(*Litopenaeus vannamei*)in outdoor biofloc systems with different sunlight exposure levels:emphasis on commercial applications[J]. Aquaculture,2020,524:735277.

[98] Albright M B N,Louca S,Winkler D E,et al. Solutions in microbiome engineering:prioritizing barriers to organism establishment[J]. The ISME Journal,2021,16(2):331-338.

[99] Wang L,Jia X Q,Xu L,et al. Engineering microalgae for water phosphorus recovery to close the phosphorus cycle[J]. Plant Biotechnology Journal,2023,21(7):1373-1382.

[100]何梅琳,迟巧云,王长海. 极地微藻对极端环境的适应机制研究进展[J]. 南京农业大学学报,2019,42(2):201-208.
He M L,Chi Q Y,Wang C H. Research progress of the adaptive mechanisms of polar microalgae in response to extreme environment[J]. Journal of Nanjing Agricultural University,2019,42(2):201-208(in Chinese with English abstract).

[101]Schwaderer A S,Yoshiyama K,de Tezanos Pinto P,et al. Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton[J]. Limnology and Oceanography,2011,56(2):589-598.

[102]Cooper M B,Smith A G. Exploring mutualistic interactions between microalgae and bacteria in the omics age[J]. Current Opinion in Plant Biology,2015,26:147-153.

[103]Natrah F M I,Bossier P,Sorgeloos P,et al. Significance of microalgal-bacterial interactions for aquaculture[J]. Reviews in Aquaculture,2014,6(1):48-61.

[104]Amin S A,Parker M S,Armbrust E V. Interactions between diatoms and bacteria[J]. Microbiology and Molecular Biology Reviews,2012,76(3):667-684.

责任编辑:周广礼