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贻贝肽对厚壳贻贝稚贝生长发育及微生物群落结构的影响*

林 倩[1,2,3] 李 政[1,2,3] 杨金龙[1,2,3①] 马 蕃[1,2,3] 梁 箫[1,2,3]

(1. 上海海洋大学水产与生命学院 科技部海洋生物科学国际联合研究中心 上海 201306;
2. 上海市水产动物良种创制与绿色养殖协同创新中心 上海 201306;
3. 中国-葡萄牙星海“一带一路”联合实验室 上海 200120)

摘要 为探究海洋生物活性肽对厚壳贻贝(*Mytilus coruscus*)生长发育的影响，本研究以厚壳贻贝稚贝为实验对象，通过投喂不同浓度的贻贝肽(0、7、9、10、70 和 90 mg/L)，测定壳长、壳高、湿重等指标，以确定最适贻贝肽浓度，并对投喂前后的稚贝微生物群落进行分析，实验周期为 56 d。结果显示，相较于未投喂贻贝肽的对照组，投喂 9 mg/L 的贻贝肽显著促进稚贝生长，且壳长、壳高和湿重分别提升了 27.37%、32.35%和 115.49%；同时发现，高浓度贻贝肽(70 mg/L 和 90 mg/L)对厚壳贻贝稚贝产生了致死效应。通过 16S rRNA 基因扩增和测序对比分析了 28 d 和 56 d 贻贝肽投喂组与未投喂组的厚壳贻贝稚贝微生物组群落结构变化。研究结果显示，投喂 9 mg/L 贻贝肽改变了稚贝微生物群落结构组成，提高了拟杆菌门(Bacteroidota)和变形菌门(Proteobacteria)的丰度，降低了放线菌门(Actinobacteriota)的丰度；同时，属水平分析发现，贻贝肽投喂组有效增加了鲁杰氏菌属(*Ruegeria*)、黏着杆菌属(*Tenacibaculum*)、居海杆菌属(*Maribacter*)、栖砂杆菌属(*Arenibacter*)、十八碳杆菌属(*Octadecabacter*)和希瓦氏菌属(*Shewanella*)等有益菌的物种丰度，显著减少了红球菌属(*Rhodococcus*)、气单胞菌属(*Aeromonas*)等潜在致病菌的丰度。综上，贻贝肽能有效促进厚壳贻贝的稚贝生长发育，并且可以优化厚壳贻贝微生物群落结构，研究成果将为后续开展贻贝肽等海洋生物活性肽对贝类稚贝中间培育以及海水贝类养殖可持续发展提供基础和数据支撑。

关键词 厚壳贻贝；生长；微生物；群落结构；贻贝肽

中图分类号 S968.3 **文献标识码** A **文章编号** 2095-9869(2025)01-0115-12

2022 年度，全国海水贻贝养殖产量为 771 230 t，较 2021 年减少 58 251 t，同比下降 7.02% (农业农村部渔业渔政管理局等, 2023)。厚壳贻贝(*Mytilus coruscus*)是我国主要养殖贻贝品种之一，隶属于软体动物门(Mollusca)、瓣鳃纲(Lanellibranchia)、异柱目(Anisomyaria)、贻贝科(Mytilidae)、贻贝属(*Mytilus*)(周轩等, 2015)，其肉质鲜美，营养丰富，经济价值高。目前，厚壳贻贝养殖产业正面临稚贝生长缓慢、成贝出肉率低和成贝个体小型化等问题，严重影响了经济和产业发展(王朝新, 2021)。

* 国家重点研发计划(2023YFD2401902; 2023YFE0115500; 2022YFE0204600)资助。林 倩，Email: m210100007@st.shou.edu.cn
① 通信作者：杨金龙，教授，Email: jlyang@shou.edu.cn
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在水产养殖中，益生元是常用的外源添加剂。益生元通过改变胃肠道形态和调节微生物群落组成等方式帮助机体吸收营养物质(Abdel-Aziz *et al*, 2020)，起到促进水生生物生长发育(Adhikari *et al*, 2017)、增强抗病原菌(Akhter *et al*, 2015)和提高饲料吸收利用率(Rohani *et al*, 2022)等作用，从而提高水产品产量(高鸣等, 2022)。贻贝肽作为一种蛋白质水解物，也属益生元，其营养价值高、安全健康，具有抗菌、抗氧化和增强免疫力等多重功能(Grienke *et al*, 2014)，特别是低分子量的贻贝肽具有抗脂质过氧化保护活性和清除多余自由基的功能，可作为天然抗菌食物添加剂(Cho *et al*, 2004; Jung *et al*, 2007; Rajapakse *et al*, 2005)。在水产养殖中，贻贝肽被认为是治疗海洋物种传染病的天然活性成分(Balseiro *et al*, 2011)。

本研究以我国东部海域主要的养殖贝类厚壳贻贝(杨金龙等, 2021)为研究对象，开展了贻贝肽对其稚贝生长发育状态以及体内外微生物群落结构组成特征变化的研究，旨在为贻贝等贝类绿色高效养殖提供理论依据和技术支撑。

1 材料与方法

1.1 材料

实验所用厚壳贻贝稚贝由中国浙江省嵊泗县东海贻贝科技创新服务有限公司提供。选择壳长为(3.28±0.05) mm、壳高为(2.21±0.03) mm 且大小规格相近的 3 600 只个体作为实验材料，在温度为 18 ℃、盐度为 30 的条件下，暂养 1 周后用于实验。实验所用贻贝肽由大连深蓝肽科技研发有限公司提供。该贻贝肽由贻贝组织经蛋白酶水解得到，其物理性状为浅黄色粉末状，其分子量小于 1 000 Da。

1.2 方法

1.2.1 贻贝肽投喂　实验设 5 个投喂处理组和 1 个未投喂对照组，处理组分别按 7、9、10、70 和 90 mg/L 的浓度投喂贻贝肽进行实验观察，每组设置 3 个重复。以青岛大扁藻(*Tetraselmis helgolandica*)和湛江等鞭金藻(*Isochrysis zhanjiangensis*)等体积混合作为培育稚贝的饵料，每日投饵 2 次(06:30 和 18:30)，每日投饵量为(4.0×10^5~5×10^5) cells/mL。为保证贻贝肽暴露浓度，每日定时定量换水，每次换水后按实验浓度添加贻贝肽。

1.2.2 生长指标测量　在第 7、14、21、28、42 和 56 天随机抽取不同处理组 50 枚稚贝，进行生长指标测量。实验中，通过电子游标卡尺测量其壳高、壳长，用分析天平测量稚贝湿重；同时，记录不同处理组稚贝存活率，存活率(survival rate, SR, %)计算公式为：

$$SR=100\times N_2/N_1$$

式中，N_1、N_2 分别为随机抽取厚壳贻贝稚贝 100 个和 100 个稚贝中存活的个数，并进行 3 个重复。

稚贝的壳高和壳长特定生长率(specific growth rate, SGR, %/d)计算公式为：

$$SGR=(\ln SL2-\ln SL1)/t\times100\%$$

式中，SL1 和 SL2 分别为实验前稚贝的初始壳高(或壳长)和实验结束后最终壳高(或壳长)，t 为实验时间(d)。

1.2.3 样品采集和微生物扩增子测序　在第 28 和 56 天分别采集不同处理组的稚贝样品。采集样品时，使用灭菌镊子夹取稚贝，并放入 1.5 mL 无酶离心管中，通过灭菌海水冲洗管中稚贝，重复冲洗 2~3 次，弃掉液体仅留下管中稚贝，最后，将冲洗过的稚贝用液氮速冻存入–80 ℃冰箱中保存，待后续分析。根据生长指标分析结果，选取第 28 天的 0 mg/L 对照组和 9 mg/L 处理组、第 56 天的 0 mg/L 对照组和 9 mg/L 处理组共 4 个分组的样品进行微生物扩增子测序分析。采用 CTAB 法(Nobleryder, 中国)标准化操作提取样品总 DNA (Bokulich *et al*, 2013)，利用 1%琼脂糖凝胶电泳(DDY-6C, 北京市六一仪器厂, 中国)和酶标仪(BIOTEK XPS, 美国)检测 DNA 的纯度和浓度。总 DNA 检验合格后，使用引物 341F (CCTAYGGGRBGCASCAG)和 806R (GGACTACNN GGGTATCTAAT)进行 PCR (T100, Bio-rad, 美国)产物获取和纯化以及 16S rDNA V3~V4 区测序文库构建。使用 NEB Next® Ultra™ II FS DNA PCR-free 建库试剂盒(New England Biolabs)，按照说明书构建基因文库，利用 Qubit 和 Q-PCR 定量检测基因文库构建质量，文库合格后，通过 NovaSeq6000 进行 PE250 上机测序。

1.2.4 生物信息分析　存活率数据以平均值±标准差(Mean±SD)表示。利用 GraphPad Prism 软件绘制生长指标柱状图。使用 JMP 统计软件进行差异性分析，$P<0.05$ 为显著差异。扩增子测序原始数据经过拼接、质量过滤和嵌合体去除后，使用 DADA2 降噪后生成扩增子序列变体(ASV) (Callahan *et al*, 2016)。使用 QIIME2 (Quantitative Insights into Microbial Ecology 2)中的 classify-sklearn 算法对每个 ASV 进行分类和物种注释，并计算 α 多样性指数和 β 多样性(Bokulich *et al*, 2018; Bolyen *et al*, 2019)。使用 SVG 函数绘制 Perl 中物种相对丰度的分布直方图。利用 R 语言绘制热图、韦恩图、主成分分析(PCA)以及进行 MetaStat

分析并绘图等。使用 LEfSe 软件进行分析绘制 LEfSe 数据图。为研究组间显著性差异的物种，本研究将不同分组间的物种相对丰度数据通过 *T*-test 方法得到假设检验的 *P* 值，再根据 *P* 值大小筛选组间显著性的差异物种。

2　结果

2.1　不同浓度贻贝肽喂养下厚壳贻贝稚贝存活率

从表 1 可见，10 mg/L 贻贝肽处理组存活率从第 21 天开始下降，而 7 mg/L 和 9 mg/L 贻贝肽处理组成活率保持稳定。贻贝肽喂养 56 d 后，7 mg/L 和 9 mg/L 贻贝肽处理组成活率高于 10 mg/L 贻贝肽处理组；同时，相比低浓度(≤10 mg/L)处理组，对照组存活率明显下降(P< 0.05)。70 mg/L 和 90 mg/L 高浓度贻贝肽处理组稚贝均在 14 d 后死亡。因此，低浓度贻贝肽对厚壳贻贝稚贝具有提高存活率的作用，而高浓度贻贝肽则具有致死效应。

2.2　不同浓度贻贝肽喂养下厚壳贻贝稚贝壳长及特定生长率

从图 1A 可见，随着稚贝中间培育时间的延长，低浓度贻贝肽处理组稚贝的壳长逐渐增加，且显著高于对照组(P<0.05)。随着贻贝肽浓度的增加，稚贝壳长呈现先升高后降低的趋势，其中，投喂 9 mg/L 贻贝肽显著促进稚贝生长，56 天后壳长提升了 27.37%，而 70 mg/L 和 90 mg/L 高浓度贻贝肽处理组稚贝壳长并无显著增加，且稚贝死亡率较高。

从图 1B 可见，实验结束时，低浓度贻贝肽处理组稚贝壳长特定生长率均显著高于对照组(P<0.05)，而高浓度贻贝肽处理组不仅无法促进稚贝壳长增加，反而导致稚贝全部死亡。

表 1　不同浓度贻贝肽喂养下厚壳贻贝稚贝的存活率/%

Tab.1　Survival rate of *Mytilus coruscus* plantigrades fed with mussel peptides of different concentrations/%

贻贝肽浓度 Concentrations of mussel peptide/(mg/L)	培养时间 culture time/d					
	7	14	21	28	42	56
0	99.33±1.15^{ab}	98.67±1.15^{abc}	96.67±1.15^{abcde}	96.00±2.00^{abcde}	93.33±1.15^{de}	92.67±2.31^{de}
7	100.00±0.00^{a}	100.00±0.00^{a}	100.00±0.00^{a}	100.00±0.00^{a}	100.00±0.00^{a}	99.33±1.15^{ab}
9	100.00±0.00^{a}	100.00±0.00^{a}	100.00±0.00^{a}	100.00±0.00^{a}	100.00±0.00^{a}	98.67±2.31^{cde}
10	100.00±0.00^{a}	100.00±0.00^{a}	98.00±0.00^{abcd}	95.33±1.15^{abcde}	94.67±1.15^{bcde}	94.00±2.00^{abc}
70	64.00±7.21^{f}	0	0	0	0	0
90	36.67±6.11^{g}	0	0	0	0	0

注：同列数据，不同小写字母表示组间有显著性差异(P<0.05)，相同小写字母表示组间无显著性差异(P>0.05)。下同。

Note: In the same column, data with different letters are significantly different at the 0.05 probability level, and data with the same letter are not significantly different. The same below.

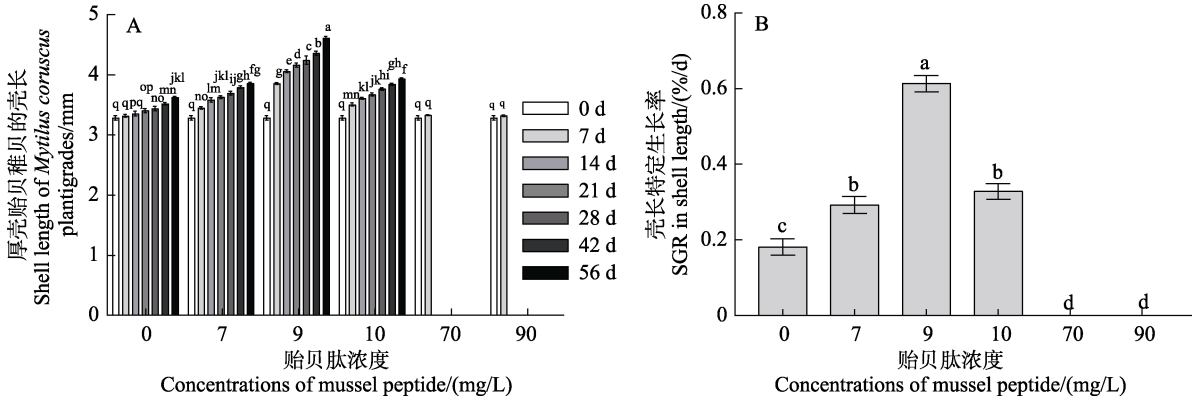

图 1　不同浓度贻贝肽喂养下厚壳贻贝稚贝的壳长(A)及特定生长率(B)

Fig.1　Shell length (A) and specific growth rate (SGR) (B) in the thick-shelled mussel *M. coruscus* plantigrades fed with mussel peptides of different concentrations

柱子标有不同小写字母表示组间有显著性差异(P<0.05)，标有相同小写字母表示组间无显著性差异(P>0.05)。下同。

Columns with different letters are significantly different at the 0.05 probability level, and the columns with the same letter are not significantly different. The same below.

2.3 不同浓度贻贝肽喂养下厚壳贻贝稚贝壳高及其特定生长率

从图 2A 可见，随着稚贝养殖时间的延长，低浓度贻贝肽处理组稚贝的壳高逐渐增加，且显著高于对照组(P<0.05)。随着贻贝肽浓度的增加，稚贝壳高呈现先升高后降低的趋势，其中投喂 9 mg/L 的贻贝肽显著促进稚贝生长，56 d 后壳高提升了 32.35%，而 70 mg/L 和 90 mg/L 高浓度贻贝肽处理组稚贝壳高并没有显著增加，且稚贝死亡率较高。

从图 2B 可见，实验结束时，低浓度贻贝肽处理组稚贝壳高特定生长率均显著高于对照组(P<0.05)，而高浓度贻贝肽处理组并不能促进稚贝壳高增加。

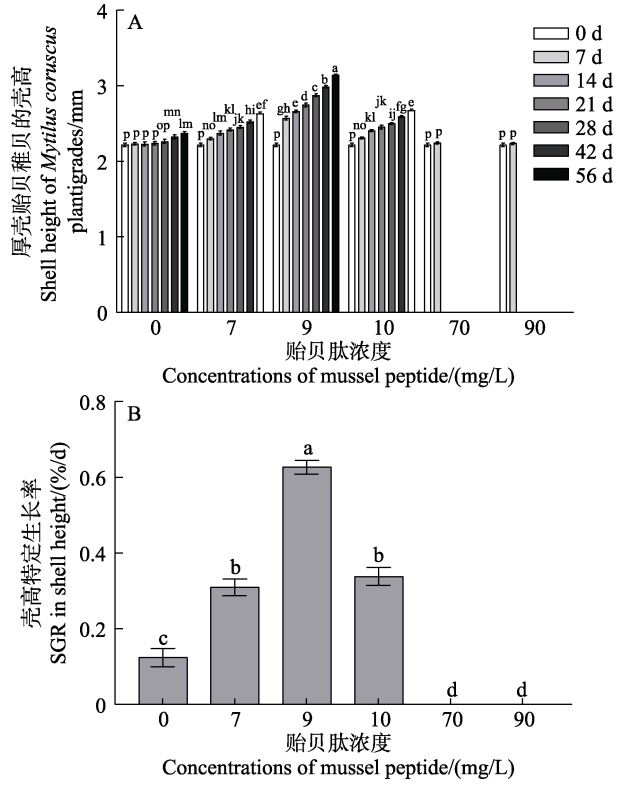

图 2 不同浓度贻贝肽喂养下厚壳贻贝稚贝的壳高(A)及特定生长率(B)

Fig.2 Shell height (A)and specific growth rate (SGR) (B) in shell height of the thick-shelled mussel *M. coruscus* plantigrades fed with mussel peptides of different concentrations

2.4 不同浓度贻贝肽喂养下厚壳贻贝稚贝湿重

从图 3 可见，随着稚贝养殖时间的延长，低浓度贻贝肽处理组稚贝的湿重逐渐增加，且显著高于对照组(P<0.05)。随着贻贝肽浓度的增加，稚贝湿重呈现先升高后降低的趋势，其中投喂 9 mg/L 贻贝肽显著促进稚贝生长，56 d 后湿重提升了 115.49%；而 70 mg/L 和 90 mg/L 高浓度贻贝肽处理组稚贝的湿重并未显著增加，且稚贝死亡率较高。

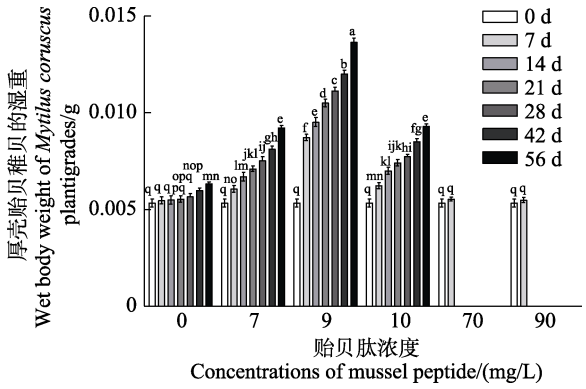

图 3 不同浓度贻贝肽喂养下厚壳贻贝稚贝的湿重

Fig.3 Wet body weight of the thick-shelled mussel *M. coruscus* plantigrades fed with mussel peptides of different concentrations

2.5 微生物群落组成

2.5.1 *扩增子序列变体(ASVs)和多样性指数* 28 d 对照组(CG.28 d)、56 d 对照组(CG.56 d)、28 d 的 9 mg/L 贻贝肽处理组(EG.28 d)和 56 d 的 9 mg/L 贻贝肽处理组(EG.56 d)共 4 组的 24 个样本平均产生 69 593 条高质量序列(SD=8 271.03)。

如图 4A 所示，CG.28 d、EG.28 d、CG.56 d 和 EG.56 d 的 ASVs 数量分别为 984、854、1 117 和 902。这 4 个组共享 316 个 ASV。EG.28 d (538)和 EG.56 d (586)的独特 ASV 数量均低于 CG.28 d (668)和 CG.56 d (801)，表明贻贝肽对厚壳贻贝稚贝微生物群落组成具有调节作用。

基于 ASV，通过主成分分析(PCA)来评估各组之间微生物群落的差异(图 4B)。PC1 (8.99%)和 PC2 (8.47%)的总交替率为 17.46%。添加贻贝肽的 28 d 和 56 d 的处理组均与对照组差异显著，表明贻贝肽对厚壳贻贝稚贝微生物群落的组成具有调节作用。

如表 2 所示，CG.56 d 的 Shannon 和 Simpson 指数显著高于其他处理组(P<0.05)，EG.56 d 组的 Shannon 和 Simpson 指数也高于 CG.28 d 组和 EG.28 d 组的 Shannon 指数，存在显著差异(P<0.05)，且 CG.56 d 与 EG.56 d 的 Shannon 和 Simpson 指数也存在显著差异(P<0.05)，表明贻贝肽可以降低厚壳贻贝稚贝微生物群落的多样性，且在 56 d 后才发挥作用。

2.5.2 *微生物群落物种组成* 由图 5A 可见，门水平的稚贝微生物群落结构主要由变形菌门(Proteobacteria)、蓝细菌门(Cyanobacteria)、拟杆菌门(Bacteroidota)、放线菌门(Actinobacteriota)、脱硫菌

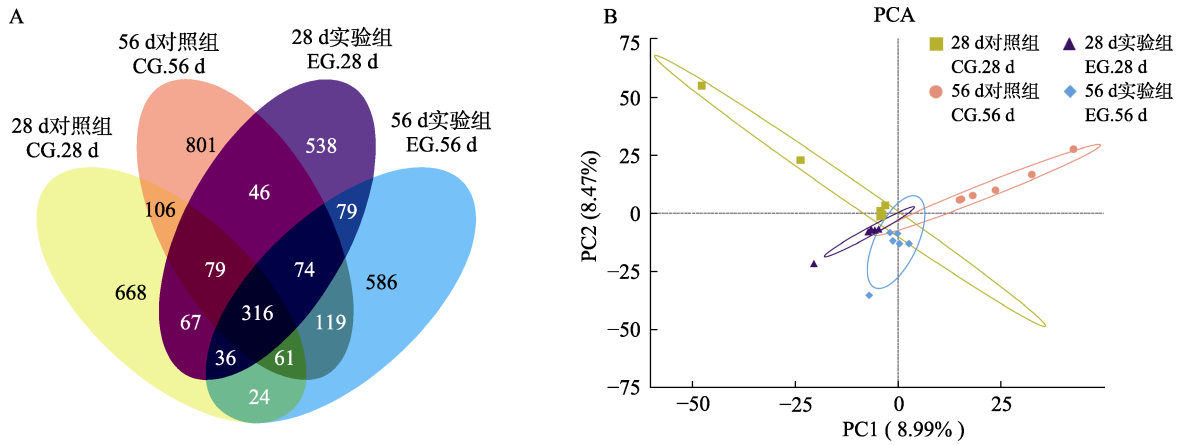

图 4　不同分组微生物群的特征序列(ASVs)的维恩图(A)和主成分分析图(B)

Fig.4　Venn diagram (A) and PCA plots (B) of microbial communities of different groups

表 2　处理组和对照组微生物群落结构 α 多样性分析

Tab.2　Analysis of alpha diversity of microbial community in the experimental group and control group

指标 Index	28 d 对照组 CG.28 d	28 d 处理组 EG.28 d	56 d 对照组 CG.56 d	56 d 处理组 EG.56 d
Shannon	5.93±0.45^{c}	5.94±0.57^{c}	7.25±0.13^{a}	6.64±0.28^{b}
Simpson	0.94±0.03^{a}	0.93±0.04^{a}	0.98±0.001^{a}	0.97±0.01^{a}
Chao1	420.57±192.07^{c}	415.84±92.38^{c}	582.28±102.17^{a}	433.96±160.97^{b}

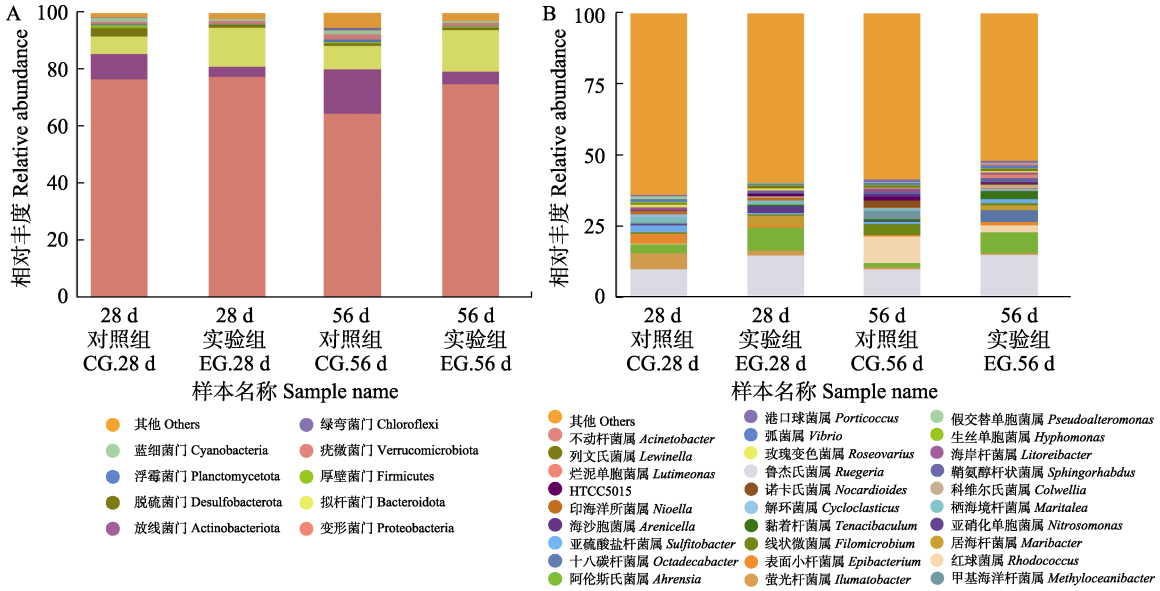

图 5　微生物群落多样性

Fig.5　Microbial community diversity

A：基于门水平的细菌多样性；B：基于属水平的细菌多样性。

A: Bacterial diversity at phylum; B: Bacterial diversity at genus.

门(Desulfobacterota)、蛭弧菌门(Bdellovibrionota)、厚壁菌门(Firmicutes)等组成。相比对照组，添加贻贝肽组优势门相对丰度出现明显变化；添加贻贝肽组其拟杆菌门和变形菌门的相对丰度高于对照组，而放线菌门相对丰度则低于对照组。

由图 5B 可知，在已鉴定的 445 个属中，某些细菌类群的相对丰度在不同养殖期间存在明显差异。例如，相比对照组，添加贻贝肽组中的鲁杰氏

菌属(*Ruegeria*)、黏着杆菌属(*Tenacibaculum*)、十八杆菌属(*Octadecabacter*)和海洋阿伦斯氏菌属(*Ahrensia*)等菌属相对丰度较高，而红球菌属(*Rhodococcus*)和线状微球菌属(*Filomicrobium*)相对丰度较低。

2.5.3 不同分组之间的具体微生物学分析

2.5.3.1 线性判别分析(LEfSe) 为了获得不同分组之间的特征微生物，进行了 LEfSe 分析。图 6 分别显示了不同时间的线性判别分析(LDA)值得分大于 4 的不同分组的特定微生物。由图 6A 可见，EG.28 d 处理组中主要是根瘤菌科(Rhizobiaceae)的海洋阿伦斯氏菌属和黄杆菌科(Flavobacteriaceae)的居海杆菌属(*Maribacter*)等微生物种类富集；在图 6B 中 EG.56 d 处理组主要是鲁杰氏菌属、十八杆菌属、黏着杆菌属等微生物种类富集。

2.5.3.2 组间物种差异分析(*T*-test) 由图 7A 可见，相比对照组，添加 9 mg/L 贻贝肽的 EG.28 d 组的鲁杰氏菌属、海洋阿伦斯氏菌属、居海杆菌属、黏着杆菌属、科维尔氏菌属(*Colwellia*)、列文氏菌属(*Lewinella*)、深海短杆菌属(*Thalassotalea*)和栖砂杆菌属(*Arenibacter*)等类群的相对丰度显著升高；而红球菌属、线状微菌属、甲基海洋杆菌属(*Methyloceanibacter*)、弧菌属(*Vibrio*)、副球菌属(*Paracoccus*)、气单胞菌属(*Aeromonas*)和亚硫酸盐杆菌属(*Sulfitobacter*)等类群的相对丰度显著降低。由图 7B 可见：与对照组相比，添加 9 mg/L 贻贝肽的 EG.56 d 组中的鲁杰氏菌属、海洋阿伦斯氏菌属、十八碳杆菌属、居海杆菌属、亚硫酸盐杆菌属、黏着杆菌属、科维尔氏菌属、烂泥单胞菌属(*Lutimonas*)、深海短杆菌属、希瓦氏菌属(*Shewanella*)、交替单胞菌属(*Alteromonas*)和假暗棕色杆菌属(*Pseudophaeobacter*)等类群的相对丰度显著升高；而萤光杆菌属(*Ilumatobacter*)、红球菌属、线状微菌属、甲基海洋杆菌属、解环菌属(*Cycloclasticus*)、HTCC5015、诺卡氏菌属(*Nocardioides*)、海沙胞菌属(*Arenicella*)和副球菌属等类群的相对丰度显著降低。

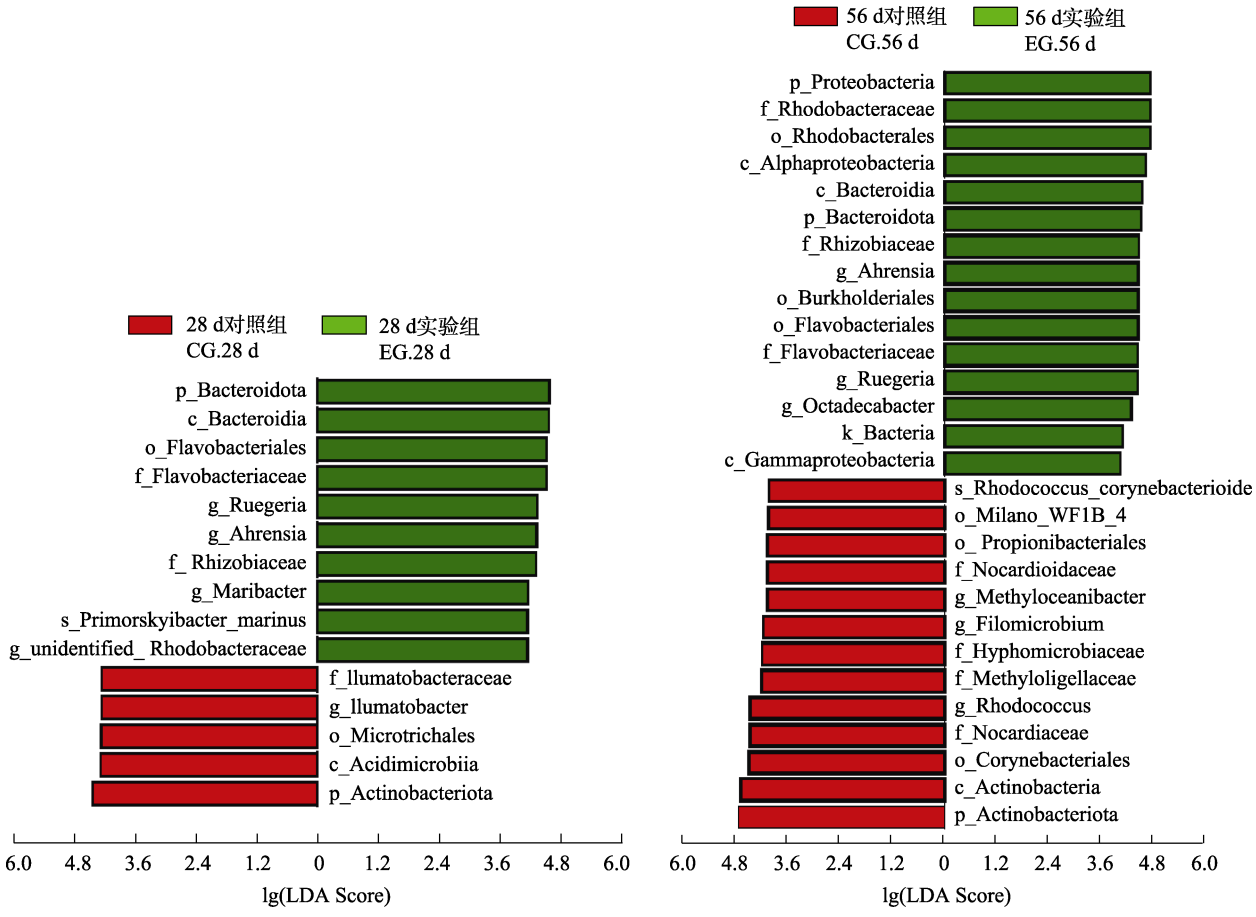

图 6 28 d (A)和 56 d (B)微生物群落的 LDA 分布柱状图

Fig.6 Histogram of the distribution of linear discriminant analysis scores of microbial communities after fed by 28 d (A) and 56 d (B)

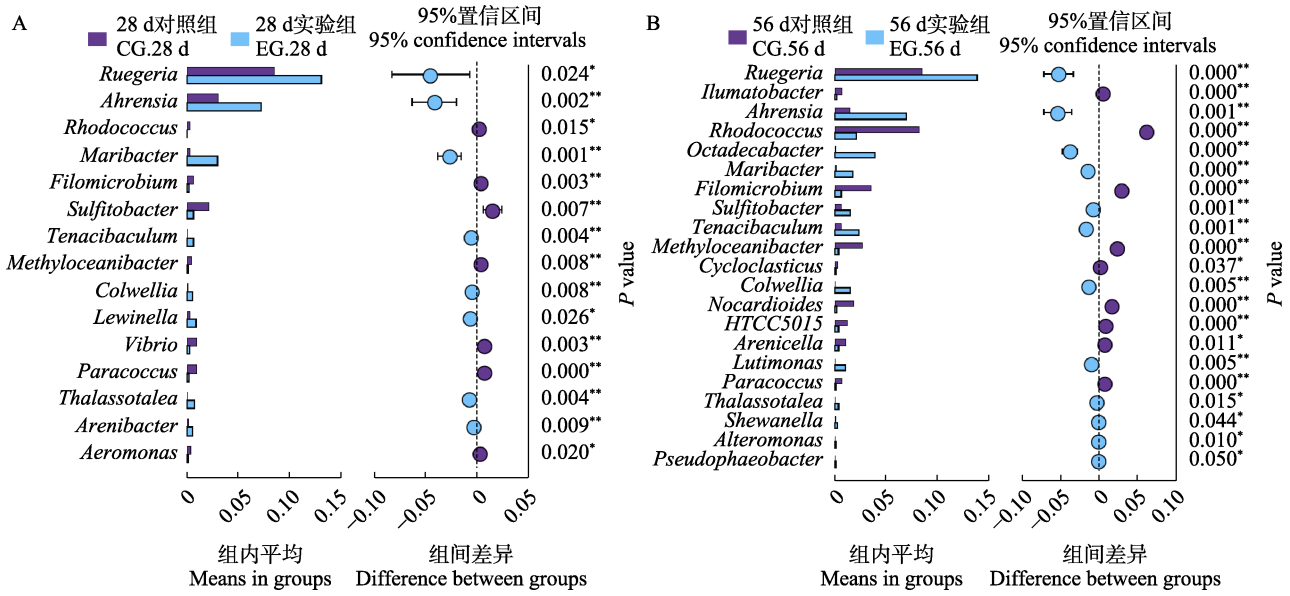

图 7　属水平微生物群落的 *T*-test 组间物种差异分析

Fig.7　*T*-test analysis of microbial communities at the genus level for species differences between groups

(A) 28 d 对照组与 28 d 实验组；(B) 56 d 对照组与 56 d 实验组。**表示差异极显著(P<0.01)；*表示差异显著(0.01<P<0.05)。

(A) CG.28 d and EG.28 d groups; (B) CG.56 d and EG.56 d groups. ** indicates highly significant difference (P<0.01); * indicates significant difference (0.01<P<0.05).

3　讨论

3.1　贻贝肽促进厚壳贻贝生长发育

研究已经证实，贻贝粉能够促进凡纳对虾(*Penaeus vannamei*)的生长(Claessens *et al*, 2023)。另外，饲料中添加 7.5 mg/kg 抗菌肽 APSH-07 也对鲍鱼(*Haliotis discus hannai*)的生长性能产生积极影响(Chen *et al*, 2020)。本研究证实了低浓度贻贝肽同样能够显著促进厚壳贻贝稚贝的生长，且提高了其存活率。不同蛋白质水平的饲料会对克氏原螯虾(*Procambarus clarkii*)的生长性能产生影响(郭赛等, 2023)；锦绣龙虾(*Panulirus ornatus*)摄食高蛋白、高脂颗粒饲料后生长良好，但摄食新鲜解冻的绿唇贻贝(*Perna canaliculus*)的软体组织对生长却没有促进作用(Barclay *et al*, 2006; Smith *et al*, 2005)。由此可见，蛋白质大分子在动物体内难以消化，其并未充分发挥作用就被排出体外。因此，易消化吸收的小分子贻贝肽在促进动物生长发育方面具有良好的研究和产业价值。

此外，贻贝肽营养组成中的 C2H2 锌指蛋白、ADP 核糖基化因子 4、α 微管蛋白白等组分是其发挥功效的重要原因之一(Nankervis *et al*, 2022)。C2H2 锌指蛋白，参与生长发育相关基因的调控、转录和表达(Seetharam *et al*, 2013)。ARF4 是哺乳动物 ADP-核糖基化因子(ARF)家族中的Ⅱ类蛋白，其在无脊椎动物中的作用尚不明确。以往研究发现，ARF 能通过与细胞生长调控蛋白结合来自由激活生长素从而响应基因的表达，进而促进生长发育(Yoon *et al*, 2010)。α 微管蛋白可以调节神经元的生长和再生，促进神经系统的发育(Gloster *et al*, 1994)。因此推测，贻贝肽促进稚贝生长发育可能是因为其组分中存在的生长发育相关的因子在发挥作用。然而，这些蛋白与基因之间的相互作用关系以及它们在生物体中发挥作用的具体机制仍需要进一步深入的研究。

3.2　贻贝肽改变厚壳贻贝微生物群落结构

海洋无脊椎动物的微生物群落组成对其生长发育具有重要作用(Ghanbari *et al*, 2015)。肠道微生物群落可以将原本无法消化的大分子化合物转化为可吸收利用的小分子代谢物(Danckert *et al*, 2021)，为海洋无脊椎动物提供丰富的消化酶并促进新陈代谢(Clements *et al*, 2014)，同时，还可以通过优化群落中的有益菌和潜在致病菌的菌群结构，为宿主提供健康保障(Ghanbari *et al*, 2015; Wang *et al*, 2018)。然而，目前贻贝的发育过程与微生物群落的关系尚不明确。

以往研究发现，水生生物的微生物群落结构与其摄食的不同饲料之间存在显著的相关性(Simon *et al*,

2020)。本研究发现，贻贝肽显著改变了厚壳贻贝的微生物群落。PCA 分析表明，贻贝肽的添加使厚壳贻贝微生物群落呈现差异。然而，稚贝养殖 28 d 后，CG.28 d 和 EG.28 d 的微生物群落组成相似；但在稚贝养殖 56 d 后，CG.56 d 与 EG.56 d 的微生物群落组成存在较大差异。这表明贻贝肽对稚贝微生物群落结构的改变是在 28 d 后才发挥作用。

研究表明，健康的贻贝以变形菌门为主(Cheikh *et al*, 2022)。同样，变形菌门也是本研究中的主要类群。添加贻贝肽后，拟杆菌门和变形菌门的丰度高于对照组，放线菌门的丰度则低于对照组。拟杆菌门可帮助宿主降解碳水化合物、蛋白质和大量宿主本身难以消化的其他物质，为宿主提供能量，促进生长，对生物体的健康平衡具有积极作用(刘艳霞等, 2023)。拟杆菌门中有许多种属能够作为益生菌用在水产养殖中发挥积极作用(Zhou *et al*, 2018)。肠道菌群组成结构的不平衡或不稳定通常会导致变形菌门的相对丰度的减少，例如，受病原体感染或生长缓慢的对虾肠道中变形菌门的数量通常较少(Holt *et al*, 2021)。

在添加贻贝肽的处理组中观察到有益菌属富集。黏着杆菌属和鲁杰氏菌属已被证实是厚壳贻贝生长发育过程中的核心物种，其中，黏着杆菌属形成的生物被膜能够诱导厚壳贻贝稚贝附着并且其诱导活性较高(杨娜等, 2017)。鲁杰氏菌属不仅可以对抗多种海洋病原体并限制其生长(Prol García *et al*, 2014；Sonnenschein *et al*, 2017)，而且能够合成对贻贝生长具有重要影响的维生素 B_{12} (Shiau *et al*, 1993)。亚硫酸盐杆菌属除了具有抗病毒和抗细菌的作用外(Long *et al*, 2011; Sharifah *et al*, 2012)，还能产生维生素 B_1、B_7 和 B_{12} 以及抗生素，对宿主的健康起到积极作用(Cheng *et al*, 2023)。科维尔氏菌属能够降解一些有机化合物(Krolicka *et al*, 2019)，是地中海贻贝(*Mytilus galloprovincialis*)受精卵和幼虫阶段最丰富的类群。这表明科维尔氏菌属伴随地中海贻贝的生长发育并为其提供营养和保护(Balbi *et al*, 2020)。有研究指出，科维尔氏菌属与太平洋牡蛎(*Crassostrea gigas*)的抗病性有关(Clerissi *et al*, 2020)。栖砂杆菌属的一些种类可产生具有抗生素活性的苯乙胺衍生物(Chen *et al*, 2013)。相对丰度较高的烂泥单胞菌属能促进凡纳对虾的生长(Tang *et al*, 2017)。居海杆菌属中的一些类群具有较高相对丰度的与碳水化合物代谢相关的基因，居海杆菌属相对丰度的升高标志着水质得到改善(Xie *et al*, 2017)。希瓦氏菌属不仅与鱼类的营养和抗病相关(Díaz-Rosales *et al*, 2009; Zadeh *et al*, 2010)，而且其形成的生物被膜具有诱导厚壳贻贝幼虫附着变态的作用(Yang *et al*, 2013)。假暗棕色杆菌属可以作为病原微生物的潜在拮抗剂(Feng *et al*, 2021)，用于对抗病原体，保护海参(*Apostichopus japonicus*)肠道(Zhang *et al*, 2023)，因此，假暗棕色杆菌属具有益生菌特性(Liang *et al*, 2021)。

贻贝肽可以降低稚贝微生物群落中致病菌属的相对丰度。例如，本研究中相对丰度下降的红球菌属是人类和动物的致病病原体(Prescott, 1991)，此外，气单胞菌属中大多数细菌种类被认为是广泛存在于水产养殖中的潜在传染性病原体，对鱼类、双壳贝类和人类具有致病性(Awan *et al*, 2018; Maki *et al*, 1998)。因此，贻贝肽可以通过提高有益菌相对丰度和降低致病菌相对丰度的方式来促进厚壳贻贝稚贝的生长发育。

综上，贻贝肽具有益生元的作用。以小分子易吸收的优势为前提，贻贝肽增加了厚壳贻贝稚贝微生物群落中鲁杰氏菌属、黏着杆菌属、居海杆菌属、栖砂杆菌属、十八碳杆菌属、亚硫酸盐杆菌属和希瓦氏菌属等益生菌的相对丰度，减少了红球菌属和气单胞菌属等潜在致病菌的相对丰度，通过优化厚壳贻贝微生物群落结构，从而促进厚壳贻贝稚贝生长发育。

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Effects of Mussel Peptides on Growth and Development and Microbial Community Structure of the Thick-Shelled Mussel *Mytilus coruscus* Plantigrades

LIN Qian[1,2,3], LI Zheng[1,2,3], YANG Jinlong[1,2,3①], MA Fan[1,2,3], LIANG Xiao[1,2,3]

(1. *International Research Center for Marine Biosciences, Ministry of Science and Technology, College of Fisheries and Life Science, Shanghai Ocean University, Shanghai* 201306, *China*; 2. *Shanghai Collaborative Innovation Center for Cultivating Elite Breeds and Green-Culture of Aquaculture Animals, Shanghai* 201306, *China*; 3. *China-Portugal Belt and Road Joint Laboratory on Space and Sea Technology Advanced Research, Shanghai* 200120, *China*)

Abstract　The thick-shelled mussel *Mytilus coruscus* belongs to Mollusca, Lanellibranchia, Anisomyaria, Mytilidae, and *Mytilus*. Due to its flavor and nutritional and high economic values, *M. coruscus* is a common commercial shellfish in the coastal area of Zhejiang and Fujian in China, and is an important cultured mussel species in China. With the increasing development of coastal areas and the changing habitat conditions, aquaculture industry of *M. coruscus* is facing problems such as slow growth of juvenile mussels, low meat production rate, and individual miniaturization of adult mussels, which affects the sustainable development of the mussel industry and economic income. Conversely, prebiotics are commonly used exogenous additives in aquaculture. Prebiotics help the organism to absorb nutrients by changing the morphology of the gastrointestinal tract and regulating the composition of the microbial community. They can promote the growth and development of aquatic organisms, enhance resistance to pathogenic bacteria, and improve the absorption and utilization rate of feed to increase the output of aquatic products. As a protein hydrolysate, mussel peptide is also a probiotic element with high nutritional value and multiple functions such as antimicrobial, antioxidant, and immune enhancement. In particular, low molecular weight mussel peptide has the function of anti-lipid peroxidation protective activity and scavenging of excess free radicals, which can be used as a natural antimicrobial food additive. In aquaculture, mussel peptides are considered to be natural active ingredients for treating infectious diseases in marine species. Till date, the relationship between mussel peptides and the growth and development of the thick-shelled mussel *M. coruscus* remains unclear. Therefore, the optimal concentration of mussel peptide for the potential application of mussel peptides in the *M. coruscus* aquaculture industry must be determined. In this study, we focused on the effects of mussel peptides on the growth and development of the thick-shelled mussel *M. coruscus* and on the structural composition of microbial communities. The

① Corresponding author: YANG Jinlong, Email: jlyang@shou.edu.cn

aim was to provide a theoretical basis for green and efficient aquaculture of the thick-shelled mussel *M. coruscus*. Here, the thick-shell mussel plantigrades used in the experiment were provided by Donghai Mussel Technology Innovation Service Co., LTD., Shengsi County, Zhejiang Province, China. It was used in the experiment after 1 week of temporary cultivation at 18 ℃ and a salinity of 30. Before the bioassays, these mussel plantigrades were cultured in the lab at 18 ℃ and 30 for 7 d. Five feeding treatment groups and one non-feeding control group were set up in the experiment. The treatment groups were fed mussel peptides at concentrations of 7, 9, 10, 70 and 90 mg/L, and each group was set up with three replicates. On days 7, 14, 21, 28, 42, and 56; 50 plantigrades were randomly selected from different treatment groups for growth measurement including shell length, shell height, and wet body weight. In addition, samples of plantigrades from different treatment groups were collected on days 28 and 56 to analyze the change in microbial communities before and after feeding. The results showed that, compared with the control group, feeding 9 mg/L of mussel peptides could significantly promote plantigrade growth and the shell length, shell height, and wet body weight were increased by 27.37%, 32.35%, and 115.49%, respectively. However, the mussel peptide concentration was too high (70 mg/L and 90 mg/L), which could cause lethal effects on the thick-shelled mussel *M. coruscus* plantigrades. The microbiome of the thick-shelled mussel plantigrades in the 28-day and 56-day treatment and control groups was analyzed by 16S rRNA gene amplification and sequencing. The results of the study showed that feeding 9 mg/L mussel peptides could alter the structural composition of the thick-shelled mussel plantigrade microbial community, such as increase in the abundance of Bacteroidota and Proteobacteria, and decrease in the abundance of Actinobacteriota. Simultaneously, an increase was observed in the diversity of beneficial bacteria such as *Ruegeria*, *Tenacibaculum*, *Maribacter*, *Arenibacter*, *Octadecabacter*, and *Shewanella* and reduction in the potentially pathogenic bacteria such as *Rhodococcus* and *Aeromonas*. Therefore, the appropriate amount of mussel peptides is useful for promoting the growth and development of the thick-shelled mussel *M. coruscus* plantigrades and optimizing their microbial community structure. In summary, mussel peptides have potential prebiotic functions and have the advantage of easy absorption of small molecules. By changing and adjusting the structure composition of the microbial community, mussel peptides increase the relative abundance of probiotics and reduce the relative abundance of potential pathogenic bacteria in the mussel microbial community of thick-shell mussel plantigrades, and promotes the growth and development of thick-shell mussel plantigrades. The current findings provide a basis and data support for the subsequent cultivation of marine bioactive peptides such as mussel peptides for enhancing shellfish juvenile aquaculture and the sustainable development of marine shellfish aquaculture.

Key words *Mytilus coruscus*; Growth; Microbe; Community composition; Mussel peptide