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The characteristics of the intestinal bacterial community from *Oreochromis mossambicus* and its interaction with microbiota from artificial fishery habitats

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Abstract

Background Artificial habitats can allow many fish to flock together and interact and have been widely used to restore and protect fishery resources. The piece of research intends to elucidate the relationship of microbial communities between tilapia (*Oreochromis mossambicus*) intestines and artificial fishery habitats (water and sediments). Hence, 16 S rDNA sequencing technology was used to study the bacterial communities from intestines, water, and sediments.

Results The results showed that the tilapia intestines had the lowest richness of Operational Taxonomic Units (OTUs) and the lowest diversity of the bacterial community compared to water and sediments. The intestine, water, and sediment microbial communities shared many OTUs. Overall, 663 shared OTUs were identified from the tilapia intestines (76.20%), the surrounding water (71.14%), and sediment (56.86%) in artificial habitats. However, there were unique OTUs that were detected in different sample types. There were 81, 77 and 112 unique OTUs observed in tilapia intestines, the surrounding water and sediment, respectively. Proteobacteria, Cyanobacteria, Actinobacteria, Firmicutes, Fusobacteria, and Bacteroidetes were the most common and dominant bacterial phyla between the tilapia intestines and habitats. In the two groups, the microbial communities were similar in the taxonomic composition but different in the abundance of bacterial phyla. Interestingly, Firmicutes increased, while Fusobacteria decreased in artificial habitats. These findings indicated that the artificial habitats had fewer effects on the water environment and indicated that the mode of artificial habitats could have an effect on the enriched bacteria in the tilapia intestines.

Conclusions This study analysed the bacterial communities of artificial habitats from the intestines, water, and sediments, which can explain the relationship between the tilapia intestines and habitats and strengthen the value of ecological services provided by artificial habitats.

Keywords Hydrobiology, 16S rRNA, tilapia, Microbial ecology

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1. Background

The *Oreochromis mossambicus* of tilapia has a high survival rate, strong disease resistance, adaptability to the environment, and rich protein content. Currently, it has become one of the main sources of animal protein [1–3]. Because of the extensive adaptability and strong fecundity in tilapias, *O. mossambicus* has become a dominant species in the Youjiang artificial habitats [4, 5]. Much research has been conducted on tilapia and fish-associated microbiota [6–8]. These studies have shown that fish-associated microbiota plays a crucial role in digestion, growth, and disease resistance [9–12]. For example, fish intestines are occupied by a variety of commensal and pathogenic microorganisms, which participate in the whole process of fish growth and development [13, 14]. Since fish live in the water environment, the composition and function of their intestinal microbiota will be strongly affected by their habitats [15]. In fact, fish intestine microbiota are enriched through those from the environment, thus completing the transfer process of microbiota from water to fish intestines [7, 16, 17]. It has been shown that the gut microbial compositions of fish, crabs, and shrimp are significantly affected by the surrounding habitats [18–20]. Most of these studies have been conducted by changing water conditions, feeding patterns, and increasing stress factors (e.g., varying temperature and dissolved oxygen). Indeed, it is rare to study the intestinal microbiota of tilapia based on complex artificial habitats. For tilapia living in artificial fishery habitats, the effects of habitat on host-related microbiota remain relatively unclear.

The role of an artificial fishery habitat is to imitate the characteristics of the natural habitat in water areas and to increase habitat heterogeneity under the condition of a single habitat [21]. Most research has clarified the role of artificial habitats in protecting fisheries, including enticing fish and improving fish abundance and biomass [22–26], providing spawning attachment substrates [27, 28], and offering a haven for juvenile fishes [29]. Additionally, when artificial habitats play these roles, they greatly affect the microbial communities in the fish intestines, water, and sediment. In recent years, researchers have conducted a few studies about the impact of artificial habitats on microbial diversity [30, 31]. However, studies on the relationship between the microbial communities of tilapia intestines and artificial fishery habitats are still rare. Although changes in feed nutrition are known to affect the environment and fish gut microbial composition [32–34], the differentiation of microbial communities between different host species remains to be clarified in unfed aquaculture systems.

In this research, we aimed to characterize the bacterial communities' relationship in the tilapia intestines and artificial habitats. The results indicated the following: (1) the compositions of bacteria in the tilapia intestines, water, and sediment were similar, while the relative abundance of bacteria varied, and (2) the microbial composition of tilapia intestines changed significantly under the influence of artificial habitats, despite no changes detected in the microbial composition of the surrounding water. This study provides new pieces of evidence for the role of artificial fishery habitats and puts forward insights into the composition, diversity, and function of tilapia intestinal microbiota, which can be affected by surrounding habitats.

2. Results

2.1 Overview of the OTUs and diversity analysis

A total of 4,601,275 sequence reads were generated by 16 S rDNA sequencing of the samples. The sequences were clustered into 830, 615, 913, 969, 1130, and 1239 OTUs from the AI, CI, AW, CW, AS, and CS, respectively (Table 1). The total intestinal OTUs were significantly different between AI and CI. The sediment groups (AS; CS) had a similar result, but there was no significant difference between the water groups (AW; CW).

The alpha-diversity indices were determined at the OTUs level to evaluate the diversity of the bacterial

Table 1 Overview of the high-throughput read analysis, including total OTUs and diversity statistics

Groups	Intestines		Water		Sediment	
	AI	CI	AW	CW	AS	CS
Total OTUs (97%)	830 ± 33 a	615 ± 21 b	913 ± 56 c	969 ± 49 c	1130 ± 101 c	1239 ± 99 d
Diversity indices						
Shannon	5.52 ± 0.27 a	4.34 ± 0.14 b	7.15 ± 0.48 c	7.22 ± 0.26 c	6.61 ± 0.08 c	6.93 ± 0.14 c
Simpson	0.0366 ± 0.0021 a	0.1573 ± 0.0018 b	0.0186 ± 0.0003 c	0.0147 ± 0.0005 c	0.0428 ± 0.0058 a	0.0125 ± 0.0043 d
Chao-1	855 ± 124 a	794 ± 96 a	932 ± 36 b	991 ± 59 b	1266 ± 106 c	1359 ± 218 c
Coverage	0.99 ± 0.01	0.99 ± 0.01	0.99 ± 0.01	0.99 ± 0.01	0.99 ± 0.01	0.99 ± 0.01

The OTUs and the bacterial community diversity analysis of all samples from intestines (I), water (W), and sediment (S) in artificial habitats (AI, AW, and AS) and control areas (CI, CW, and CS) are shown. The means ± SD data of Table 1 in the same row with different letters differ significantly ($P < 0.05$)

communities in all groups (Table 1). The Shannon index was in the range of 4.34 to 5.52 in the intestines, 7.15 to 7.22 in the water, and 6.61 to 6.93 in the sediment. The Simpson index was used to estimate the bacterial community dominance within a range of 0.1573 to 0.0366 in intestines, 0.0147 to 0.0186 in water, and 0.0125 to 0.0428 in sediment. The coverage was always kept at 0.99. These results indicated that tilapia intestines had the lowest OTU abundance and bacterial community diversity compared with the sampled habitats. The Chao-1 index was used to estimate bacterial community richness which ranged from 794 to 855 phylotypes in intestines, 932 to 991 phylotypes in water, and 1266 to 1359 phylotypes in sediment. There were no significant differences in the Chao-1 index.

Principal coordinate analysis (PCoA) by Bray-Curtis distances showed that bacterial communities from intestines and sediment were obviously divided (Fig. 1A and C), while bacterial communities in water were similar between the two habitats, with a certain degree of convergence (Fig. 1B). Moreover, the analysis revealed a stable clustering of microbial communities in habitats (Fig. 1D, E). These results revealed that the differences between fish gut groups were high and that the similarities between habitat groups were stable.

2.2 Taxonomic composition

The dominant bacterial phyla in the groups were Proteobacteria, Cyanobacteria, Actinobacteria, Firmicutes, etc. (Fig. 2). It was similar in taxonomic composition to the microbial communities, but the bacterial phyla distribution was different in abundance. In artificial habitats, the most abundant phylum was Proteobacteria in tilapia intestines, water, and sediment, with a relative abundance of 34.85% in the AI groups, 32.19% in the AW groups, and 41.36% in the AS groups. The second most abundant phylum was Cyanobacteria, with a relative abundance of 17.17% in the AI groups, 24.31% in the AW groups, and 33.15% in the AS groups. In control areas, Proteobacteria was also the most abundant phylum in tilapia intestines and habitats, with a relative abundance of 33.87% in the CI groups, 27.51% in the CW groups, and 43.52% in the CS groups. The second most abundant phylum was also Cyanobacteria, with a relative abundance of 10.12% in the CI groups, 23.42% in the CW groups, and 24.37% in the CS groups. In the tilapia intestine, Proteobacteria, Cyanobacteria, Actinobacteria, Firmicutes, and Fusobacteria were the five most dominant phyla in both habitats. The Fusobacteria abundance in tilapia intestines was higher when compared to that found in the surrounding habitats.

In artificial habitats, the closest relatives were separated into 218 genera of Proteobacteria, 55 genera of Cyanobacteria, 60 genera of Actinobacteria, 65 genera of Firmicutes, 63 genera of Bacteroidetes, and 124 genera of other phyla (Table 2). Meanwhile, in control areas, the closest relatives were divided into 215 genera of Proteobacteria, 53 genera of Cyanobacteria, 2 genera of Fusobacteria, 55 genera of Actinobacteria, 61 genera of Firmicutes, and 199 genera of other phyla (Table 3).

The bacterial OTUs in the tilapia intestines and habitats were investigated between two modes of habitats and are shown quantitatively in Fig. 3. In the mode of artificial habitats, a total of 663 collective OTUs were found among tilapia intestines, the surrounding water, and sediment (Fig. 3A), with an average of 76.20%, 71.14%, and 56.86% shared OTUs for the AI, AW and AS groups, respectively. In addition, 81, 77, and 112 unique OTUs were found in the intestines, water, and sediment, respectively.

In the control areas, 605 collective OTUs were detected in the intestines, water, and sediment (Fig. 3B). The number of shared OTUs accounted on average for 65.97%, 61.67%, and 48.05% of the total bacterial communities in the CI, CW, and CS groups, respectively. In addition, 81, 77 and 112 unique OTUs were observed in the intestines, surrounding water, and sediment, respectively.

2.3 Effects of artificial habitats on the bacterial communities of tilapia intestines, water, and sediment

This piece of research explored the effect of artificial habitats on the bacterial community, and the linear discriminant analysis effect size (LEfSe) method was used to identify differently enriched taxa between the artificial habitats (AH) and control areas without artificial structures (CW). At the taxonomic level, LEfSe could effectively analyse the data [35]. When the linear discriminant analysis (LDA) value setting was 2, there were 658 bacterial groups. To make the cladograms clearer, the LDA value was set to 4 [30, 36].

The dominant species in the bacterial community changed significantly (Fig. 4), while the LEfSe analysis revealed that artificial habitats influenced some biomarkers ($P < 0.05$, LDA > 4.0). There were 16 biomarkers enriched in intestines from the AI (Fig. 4A), including Actinobacteria, Alphaproteobacteria, Micrococcales, Peptostreptococcaceae, and *Rhodobacteraceae*. Moreover, there were 11 biomarkers enriched in intestines from the CI group (Fig. 4A), including Fusobacteria, Fusobacteriia, Fusobacteriales, Fusobacteriaceae, and *Cetobacterium*. The water samples had the lowest number of biomarkers. There were 7 bacteria biomarkers enriched in water samples from the AW groups (Fig. 4B), including Actinobacteria, Microtrichales, Ilumatobacteraceae, *Microbacterium*, and *CL500_29_marine_group* (at the genus level), among others. However, there were only two

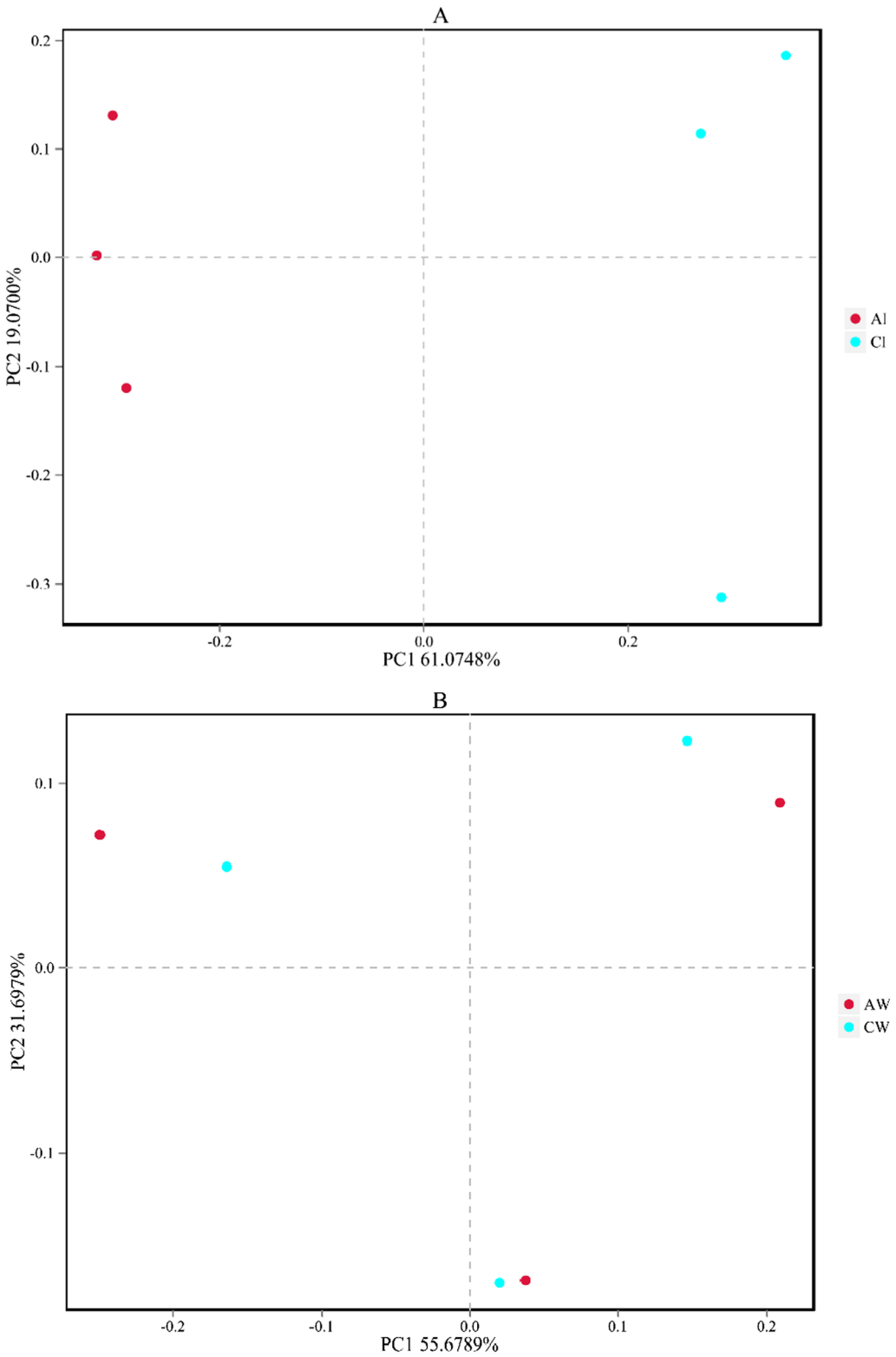
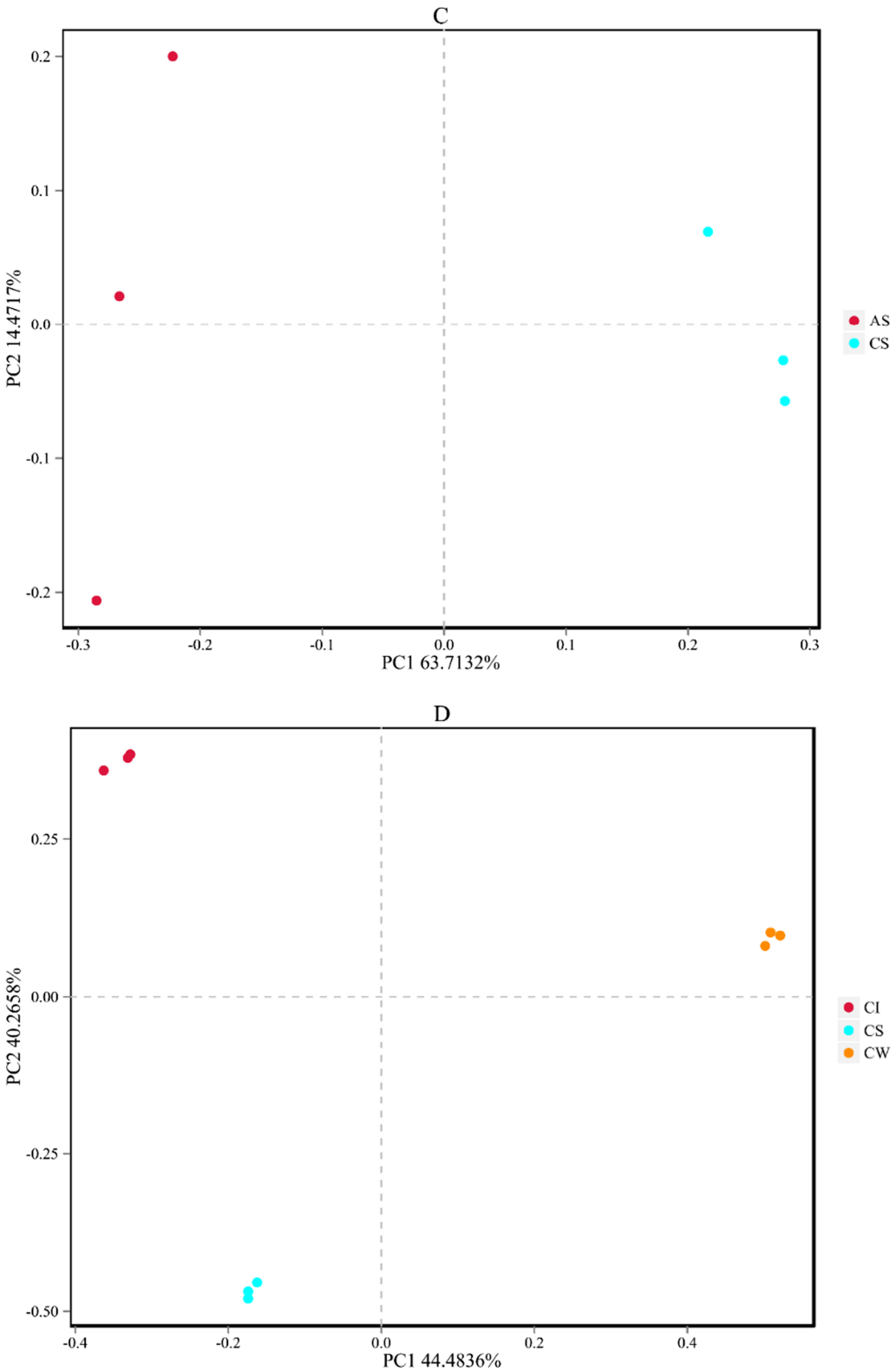


Fig. 1 The PCoA in intestines, water, and sediment samples between artificial habitats and control areas. Figure **A**–**C** provides comparisons of intestines, water, and sediment within different habitats. Figure **D** shows the comparison of bacterial communities in control areas. Figure **E** shows the comparison of bacterial communities in artificial habitats. AI, intestines of tilapia in the artificial habitats; AS, sediment in the artificial habitats; AW, water in the artificial habitats; CI, intestines of tilapia in the control areas; CS, sediment in the control areas; CW, water in the control areas



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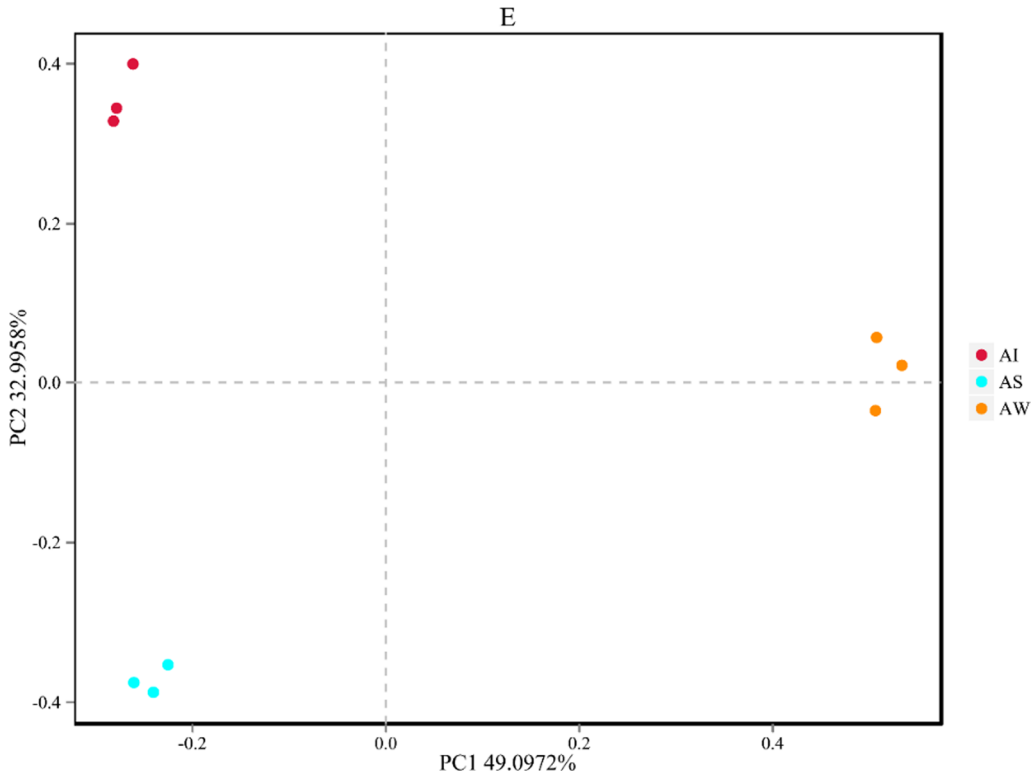

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bacteria biomarkers enriched in water samples from the CW group (Fig. 4B), namely, Bacteroidetes and Bacteroidia. The sediment samples had the highest number of biomarkers. There were 18 bacteria biomarkers enriched in sediment samples from the AS group (Fig. 4C), including Firmicutes, Bacilli, Bacillales, Pseudomonadales, Bacillaceae, and others. Moreover, there were 23 bacteria biomarkers enriched in sediment samples from the CS (Fig. 4C), including Alphaproteobacteria, Bacteroidetes, Betaproteobacteriales, Nostocales, Burkholderiaceae, and others.

4. Discussion

It is generally believed that the microbiota plays a crucial role in host nutrition and health [37–39]. Increasing evidence indicates that environmental microbes are associated with microbial digestive system diseases in the intestines of aquatic organisms (such as fishes, crabs, and shrimp) [17, 40, 41]. Studies to investigate the bacterial community composition in sediment [6], water [17], and tilapia intestines [7] have been previously conducted. Nevertheless, studies on the relationship of microbial communities between the tilapia intestines and artificial fishery habitats are still rare. Here, we attempt to elucidate the relationship between bacterial communities in intestines and habitats and then propose a method for studying bacterial communities in unfed aquaculture ecological systems. Moreover, we compared the bacterial community between fish intestines and the surrounding environment in artificial habitats.

The Shannon index was used to estimate the bacterial diversity, and the Simpson index was used to confirm it. There was a lower diversity in tilapia intestines when compared to the surrounding habitats ($P < 0.05$) (Table 1). It has been shown that the intestinal bacterial diversity is lower than that in water and sediment [6]. Similar results have been found for other aquatic organisms, including shrimps (*Litopenaeus vannamei* and *Litopenaeus stylirostris*) and crabs (*Eriocheir sinensis*) [19, 20, 42]. This study hypothesized that habitats would have a higher diversity compared to the intestines of tilapia due to environmental differences between habitats. However, the results showed that not all microbes in habitats could be ingested by the intestines of tilapia (Fig. 3). In fact, the tilapia intestines were less aerobic than water and sediment and had immunological factors that may select specific types of bacteria [43–46]. The intestines, water, and sediment exhibited marked similarities in the field of shared OTUs, core taxa, and composition. Shared OTUs were found for tilapia intestines, the surrounding water, and sediment, indicating that there are considerable microbes coexisting among these samples (Figs. 2

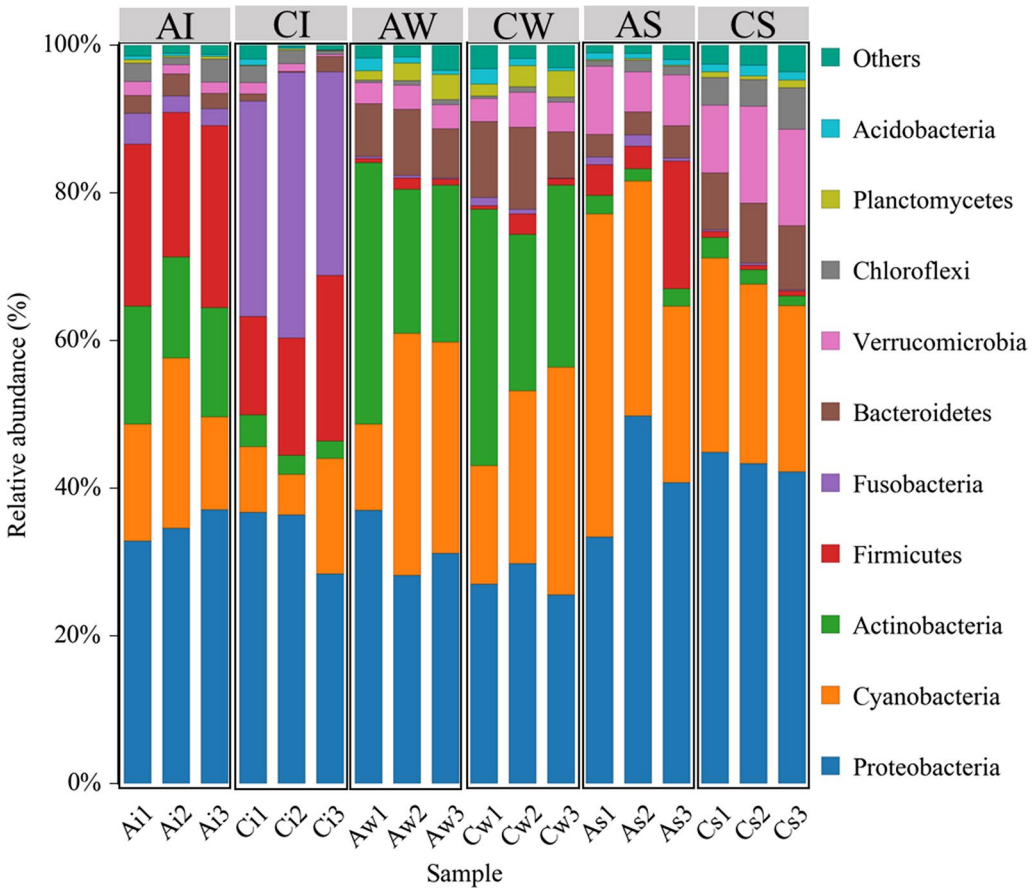

Fig. 2 Bacterial community composition at the phylum level in tilapia intestines, water, and sediment

Table 2 Genus level differences in dominant phyla in artificial habitats

Phylum	Numbers of genera	Genera
Proteobacteria	218 genera	*Rhodopila, Roseococcus, Rubritepida, Brevundimonas, Phenylobacterium*, etc.
Cyanobacteria	55 genera	*Limnothrix, Chlorotetraedron_incus, Leptolyngbya_PCC-6306*, etc.
Actinobacteria	60 genera	*Ilumatobacter, Brevibacterium, hgcI_clade, Brachybacterium*, etc.
Firmicutes	65 genera	*Bacillus, Fictibacillus, Allobaculum*, etc.
Bacteroidetes	63 genera	*Bacteroides, Alloprevotella, Runella*, etc.
Others	124 genera	*Bryobacter, Brevifollis, Luteolibacter*, etc.

Table 3 Genus level differences in dominant phyla in control areas

Phylum	Numbers of genera	Genera
Proteobacteria	215 genera	*Rhodopila, Roseococcus, Rubritepida, Methylobacterium, Arenimonas*, etc.
Cyanobacteria	53 genera	*Limnothrix, Prochlorococcus_MIT9313, Leptolyngbya_PCC-6306*, etc.
Fusobacteria	2 genera	*Cetobacterium, Hypnocyclicus*
Actinobacteria	55 genera	*Ilumatobacter, Micrococcus, Microbacterium, hgcI_clade*, etc.
Firmicutes	61 genera	*Blautia, Fictibacillus, Lactobacillus*, etc.
Others	199 genera	*Sulfurospirillum, Helicobacter, Gemmatimonas*, etc.

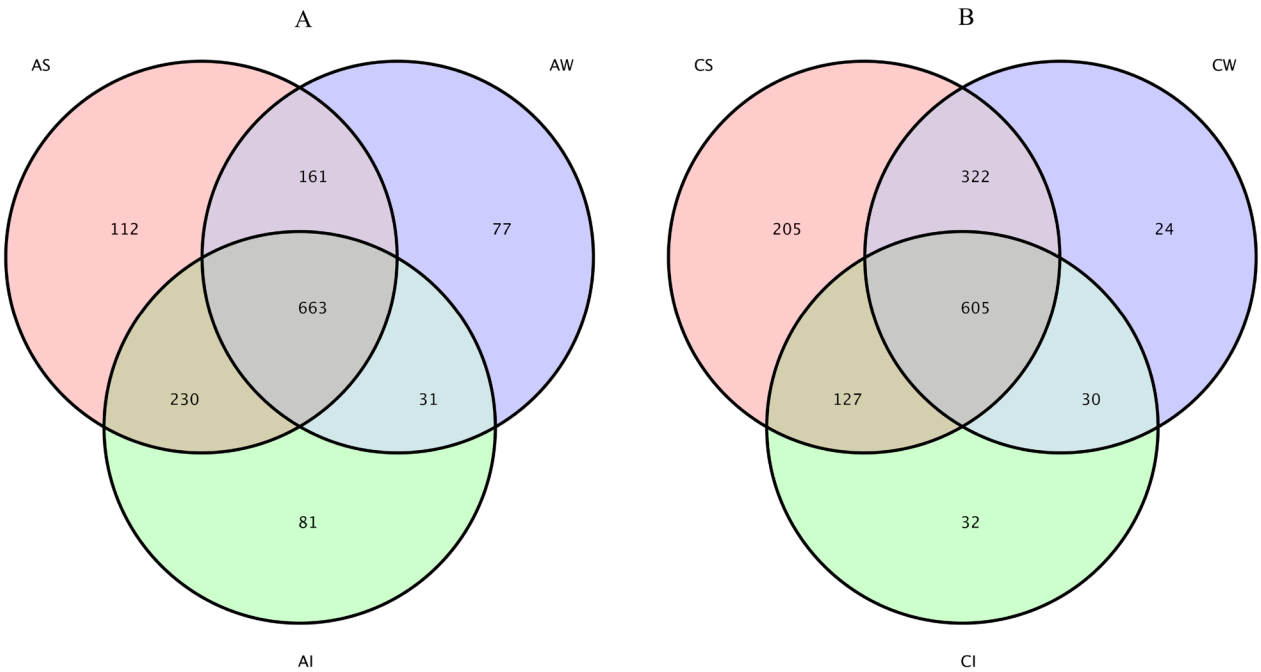

Fig. 3 **A** Venn plot showing OTUs overlap of the AI, AS and AW groups; **B** Venn plot showing overlap of the CI, CS, and CW groups. AI, intestines in artificial habitats; AS, sediment in artificial habitats; AW, water in artificial habitats; CI, intestines in control areas; CS, sediment in control areas; CW, water in control areas

and 3). In the artificial habitat, the dominant bacterial phyla in the groups were Proteobacteria, Cyanobacteria, Actinobacteria, Firmicutes, and so on. This was similar to the composition of bacteria in the tilapia intestines, water, and sediment, while the relative abundance of bacteria varied. Taking Firmicutes and Fusobacteria as examples, the relative abundance of bacteria in the intestines was significantly higher than that in the habitats. Firmicutes increased while Fusobacteria decreased in artificial habitats when compared to those of the control areas. Previous research has shown that Firmicutes can promote caloric extraction of ingested food substances and energy regulation [47, 48], while Fusobacteria is a potential intestinal pathogen that can cause inflammation and abdominal infection [49, 50]. Changes in tilapia intestinal microflora showed that artificial habitats could play a better role in promoting the growth of tilapia and decreasing the risk of infection.

The main difference between samples from different environments (intestine, water, and sediment) regardless of habitat was the relative abundance. Furthermore, there was a discrepancy in enriched bacteria within the same sample type under different habitats. LEfSe (LDA > 4.0) analysis found that the bacterial communities of the tilapia intestine had significant changes (Fig. 4). The relative richness of Actinobacteria (at the phylum level) was higher in AI than in CI, while Fusobacteria (at the phylum level) was significantly higher in CI than in AI (Fig. 4A). However, the microbial community changes in habitat samples were strikingly different under the two habitat modes. The water samples had the lowest numbers of biomarkers (Fig. 4B), while sediment samples had the highest (Fig. 4C). These results showed that the artificial habitat had a lower impact on the water environment and indicated that artificial habitats could affect enriched bacteria in the tilapia intestines. It is generally believed that the intestinal microflora of freshwater fishes comes from the environment [51], and differences in intestinal microflora among different habitats may be caused by bacteria gathered in specific habitats [36, 52].

Findings from this piece of research were consistent with results previously obtained by other researchers that showed a similar bacterial community composition between fish intestines and surroundings [6, 53]. In addition, the interaction between the intestinal bacterial community and the surrounding environment was associated with aquatic animal diseases [17, 54, 55]. Some potential pathogenic bacteria were also identified in the tilapia intestines and surroundings, such as *Flavobacterium* and *Pseudomonas* in water and *Vibrio* in the intestines, which may be linked to aquatic animal diseases. Indeed, *Vibrio* was shown to amplify the chance of Hepato pancreas necrosis syndrome (HPNS) outbreaks [40]. Our results showed that taxa and microbial diversities were

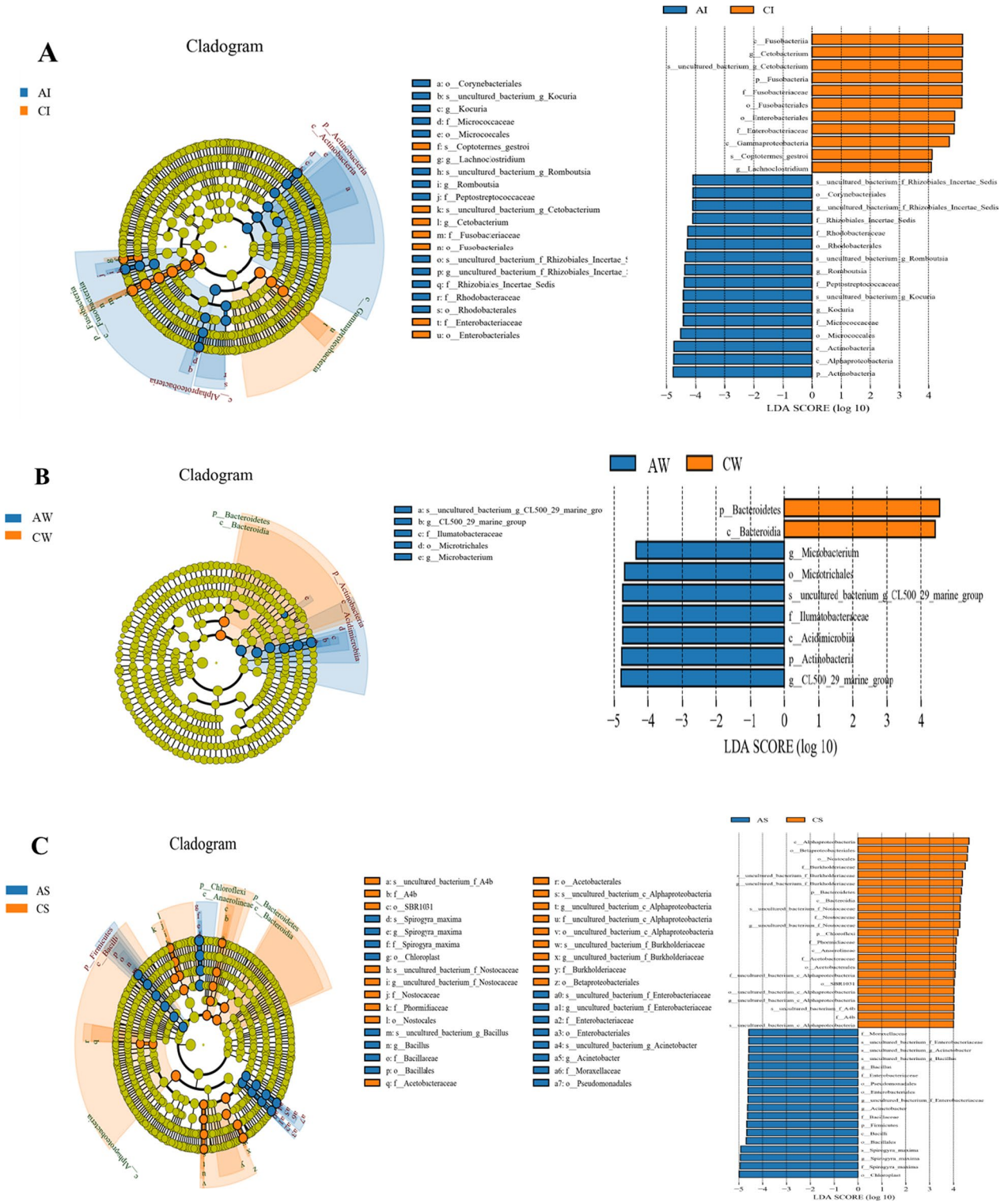

Fig. 4 LEfSe analysis ($P < 0.05$) of intestinal microflora (**A**), water (**B**), and sediment (**C**) between artificial and control habitats

significantly different between the tilapia intestines and habitat, demonstrating that the habitat mode may also affect the composition of the bacterial community in fish intestines and the surrounding environment. Altogether, the relationship between fish intestines and the surrounding environment still needs further investigation in addition to the influence of habitat change, including the role of environmental factors and food intake.

5. Conclusions

This research represented an attempt to study bacterial communities related to tilapia intestines, water, and sediment in artificial fishery habitats. In short, we generated profiles of microbial communities in tilapia intestines, water, and sediment. It was evident that the microbial community composition was similar, but the bacterial distribution abundance was different between habitats. The microbial composition of tilapia intestines changed significantly under the influence of artificial habitats; however, the microbial composition of water was unaffected. Overall, we provide insights into the relationship between bacterial communities in intestines and habitats. This study provides new scientific evidence for the role of artificial fishery habitats and provides insights into the composition, diversity, and function of tilapia microbiota, which strengthens the value of ecological services by artificial habitats.

6. Materials and methods

6.1 Study sites

The artificial habitats were located in the Youjiang River of the Pearl River Basin, China (23.46° N, 106.41° E). An unfed aquaculture program was previously carried out in this river. The artificial habitats were operated in the experimental site of the Youjiang River in December 2015 (Fig. 5) [4, 5].

6.2 Sample collection

Samples of the surrounding water, sediment, and tilapia intestines were collected from two distinctive habitats: artificial habitats (AH) and control areas without artificial structures (CW). A total of 180 tilapia were captured, 90 of which came from AH and 90 from CW. The large sample size excluded individual differences in experimental results.

Samples were collected from three random sites for each habitat, and the AH and CW samples were collected at the same time. Thirty samples were taken from each site, totalling 180 intestinal samples (from tilapias captured in artificial habitats AI1, AI2, and AI3, in control areas CI1, CI2, and CI3), 180 water samples (from AH groups AW1, AW2, and AW3, from CW groups CW1, CW2, and CW3) and 180 sediment samples (from AH groups AS1, AS2, and AS3, from CW groups CS1, CS2, and CS3). The entire intestines were sampled to minimize bias caused by the spatial structure [56]. Water samples (1000 mL) were filtered through a 0.22 μm membrane [57]. All the above experimental fish were anesthetized with a high concentration of 50 mg/L tricaine methanesulfonate MS-222 (Beijing Green Hengxing Biological Technology Co). and the surgery and sampling were made after a respiratory arrest.

All animal experimental protocols were approved by the Institutional Animal Care and Use Committee of Sun Yat-sen University, and all methods were carried out following relevant guidelines and regulations.

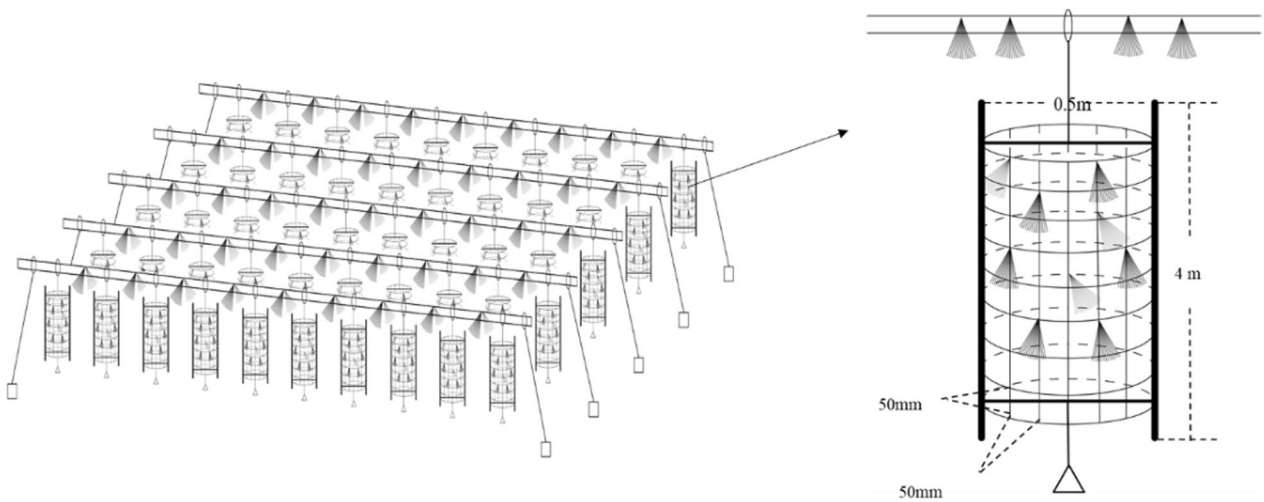

Fig. 5 Schematic diagram of the artificial habitats [5]

6.3 16 S rDNA sequencing and statistical analysis

V3-V4 hypervariable regions were amplified using the 338 F (ACTCCTACGGGAGGCAGCA) and 806R (GGACTACHVGGGTWTCTAAT) primers [58, 59]. The sequencing work was completed by HiSeq2500 at Biomarker Technologies Co., Ltd. (Beijing, China). The datasets analysed during the current study are available in the NCBI's GenBank Sequence Read Archive (PRJNA941103).

The diversity index was determined from the OTUs to compare the bacterial community diversity in all groups [60]. The bacterial diversity and OTU richness of habitats and intestines were compared by Kruskal–Wallis tests ($P < 0.05$). PCoA analysis was used to visualize the difference in groups by the R program. BMKCloud (https://international.biocloud.net/zh/dashboard) can be used to analyse Venn diagrams. LEfSe analysis was performed to identify indicator species also using the online BMKCloud.

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Author contributions
GL and GX conceived the study. GL and SB designed the experiments and drafted the work or revised it critically for important content. H. La, DG, HY, XL, QC, JC, H. Li and SB collected the samples and performed the experiments. H. La, DG, ZZ, XW, H. Li and SB analysed data and prepared the figures and tables. SB led the writing on the manuscript, with substantial contributions from GL, GX, HY and XL. QC, JC, ZZ, and XW managed the project and revise the manuscript. All the authors contributed critically to the drafts and approved the submitted version. All authors read and approved the final manuscript.

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Availability of data and materials
All sequence data have been uploaded to NCBI's GenBank Sequence Read Archive under accession number PRJNA 941,103.

Declarations

Ethics approval and consent to participate
This study was conducted with animal ethicsapproval of Sun Yat-sen University under a research permit(SYSU-IACUC-2020-B0423). We confirmed that all methods were reported followingthe ARRIVE guidelines (https://arriveguidelines.org) for the reporting ofanimal experiments. All methods were carried out in accordance with relevantguidelines and regulations.

Consentfor publication
Not applicable.

Competing interests
The authors declare that they have no conflicts of interest. This paper is contributed by the Sun Yat-senuniversity. The National Natural Science Foundation of China (Grant No. 31772853)takes part inthe design of the study and collection, analysis, interpretation of data.

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