

MICROBIAL DIVERSITY OF FERMENTED SEAFOOD PRODUCTS FROM MUNCAR, BANYUWANGI: INSIGHTS FROM 16S rRNA METABARCODING FOR BIOPROSPECTING AND FOOD SAFETY

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ABSTRACT

Fermented seafood products such as *petis*, salted fish, and *terasi* are integral to Indonesian cuisine, yet their bacterial community structures remain underexplored. This study utilized 16S rRNA-based metabarcoding to identify the microbial diversity in these products from Muncar, one of the largest fishing ports in Indonesia. The analysis revealed dominant genera, including *Ligilactobacillus*, *Kocuria*, *Weissella*, and *Staphylococcus*, many of which possess significant biotechnological potential. Notably, we identified bacteria capable of producing industrially valuable enzymes and metabolites, along with probiotic genera (*Limosilactobacillus*, *Weissella*) that have applications in food biotechnology. Conversely, opportunistic pathogens such as *Staphylococcus epidermidis*, *Cutibacterium acnes*, and *Enterococcus faecalis* were detected, highlighting the need for improved hygiene practices. By linking microbial biodiversity to both bioprospecting opportunities and food safety challenges, this work advances the understanding of traditional fermentation ecosystems while providing actionable insights for optimizing food quality and safety in artisanal production.

Keywords: 16S rRNA metabarcoding, Fermented seafood, Biodiversity, Food safety, Probiotics, Indonesia

INTRODUCTION

Indonesia, an archipelagic nation, is endowed with vast marine biodiversity, making it one of the world's leading seafood producers (Tran *et al.*, 2017). Marine resources are a cornerstone of the national economy, contributing significantly to livelihoods, nutrition, and trade. In addition to fresh seafood, Indonesia produces a variety of processed seafood products, including shrimp paste, fish chips, and salted fish, which are staples of local diets and cultural heritage (Prihanto & Muyasyaroh, 2021). Among the prominent fishing centers in Indonesia is the Muncar subdistrict, Banyuwangi, one of the largest fish producers in the country, highlighting its critical role in the seafood supply chain (Umroh *et al.*, 2020).

Muncar, a major Indonesian fishing hub, relies on traditional small-scale seafood processing, with fermented products like salted fish, *terasi* (sun-dried fermented shrimp paste), and *petis* (fermented shrimp/fish paste) being central to local cuisine and livelihoods. These three products were selected for their cultural and economic significance, representation of distinct fermentation processes, and understudied microbial profiles. Salted fish, preserved through dry salting, exemplifies halotolerant microbial communities critical to preservation and flavor development. *Terasi*, a sun-dried shrimp paste, undergoes semi-solid fermentation driven by complex microbial interactions, while *petis*, a thick condiment, relies on prolonged shrimp or fish fermentation in carbohydrate-rich substrates (Herlina & Setiarto, 2024; Surya *et al.*, 2024).

These products harbor complex microbial communities, some of which provide functional benefits. For example, lactic acid bacteria (LAB) often isolated from fermented seafood products are associated with health-promoting properties such as improved gut microbiota, antimicrobial activity, and potential immunomodulatory effects (Narzary *et al.*, 2021; Nofiani *et al.*, 2022). LAB have been widely reported in Indonesian seafood products, such as salted fish (Karyantina *et al.*, 2020), fermented fish, shrimps, and marine worms, where they play an important role in fermentation, preservation, and flavor enhancement (Mahulette & Kurnia, 2020; Prihanto *et al.*, 2021).

However, artisanal production practices often lack strict hygiene protocols, increasing the risk of contamination by pathogenic bacteria. Pathogens such as *Escherichia coli*, *Salmonella* spp., and *Listeria monocytogenes* are frequently detected in inadequately processed seafood, posing significant health risks to consumers (Axelsson *et al.*, 2020; Roy *et al.*, 2024). While previous studies have focused on these pathogens, there remains a critical gap in understanding the full

microbial ecology of traditional fermented seafood like *petis*, salted fish, and *terasi*. These products host complex microbial communities that include not only hazards but also undercharacterized beneficial taxa with biotechnological potential, such as probiotic lactic acid bacteria or enzyme-producing strains. By mapping both risks and microbial resources, this study bridges the gap between food safety and the preservation of artisanal fermentation ecosystems, offering actionable strategies to enhance product quality while enabling the bioprospecting of industrially valuable microorganisms.

Advances in next-generation sequencing (NGS) techniques, particularly 16S rRNA gene-based metabarcoding, have revolutionized the characterization of microbial communities in food. This high-throughput approach allows for comprehensive profiling of bacterial diversity and abundance, enabling the simultaneous detection of both beneficial and harmful taxa (Maria Sirangelo & Calabrò, 2020; Parente *et al.*, 2022). Recent studies have successfully used metabarcoding to analyze the microbial composition in various fermented products, such as fish paste, cheese, and kimchi, demonstrating its efficacy in revealing the dynamics of microbial communities (Helmi *et al.*, 2022a; Jung *et al.*, 2022; Levante *et al.*, 2021).

This study aims to use 16S rRNA-based metabarcoding to elucidate the bacterial community structure in *petis*, shrimp paste, and salted fish from Muncar, Banyuwangi. By identifying both beneficial and harmful bacteria, the results will provide valuable insights into microbial ecology, inform strategies to improve food safety, and support the sustainable production of these culturally important seafood products.

MATERIAL AND METHODS

Genomic DNA Extraction

Sampling was conducted in October 2024. Samples of *petis* (fish paste), *terasi* (sun-dried fermented shrimp paste), and salted fish (*Auxis rochei*) were purchased from three different vendors at Muncar Harbor, Banyuwangi, Indonesia. All samples were made using the same type of shrimp and fish species based on information provided by the vendors. The samples were transported in sealed, sterile containers under chilled conditions (4°C) to maintain their integrity. Upon arrival at the laboratory, samples of the same type were homogenized to obtain a representative composite sample for each product. Genomic DNA was extracted

using the ZymoBIOMICS DNA Miniprep Kit (Zymo Research, Cambridge, UK). DNA concentration was quantified using both a NanoDrop spectrophotometer and a Qubit fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). DNA quality was evaluated via agarose gel electrophoresis, and the DNA bands were visualized using the Gel-Doc EZ imaging system (Bio-Rad, Hercules, CA, USA).

Amplification of the 16S rRNA V1-V9 Region

To identify bacterial communities, the hypervariable V1-V9 regions of the 16S rRNA gene were amplified using universal primers 27F and 1492R at a final primer concentration of 10 μ M. The PCR was conducted using MyTaq™ HS Red Mix 2X (Bioline, Essex, UK) under the following conditions: initial denaturation at 95°C for 3 minutes, followed by five cycles of 95°C for 15 seconds, 55°C for 15 seconds, and 72°C for 30 seconds. Subsequently, 30 cycles of 95°C for 15 seconds, 62°C for 15 seconds, and 72°C for 30 seconds were completed, with a final extension at 72°C for 1 minute.

Library Preparation and Sequencing

Sequencing libraries were generated using the Native Barcoding Kit 24 V14 (SQK-NBD114.24) from Oxford Nanopore Technologies (Oxford, UK). A total of 130 ng of the amplified 16S rRNA product was used for full-length sequencing. The library was sequenced using an R9.4 flow cell on the GridION platform (Oxford Nanopore Technologies, UK). Basecalling and data collection were performed using MinKNOW software version 22.05.7.

Bioinformatic Analysis

Basecalling of raw sequencing data was performed using Guppy version 6.1.5 with the high-accuracy model (Wick et al., 2019). The quality of sequencing reads was analyzed using NanoPlot (De Coster et al., 2018). Taxonomic assignments were made using Centrifuge (D. Kim et al., 2016) and a customized bacterial and

archaeal index constructed from the NCBI 16S RefSeq database. Visualization and downstream data analysis were performed with Pavian, Krona Tools, and RStudio, using R version 4.2.0 for R-based analyses.

RESULTS AND DISCUSSION

Metagenomic Data

The bacterial diversity in fermented seafood products was analyzed by sequencing the hypervariable V1-V9 regions of the 16S rRNA gene. This gene, which is highly conserved and specific to bacteria and archaea, serves as a robust marker for identifying microbial communities in various samples, including food products (Bahram et al., 2019). Sequencing the full-length 16S rRNA gene, encompassing all variable regions, enables detailed taxonomic and phylogenetic resolution, facilitating precise identification of bacterial species (Fang et al., 2015).

To evaluate bacterial diversity, Shannon and Simpson diversity indices were applied, quantifying both species richness (the number of species present) and evenness (relative species abundance). Additional metrics, including observed species count, Chao1, and abundance-based coverage estimators (ACE) indices, were used to further assess species richness. Figure 1 illustrates the values for these diversity indices, highlighting that salted fish exhibited the highest bacterial diversity, followed by *petis* and *terasi*. Specifically, the Shannon and Simpson indices indicated that salted fish contained a significantly more diverse bacterial community compared to *petis* and *terasi*. The observed species counts and ACE estimates further confirmed that salted fish harbors the richest and most diverse bacterial community, likely a consequence of its simple dry salting process without added fermentation starters, which allows a wider array of environmental and halotolerant bacteria to persist (B.-K. Kim & Kim, 2023). In contrast, the concentrated fermentation and heat-treatment steps used in *petis* and *terasi* selectively promote shrimp-derived lactic acid bacteria, thereby limiting overall community complexity (Surya et al., 2023).

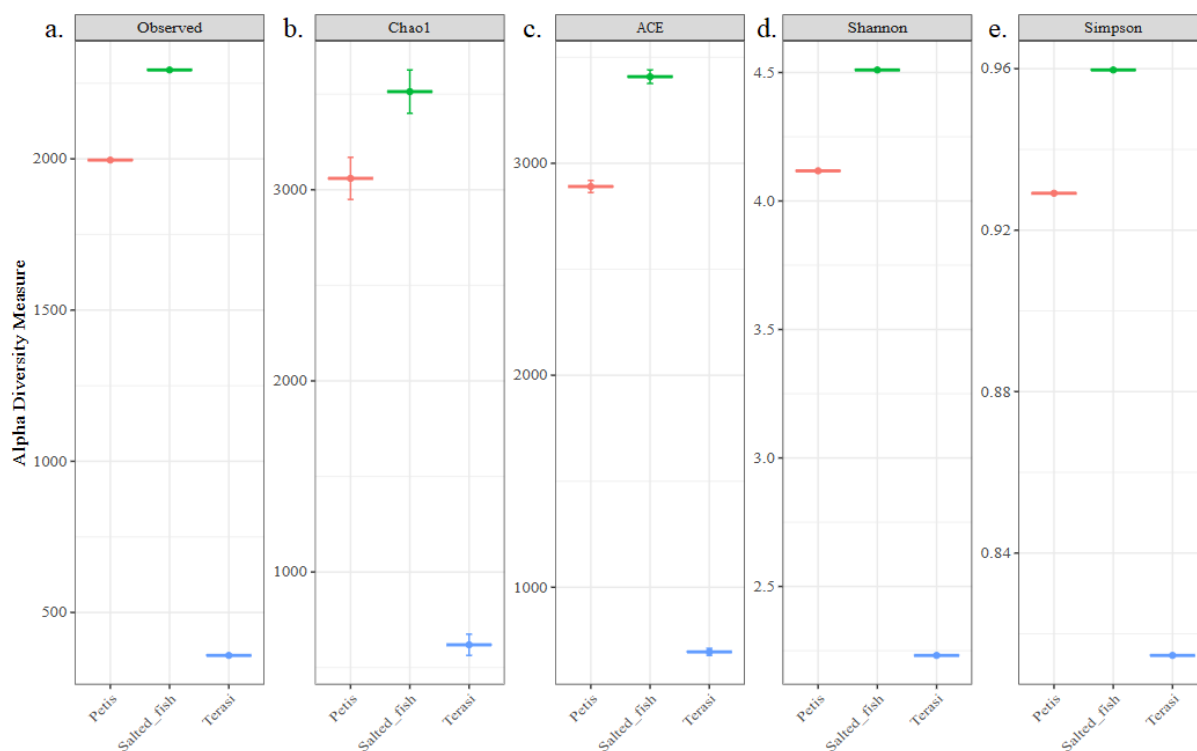


Figure 1 Diversity index box plot for bacterial communities in *petis*, salted fish, and *terasi*. a: Observed species index; b: Chao1 index; c: ACE index; d: Shannon index; e: Simpson index.

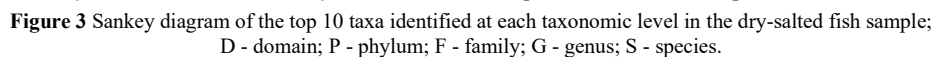
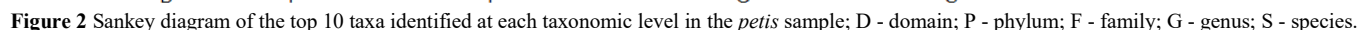
Bacterial Diversity

To date, no reports have been made on the bacterial community structure in *petis*. *Petis* is a unique fermented seafood product whose bacterial taxa are primarily dominated by the genera *Atopostipes* and *Staphylococcus* (Figure 2). *Atopostipes*, a lactic acid bacterium, and *Staphylococcus* are commonly associated with fermented seafood products such as alkaline-fermented skates and sharks (Jang et al., 2017; Jensen et al., 2023).

In *petis* samples, three dominant species from the genus *Staphylococcus* were identified: *S. simulans*, *S. epidermidis*, and *S. pasteurii*. *S. simulans*, a normal flora of human skin, has previously been detected in fermented foods such as traditional Italian and Chinese sausages, as well as *budu*, a Southeast Asian fermented fish product (Casaburi et al., 2005; Kanjan & Sakpetch, 2020; M. Sun & Ning,

2021). This species is recognized as a potential producer of nitrate reductase and lipase enzymes (J. Sun et al., 2019). Moreover, *S. simulans* exhibits medical potential, including the inhibition of methicillin-resistant *Staphylococcus aureus* and protective activity for skin health (Brown et al., 2020). *S. epidermidis*, another human skin commensal, has also been isolated from fermented foods, including *lanhouin* (a West African fermented fish product) and *miso* (a Japanese fermented soybean product) (Kindossi et al., 2021; Shirasawa et al., 2023). Meanwhile, *Staphylococcus pasteurii* has been isolated from fish sauce and fermented jellyfish products (Ma et al., 2021; Ramirez et al., 2022).

Other bacteria associated with fermentation, such as *Tetragenococcus*, were also detected in *petis*. *Tetragenococcus* is known as a key fermentative bacterium in seafood-based fermented products (Belleggia & Osimani, 2023). Additionally, *Salinicoccus*, which is frequently found in Asian fermented fish products, was



Fish Species	Origin	Dominant Bacterial Genera	References
Bullet tuna (<i>Auxis rochei</i>)	Muncar, Banyuwangi, Indonesia	<i>Kocuria</i> , <i>Lentibacillus</i> , <i>Enterococcus</i> , <i>Ligilactobacillus</i> , <i>Limosilactobacillus</i> , <i>Weisella</i> , <i>Staphylococcus</i> , <i>Streptococcus</i> , <i>Bartonella</i> , <i>Enterobacter</i>	This study
Ribbon fish (<i>Trichiurus haumela</i>)	Bangladesh	<i>Photobacterium</i> , <i>Psychrobacter</i> , <i>Vibrio</i> , <i>Shewanella</i> , <i>Cetobacterium</i> , <i>Staphylococcus</i>	(Bahrndorff <i>et al.</i> , 2022)
Flatfish dab (<i>Limanda limanda</i>)	Denmark	<i>Photobacterium</i> , <i>Psychrobacter</i> , <i>Pseudoalteromonas</i> , <i>Staphylococcus</i>	
Cod (<i>Gadus</i> sp)	Iceland	<i>Photobacterium</i> , <i>Psychrobacter</i> , <i>Vibrio</i> , <i>Kocuria</i> , <i>Carnobacterium</i>	
Black carp (<i>Mylopharyngodon piceus</i>)	Zhejiang, China	<i>Staphylococcus</i> , <i>Macrococcus</i> , <i>Acinetobacter</i>	(Zhang <i>et al.</i> , 2021)
Grass carp (<i>Ctenopharyngodon idellus</i>)	Hangzhou, China	<i>Cobetia</i> , <i>Staphylococcus</i> , <i>Ralstonia</i>	(Zhao <i>et al.</i> , 2022)

Ligilactobacillus, a lactic acid bacterium, is recognized for its probiotic properties, particularly its ability to promote digestive health (O. Liu *et al.*, 2024; Shen *et al.*,

2024). Notably, this genus has not been previously reported in seafood fermentation products. Other lactic acid bacteria identified in salted fish include *Limosilactobacillus* and *Weissella*. Both genera are known for their probiotic properties, including antimicrobial and immunomodulatory activities, and are commonly used in fish and fish sauce fermentation (E. Kim *et al.*, 2022; Kingkaew *et al.*, 2023; Prima *et al.*, 2022; Teixeira *et al.*, 2021). *Kocuria* is another noteworthy genus found in salted fish and is known for its potential to produce industrial enzymes, biosurfactants, and carotenoids (de Paiva Anciensi Ramos *et al.*, 2021; Ghasemi *et al.*, 2024). In food-related studies, *Kocuria* has been isolated from milk, cheese, sake, and carp fermentation products (Terasaki *et al.*, 2021; Zang *et al.*, 2022).

To our knowledge, this study represents the first comprehensive analysis of the bacterial community in dry-salted *Auxis rochei*. The dominant genera identified

here show a unique composition compared to other tropical marine dry-salted fish, such as those from Bangladesh, and even those from colder regions like the North Atlantic and North Sea (e.g., Denmark and Iceland) (Table 1). This distinct microbial profile also differs from dry-salted freshwater species, such as grass carp and black carp, highlighting how ecological and processing factors shape bacterial communities (Department of Food Science Foshan 528137 China *et al.*, 2025). Notably, *Staphylococcus* was consistently dominant across all studied products, regardless of fish species or geographic origin. Known for thriving in high-salinity environments, this genus also contributes to flavor development. Its lipase and protease enzymes break down fats and proteins into free fatty acids and amino acids, compounds that shape the distinct savory and aromatic qualities of fermented dry-salted fishes (J. Liu *et al.*, 2023).

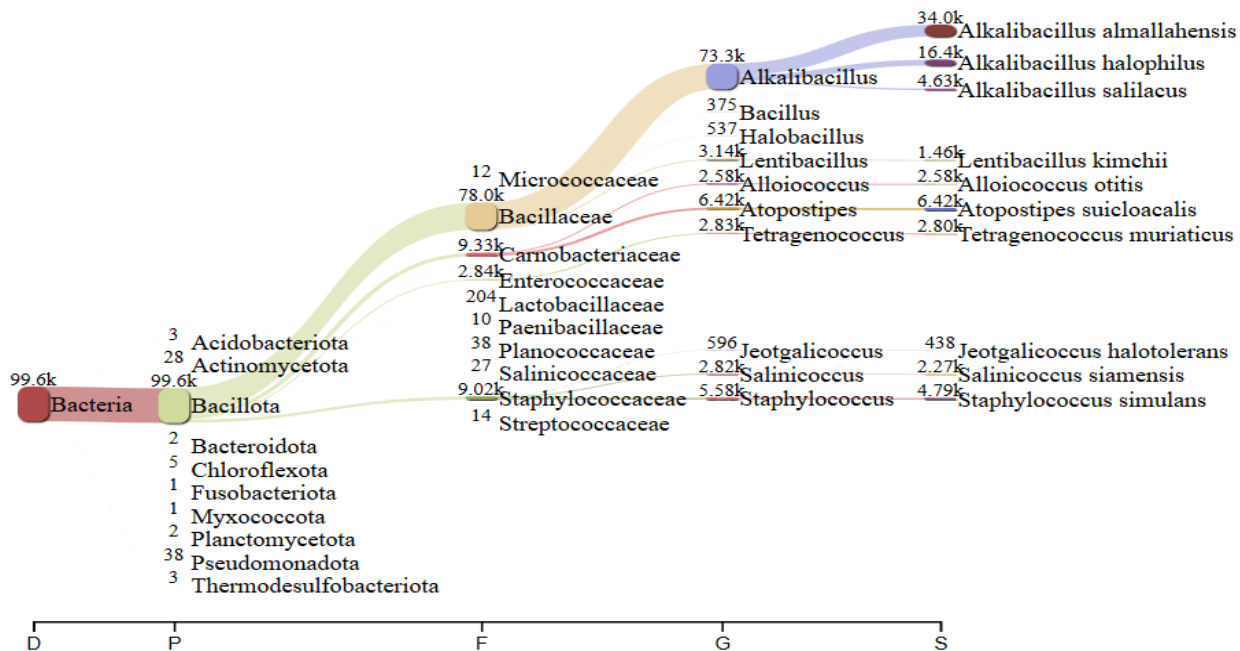


Figure 4 Sankey diagram of the top 10 taxa identified at each taxonomic level in the *terasi* sample; D - domain; P - phylum; F - family; G - genus; S - species.

Table 2 Top genera observed in *terasi* from this study and other studies.

Sample	Dominant Bacterial Genera	References
<i>Terasi</i> from Muncar, Banyuwangi, East Java, Indonesia	<i>Alkalibacillus</i> , <i>Bacillus</i> , <i>Halobacillus</i> , <i>Lentibacillus</i> , <i>Alloiococcus</i> , <i>Atopostipes</i> , <i>Tetragenococcus</i>	This study
<i>Terasi</i> made from <i>Acetes japonicus</i> with 5% salt concentration	<i>Tetragenococcus</i> , <i>Alloiococcus</i> , <i>Alkalibacillus</i> , <i>Atopostipes</i> , <i>Alkalibacterium</i>	(Helmi <i>et al.</i> , 2022b)
<i>Terasi</i> made from <i>Acetes</i> sp. with a 5% salt concentration	<i>Vibrio</i> , <i>Macroccoccus</i> , <i>Staphylococcus</i> , <i>Exigubacterium</i> , <i>Jeotgaliococcus</i> , <i>Salinococcus</i> , <i>Bacillus</i> , <i>Pseudoarthrobacter</i> , <i>Vagococcus</i>	(Utama <i>et al.</i> , 2025)
<i>Terasi</i> made from <i>Acetes japonicus</i> with 10% and 15% salt concentration	<i>Alkalibacillus</i> , <i>Alkalibacterium</i> , <i>Tetragenococcus</i> , <i>Salimicrobium</i> , <i>Staphylococcus</i> , <i>Corticococcus</i> , <i>Alkalibacterium</i> , <i>Lentibacillus</i>	(Helmi <i>et al.</i> , 2024)

Meanwhile, *terasi*, one of Indonesia's most extensively studied fermented seafood products, is dominated by *Alkalibacillus*, *Staphylococcus*, and *Tetragenococcus* (Figure 4). These three genera are consistently reported as dominant across multiple studies of *terasi* (Table 2). *Alkalibacillus* and *Staphylococcus* contribute to *terasi*'s distinct aroma and flavor through proteolytic and lipolytic activities, which generate volatile low-molecular-weight compounds such as peptides, amino acids, fatty acids, and aldehydes (Helmi *et al.*, 2024). *Tetragenococcus*, a

halophilic lactic acid bacterium, enhances both flavor development and preservation via proteolysis and lactic acid production (Prihanto *et al.*, 2024). These findings highlight the diverse and potentially valuable bacterial communities present in *petis*, salted fish, and *terasi* from Muncar. These bacteria not only contribute to the fermentation process but also have potential for biotechnological applications. Future studies should focus on isolating these promising bacteria using specific media to develop them as probiotics, producers of industrial enzymes, and valuable metabolites, as well as standardized starters for fermented foods.

Our analysis also revealed the presence of opportunistic pathogens of human origin. *Petis* harbored *Staphylococcus epidermidis* and *Cutibacterium acnes*, while dry-salted fish contained *S. epidermidis* and *E. faecalis*. These findings align with studies reporting *S. epidermidis* as a common contaminant in high-protein fermented foods due to its biofilm-forming capacity in nutrient-rich environments (Podkowik *et al.*, 2016; Sabat  Bresc  *et al.*, 2017), whereas *C. acnes*, typically associated with human skin microbiota, may reflect cross-contamination during manual processing (Mollerup *et al.*, 2016). The detection of *E. faecalis*, a known opportunistic pathogen with antibiotic resistance traits (Rana *et al.*, 2023), in dry-salted fish raises public health concerns, particularly given its persistence in high-salt matrices (Ullah *et al.*, 2024).

The higher prevalence of *C. acnes* in *petis* compared to dry-salted fish may stem from differences in raw material handling, as *petis* production involves prolonged exposure to ambient conditions during shrimp paste fermentation. In contrast, the dominance of *E. faecalis* in dry-salted fish likely reflects its halotolerance and ability to colonize protein-rich substrates (Heo *et al.*, 2019). The presence of these bacteria poses challenges for scaling up production, as they may not meet food quality and safety standards.

While this study advances our understanding of the microbial ecology of Muncar's fermented seafood, several limitations warrant consideration. The current findings are derived solely from taxonomic presence data and, therefore, must be complemented by strategic isolation efforts. Future research should focus on isolating and characterizing key microorganisms for three primary applications: industrial enzyme production, probiotic strain development, and the formulation of defined starter cultures to facilitate the standardization and quality enhancement of fermented seafood products. At the same time, traditional artisanal practices will be preserved, with producers equipped with comprehensive profiles of both beneficial and potentially pathogenic bacteria to inform targeted hygiene

improvements and strengthen the marketing of their products' health and quality attributes.

CONCLUSION

This study successfully characterized the bacterial diversity of Muncar's traditional fermented seafood products (*petis*, dry-salted fish, and *terasi*) using 16S rRNA-based metabarcoding, assess their microbial safety, and identify taxa with biotechnological potential. Our methodology revealed distinct, product-specific bacterial profiles shaped by raw materials and fermentation conditions. Key findings include: the dominance of *Priestia flexa* in *petis* and *Ligilactobacillus* in dry-salted fish, novel observations in seafood fermentation, with implications for probiotic development, enzyme production (e.g., proteases, lipases), and bioplastic biosynthesis; the detection of opportunistic pathogens (*Staphylococcus epidermidis*, *Cutibacterium acnes*, *Enterococcus faecalis*), highlighting hygiene-related risks in artisanal production. These results underscore the dual novelty of our work: resolving previously unreported microbial dynamics in Indonesian fermented seafood products and demonstrating how 16S metabarcoding can simultaneously advance food safety surveillance and bioprospecting. To translate these findings, we recommend targeted isolation of beneficial strains for starter cultures, coupled with hygiene optimization to mitigate pathogen risks, ensuring these culturally significant products meet modern safety and market standards.

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