A modern scientific perspective on the flavor and functional properties of diverse teas in traditional cuisine "tea-flavored fish": From macroscopic quality to microscopic variations

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ABSTRACT

The historical appreciation of tea dates back to ancient times, while technological limitations have long hindered in-depth exploration of its flavor complexity and functional attributes. This study investigated the effects of various teas on a traditional delicacy, "tea-flavored fish", using teas processed via traditional methods. Analysis of functional components revealed that processing and fermentation reduced catechin levels (186.3 mg/g to 58.8 mg/g) while increasing theaflavins (16.6 mg/g to 39.6 mg/g), leading to decreased antioxidant and anti-microbial activities. Tea flavored fish was prepared following traditional techniques. The results indicated that the teas preserved their sensory qualities such as texture and color, inhibited metabolic activity and microbial growth, delayed lipid oxidation and protein degradation, and inhibited biogenic amine accumulation. Furthermore, minor compositional variations were observed in the final product. These findings offer novel insights into the application of modern scientific concepts to elucidate the principles underlying traditional craftsmanship.

1. Introduction

Tea, derived from the leaves of the *Camellia genus*, is one of the most widely consumed beverages worldwide, celebrated for its refreshing and healthful properties. Its versatility allows for diverse preparations — liquid, paste, or powder, served hot or cold, and enhanced with sugar, milk, or lemon — catering to various occasions and preferences (Dasdemir et al., 2023). In East Asia, tea represents philosophical ideals of mindfulness, respect, and harmony. In India, chai, a spiced milk tea, is a ubiquitous part of daily life, transcending social boundaries. In the Middle East and North Africa, tea infused with mint and sugar plays a central role in social rituals, fostering communication and hospitality. In Europe, the tradition of afternoon tea embodies the elegance and leisure of the Victorian era, highlighting tea's integration into diverse cultural practices.

While ancient cultures valued tea for its invigorating characteristics and ceremonial significance, contemporary society increasingly emphasizes its functional components and health benefits. Fresh tea leaves contain 25–40 % phenolic compounds (e.g. flavonoids, phenolic acids, etc.), 20–25 % carbohydrates (e.g. glucose, fructose, sucrose, and polysaccharides, etc.), 20–30 % crude protein, and ∼ 8 % lipids (e.g. fats, phospholipids, glycerides, sugar esters, thioesters, etc.) (Bortolini et al., 2021; Salman et al., 2022; Wang et al., 2024). Phenolic compounds, particularly catechins, followed by theaflavins and caffeine, are the primary contributors to tea's bioactivity (Truong & Jeong, 2021). Numerous studies showed these components can neutralize free radicals, mitigating oxidative stress and cellular damage, thereby reducing risks of carcinogenesis and aging (Alam et al., 2022; Trisha et al., 2022). Additionally, they support cardiovascular health by regulating blood pressure and improving vascular function, while offering neuroprotective effects that may lower the risk of neurodegenerative diseases and enhance cognitive performance (Bortolini et al., 2021).

Freshly harvested tea leaves can produce six main categories of teas, classified by fermentation degree: green tea (unfermented), white tea

(slightly fermented), yellow tea (lightly fermented), oolong tea (semifermented), red tea (fully fermented), and dark tea (post-fermented) (Fig. 1) (Aaqil et al., 2023; Azeem et al., 2020; Bortolini et al., 2021). Green tea retains high levels of chlorophyll, theanine, and catechins, due to its minimal oxidation, contributing to its bright green color and potent antioxidant properties. White tea undergoes minimal processing, retaining a high catechin content that contributes to its mild sweetness and delicate flavor profile. Yellow tea undergoes an additional "yellowing" stage, where chlorophyll degradation results in its distinct hue and flavor. Oolong tea, with partial fermentation converting some catechins into theaflavins and thearubigins, yields a diverse range of flavors. Red tea is fully fermented, containing abundant theaflavins and thearubigins, which give it a rich flavor and deep color. Dark tea, known as post-fermented tea, features a breakdown of catechins and theanine into smaller molecules, producing unique earthy and woody flavors.

In the food industry, various types of tea are increasingly utilized as natural preservatives and flavor enhancers. Their bioactive components effectively inhibit microbial growth, reduce lipid oxidation, and mitigate protein degradation, thereby preserving food safety and quality (Hamann et al., 2024; He et al., 2018; Paglarini et al., 2022; Robalo et al., 2022). However, current research still faces several challenges. For instances, key factors such as tea variety, application field and application method, can markedly influence its efficacy. Additionally, potential changes in sensory attributes, variability in the bioactive components of tea, and the lack of standardized extraction protocols hinder its broader adoption. Addressing these challenges through systematic research is critical to fully harness the potential of tea extracts.

This study focused on the application of different teas in the preparation of "tea-flavored fish", a traditional Chinese cuisine. By combining ancient culinary techniques with contemporary technological principles, the findings provide innovative approaches to enhance food preservation and enrich cultural heritage practices. These insights offer a pathway for integrating traditional knowledge into modern food science and industry applications.

2. Materials and methods

2.1. Materials

Freshly harvested tea leaves were obtained by manually picking tender buds with 2–3 leaves from *Camellia sinensis* trees in April 2024 at local tea plantations in Guangzhou City, Guangdong Province, China (~23° N, ~114° E, annual average temperature of 22 °C, ~ 300 m above sea level, ~1200 mm annual rainfall).

Tilapia (*Pagrus major*) fillets, measuring approximately 40 mm × 20 mm × 2.5 mm and weighing around 2 g each, were sourced from an aquatic processing facility in Foshan City, Guangdong Province, China (~23° N, 113° E, average annual temperature of 23 °C, and annual rainfall of approximately 1800 mm). More than 200 tilapia individuals (average weight: 947 g ± 81 g) were processed according to modern technological standards, ensuring cold chain transport at 1 °C within a 4 h limit.

The primary reagents were sourced from Shanghai Macklin Biochemical Technology Co., Ltd., and Guangzhou Chemical Reagent Co., Ltd., China.

Fig. 1. Traditional processing techniques for different teas.

2.2. Teas processing

A total of 40 kg of tea leaves were randomly divided into 4 groups for processing into various tea products, following traditional techniques (Fig. 1) (Wang et al., 2024). The fresh tea group (F) was prepared by direct drying at ~100 °C for 120 min using a dryer (6CHZ-9B, Fujian Jiayou Co., Fuzhou, China). The green tea group (G), oolong tea group (O) and red tea group (R) underwent steaming (115 °C for 2 min) followed by rolling (5 min of pressure + 5 min of non-pressure) using a rolling machine (6CRZ-35, Zhejiang Shangyang Co., Quzhou, China) for a total of 120 min. The resulting tea leaves were naturally fermented aerobically (~30 °C, ~95 % relative humidity) for 0, 5, and 10 h, respectively, before being dried under the same conditions to obtain the final products.

2.3. Composition analysis and activities characterization of the teas

Tea extracts were obtained according to Chinese national standards GB/T 8313–2018 (Wang et al., 2024) by sufficiently immersing tea leaves (20 g) from each group in 70 % ethanol (2 L) at 70 °C for 3 h. Identification of key bioactive compounds was performed using high-performance liquid chromatography (HPLC) (LC-20AT, Shimadzu Corp., Tokyo, Japan) with an Inertsil ODS 3 column (250 × 4.6 mm, 5 μm). Approximately 10 μL of each extract was injected into the HPLC system, and data were obtained following the standard protocol (Wang et al., 2024).

Antioxidant activity of each tea was assessed using the radical scavenging capacity of 2,2-diphenyl-1-picrylhydrazyl (DPPH) and 2,2-azinobis (3-ethylbenzothiazoline-6-sulfonic acid) radical cation (ABTS$^+$) according to the method described by Zhang et al. (2024). Antimicrobial activity was evaluated by measuring inhibition zones of the tea extracts on Mueller-Hinton agar plates inoculated with *Escherichia coli*, *Pseudomonas aeruginosa*, and *Staphylococcus aureus* (~100 CFU/mL) (He et al., 2020). Each tea extract (20 μL) was applied to the plates, which were incubated at 37 °C for 24 h.

2.4. Processing and storage of the fish

Over 5000 pieces of fish fillets was randomly divided into five groups: control (C), fresh tea (F), green tea (G), oolong tea (O), and red tea (R). The control group was preserved at 1 °C without any treatment, while the F, G, O, and R groups were soaked in the respective tea extracts for 15 min and then drained before being stored under identical conditions. Fish from each group were sampled for analysis every two days.

2.5. Sensory evaluation of the preserved fish

Sensory evaluation focused on key attributes of the fish, including color, odor, taste, texture, and overall acceptability, following the methodology established by He et al. (2019). A panel of 28 trained assessors (aged 21 to 44 years) participated in the evaluation after providing informed consent and receiving ethical approval from the relevant institutions. Fish from each group were presented anonymously on white porcelain plates in a sensory laboratory maintained at approximately 25 °C. Panelists scored the samples on a scale from 0 (extremely unacceptable) to 5 (extremely fresh).

Color analysis was conducted using a colorimeter (CR-8, 3NH Co., Shenzhen, China), utilizing the CIE color system to determine *L** (lightness/darkness), a* (redness/greenness), and b* (blueness/yellowness) values of the fish (Wang et al., 2020).

Texture analysis was performed using a texture analyzer (Brookfield-CT3, Brookfield Co., Middleboro, USA) equipped with a 6 mm cylindrical probe to assess hardness and springiness. Each sample was subjected to two compressions at a speed of 5 mm/s and a depth of 2 mm to obtain measurements of hardness and springiness (Liu et al., 2024).

2.6. Metabolic activity of the preserved fish

The metabolic activity of the fish was evaluated by measuring the k-value, as the method described by Li et al. (2020). In this process, 2 g of the fish was homogenized in 2 mL of perchloric acid (50 *g*/L) and then centrifuged at 2000 ×*g* for 3 min. The supernatant (20 μL) was filtered and analyzed by high-performance liquid chromatography (HPLC, LC-20AT, Shimadzu Corp., Kyoto, Japan) with a C18 column (Agilent ZORBAX Eclipse Plus, 5 μm, 4.6 mm × 250 mm, Agilent Technologies, Santa Clara, USA). Absorbance was measured at 254 nm to determine the k-value.

Additionally, the activity of Ca^{2+}-ATPase in the fish was assessed using commercially available assay kits (Solarbio Co., Beijing, China) as per the method outlined by Ji et al. (2021). Results were expressed as the amount of inorganic phosphate (Pi) released per milligram of sample per minute (μmol/mg/min).

2.7. Microbial counts in the preserved fish

Microbial counts were assessed through total bacterial count (TBC) and total aerobic count (TAC) as described by He and Xiao (2016). A 0.2 g sample of the fish was homogenized in 45 mL of sterile physiological saline for 1 min. The homogenate (1 mL) was then serially diluted with 9 mL of sterile saline. TBC was determined using spread plates of iron agar (Scharlab, Barcelona, Spain) supplemented with NaCl (10 g/L) and incubated at 15 °C for 72 h. TAC was evaluated using plate count agar, with plates incubated at 37 °C for 24 h.

2.8. Lipid oxidation in the preserved fish

The peroxide value (PV) of the fish was measured following Lea (1952). A 50 g sample of the fish was extracted using a solvent mixture of distilled water (25 mL), methanol (100 mL), and chloroform (100 mL). The resulting extract (1 g) was dissolved in a solvent comprising chloroform (10 mL) and acetic acid (15 mL). A saturated aqueous solution of potassium iodide (1 mL) was added, and the mixture was kept in the dark for 10 min. Following this, distilled water (30 mL) and starch solution (1 mL, 10 g/L) were added, and the mixture was titrated with sodium thiosulfate (0.01 mol/L). The results were calculated based on the volume of sodium thiosulfate consumed.

Thiobarbituric acid reactive substances (TBARS) were quantified according to the method described by He and Xiao (2016). A 0.2 g sample of the fish was dissolved in 1 mL of n-butanol and diluted to 25 mL. A 5 mL aliquot of this mixture was combined with 5 mL of a thiobarbituric acid solution (2 g/L of 2-thiobarbituric acid in n-butanol) and incubated in a water bath at 95 °C for 120 min. Absorbance was measured using a UV spectrophotometer (UV-1800, Shimadzu Corp., Kyoto, Japan) to determine TBARS levels.

2.9. Protein degradation in the preserved fish

Trichloroacetic acid (TCA)-soluble peptides in the fish were quantified using the method of Zhang et al. (2025). A 3 g sample of the fish was homogenized in 27 mL of TCA (50 g/L) and incubated on ice for 30 min. The mixture was then centrifuged at 4 °C and 2000 ×*g* for 5 min, and the soluble peptides in the supernatant were measured using a UV spectrophotometer (UV-1800, Shimadzu Corp., Kyoto, Japan).

Total volatile basic nitrogen (TVB-N) was determined using the semi-micro Kjeldahl method (He et al., 2015). Approximately 10 g of the fish was mixed with 50 mL of distilled water, stirred for 30 min, and filtered. The filtrate was alkalinized using a suspension of magnesium oxide (100 g/L) and analyzed with a Kjeldahl apparatus (KDY-9820, Ruibangxingye Co., Beijing, China). Volatile nitrogen compounds were collected in an acid receiver and titrated with hydrochloric acid (1 mL/L) to obtain the TVB-N values.

2.10. Accumulation of biogenic amines in the preserved fish

The main biogenic amines, including histamine, putrescine, cadaverine, spermine, spermidine, tyramine, and tryptamine, were assessed following the protocol outlined by Hui et al. (2023). A 5 g sample of the fish was homogenized with 20 mL of hydrochloric acid (0.1 mol/L) and centrifuged at 4 °C and 8000 ×g for 5 min. The supernatant (0.3 mL) was mixed with saturated sodium bicarbonate (0.05 mL) and sodium hydroxide (0.05 mL, 2 mol/L), followed by incubation with dansyl chloride solution (0.3 mL, 10 mg/mL) in acetone. The resulting mixture was analyzed using HPLC (LC-20AT, Shimadzu Corp., Kyoto, Japan), with biogenic amine concentrations determined by absorbance at 254 nm.

2.11. Microstructure variations of the preserved fish

Surface hydrophobicity of the fish was evaluated according to the method described by Gao et al. (2023). A 0.1 g sample of the fish was diluted in 2 mL of distilled water, followed by the addition of 200 μL of bromophenol blue (1 g/L). The mixture was centrifuged at 4000 ×g for 15 min, and the absorbance of the supernatant was measured at 595 nm to determine surface hydrophobicity.

Total sulfhydryl content in the fish was measured using Ellman (1959). A 0.1 g fish was homogenized in 0.4 mL of phosphate-buffered saline (PBS, 10 mmol/L) containing NaCl (0.1 mol/L), and then mixed with 4.5 mL of Tris-HCl buffer (pH 8.0, 0.2 mol/L). After the addition of 0.5 mL of 5,5′-dithiobis-2-nitrobenzoic acid (DTNB, 10 mmol/L in Tris-HCl buffer), the mixture was incubated in a water bath at 40 °C for 25 min. The sulfhydryl content was quantified by measuring absorbance at 412 nm using a UV spectrophotometer (UV-1800, Shimadzu Corp., Kyoto, Japan).

Total carbonyls content in the fish were assessed following Oliver et al. (1987). Fish (~ 0.1 g) were homogenized in phosphate-buffered saline (PBS, 0.4 mL, 10 mmol/L) containing sodium chloride (NaCl, 0.1 mol/L). The homogenate was treated with 2,4-dinitrophenylhydrazine (DNPH) solution (1 mL, 10 mmol/L) and incubated in the dark at room temperature for 1 h. Subsequently, trichloroacetic acid (TCA, 1 mL, 20 % w/w) was added, and the mixture was centrifuged at 8000 ×g for 5 min at 4 °C. The precipitate was dissolved in guanidine hydrochloride (3 mL, 6 mol/L) and incubated in a water bath at 37 °C for 15

min. Carbonyl content was quantified by measuring absorbance at 370 nm using a UV spectrophotometer (UV-1800, Shimadzu Corp., Kyoto, Japan).

2.12. Statistical analysis

Each assay included at least five independent replicates from different samples. Results are expressed as mean ± standard deviation. Statistical analyses were conducted using SPSS software (version 22.0, SPSS Inc., USA), with significance set at $p < 0.05$ (Li et al., 2022).

3. Results and discussion

3.1. Composition analysis of the teas

As shown in Fig. 2, processing and fermentation significantly altered the levels of key bioactive compounds in the teas, which can be classified into three categories based on their transformation patterns: (1) Catechins with significant reductions. Catechin (C), epigallocatechin-3-gallate (EGCG), epicatechin (EC), and epicatechin-3-gallate (ECG) were abundant in fresh tea leaves but decreased substantially during processing and fermentation. These catechins primarily underwent enzymatic oxidation, transforming into theaflavins (TFs) and derivatives like theaflavin-3-O-gallate (TFG) and theaflavin-3,3′-digallate (TF33G) (Wang et al., 2024), resulting in an increase in theaflavin content. (2) Catechins with irregular fluctuations. Epigallocatechin (EGC) and gallocatechin gallate (GCG) exhibited variable concentrations, influenced by fermentation conditions and processing methods. (3) Stable compounds. Gallocatechin (GC) and catechin gallate (CG) were present at low initial levels and showed minimal changes during processing and fermentation. A stability also observed for caffeine.

In this study, teas were produced using traditional processing methods, involving 4 main stages: steaming, rolling, fermentation, and drying: (1) Steaming is a critical initial step to reduce the bitterness and aroma while deactivating oxidative enzymes (e.g., PPO, POD) (Donlao & Ogawa, 2019). Although minor structural changes occur (e.g., EGCG to GCG epimerization), these are less significant compared to fermentation. (2) Rolling mechanically disrupts tea leaves, exposing cellular contents to oxygen and partially oxidizing catechins into theaflavins.
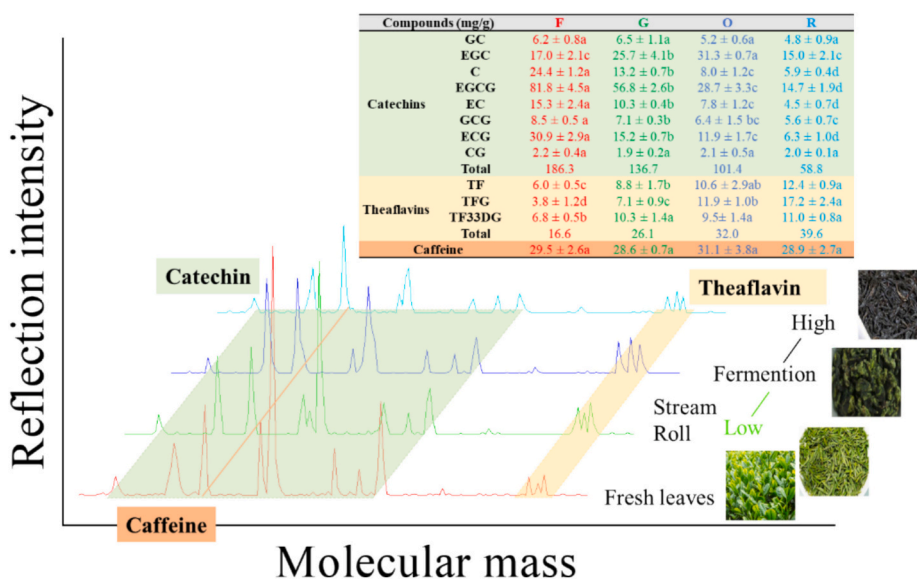

Compounds (mg/g)		F	G	O	R
	GC	6.2 ± 0.8a	6.5 ± 1.1a	5.2 ± 0.6a	4.8 ± 0.9a
	EGC	17.0 ± 2.1c	25.7 ± 4.1b	31.3 ± 0.7a	15.0 ± 2.1c
	C	24.4 ± 1.2a	13.2 ± 0.7b	8.0 ± 1.2c	5.9 ± 0.4d
	EGCG	81.8 ± 4.5a	56.8 ± 2.6b	28.7 ± 3.3c	14.7 ± 1.9d
Catechins	EC	15.3 ± 2.4a	10.3 ± 0.4b	7.8 ± 1.2c	4.5 ± 0.7d
	GCG	8.5 ± 0.5 a	7.1 ± 0.3b	6.4 ± 1.5 bc	5.6 ± 0.7c
	ECG	30.9 ± 2.9a	15.2 ± 0.7b	11.9 ± 1.7c	6.3 ± 1.0d
	CG	2.2 ± 0.4a	1.9 ± 0.2a	2.1 ± 0.5a	2.0 ± 0.1a
	Total	186.3	136.7	101.4	58.8
	TF	6.0 ± 0.5c	8.8 ± 1.7b	10.6 ± 2.9ab	12.4 ± 0.9a
Theaflavins	TFG	3.8 ± 1.2d	7.1 ± 0.9c	11.9 ± 1.0b	17.2 ± 2.4a
	TF33DG	6.8 ± 0.5b	10.3 ± 1.4a	9.5± 1.4a	11.0 ± 0.8a
	Total	16.6	26.1	32.0	39.6
Caffeine		29.5 ± 2.6a	28.6 ± 0.7a	31.1 ± 3.8a	28.9 ± 2.7a

Fig. 2. Changes in the content of main active components in the teas with various processing and fermentation.
GC: gallocatechin; EGC: epigallocatechin; C: catechin; EGCG: epigallocatechin-3-gallate; EC: epicatechin; GCG: gallocatechin gallate; ECG: epicatechin-3-gallate; CG: catechin gallate; TF: theaflavin; TFG: theaflavin gallate; TF33DG: theaflavin 3,3′-digallate.
Different letters (a ~ d) indicate the significant difference (p < 0.05) between each treatment.

This process enhances caffeine extraction, which remains chemically stable during this phase (Wang et al., 2024). (3) Fermentation drives enzymatic oxidation of key catechins (e.g., EGCG, ECG) by PPO and POD, producing polyphenolic compounds (e.g. theaflavins) that contribute to the distinctive color and flavor of oolong tea and red tea. Notably, caffeine remains unaffected due to its chemical stability (Ito & Yanase, 2022; Jakubczyk et al., 2024). (4) Drying removes moisture for storage and transportation while influencing thermosensitive components, imparting a unique flavor to the final product.

3.2. Antioxidant and antimicrobial activities of the teas

As shown in Table 1, the antioxidant activity of the teas was positively correlated with total catechin content. This relationship can be explained by the following mechanisms (Truong & Jeong, 2021; Oliveira et al., 2022): (1) Free radical scavenging. Catechins donate hydrogen atoms from their hydroxyl groups, neutralizing free radicals and converting them into more stable species. EGCG exhibited the highest activity due to its 3′, 4′, 5′-trihydroxyl (gallate) group on the B-ring, which enhanced hydrogen donation efficiency (Ma et al., 2022). (2) Metal chelation. Catechins chelate transition metals, such as Fe^{2+} and Cu^{2+}, that act as catalysts in Fenton and Haber-Weiss reactions. By reducing the availability of these metals, catechins inhibit the generation of reactive hydroxyl radicals, effectively mitigating oxidative stress. (3) Regulation of endogenous antioxidant systems. Catechins upregulate endogenous antioxidant enzymes, including superoxide dismutase, catalase, and glutathione peroxidase, by modulating cellular signaling pathways. These enzymes play a critical role in maintaining redox balance and protecting cells from oxidative damage.

Table 1 also highlighted the antimicrobial activity of the teas, which was positively associated with catechin content. The strongest activity was observed against *S. aureus*, followed by *P. aeruginosa*, with weaker effects on *E. coli* (Salman et al., 2022). This variation reflected the primary antimicrobial mechanism of catechins: disruption of microbial cell membranes. Catechins interact with the membrane proteins and phospholipids, increasing permeability and leading to cell death (Ruengdech & Siripatrawan, 2021; Salman et al., 2022). However, Gram-negative bacteria, such as *E. coli*, possess an outer membrane enriched with lipopolysaccharides, which serve as a barrier that limits direct catechins interaction. Despite this, catechins exert antimicrobial effects on Gram-negative bacteria through alternative mechanisms, such as inhibiting key metabolic enzymes (e.g., DNA gyrase and F1-ATPase) or chelating essential metal ions (e.g., Fe^{3+} and Zn^{2+}) required for microbial growth (Salman et al., 2022).

3.3. Sensory evaluation of the preserved fish

The sensory scores of the preserved fish, declined over the storage period (Fig. 3A), reflecting a gradual reduction in quality. However, the tea treatments significantly alleviated this deterioration. In addition, quantitative analysis of textural properties (hardness and springiness; Fig. 3B) and color parameters ($L*$, a*, b*; Fig. 3C), which are crucial factors determining consumer acceptance and purchasing decisions (He et al., 2017), revealed a progressive decline over time. Notably, tea-

Table 1
Antioxidant and antimicrobial activities of different teas.

Tea	Antioxidant activity (%)		Antimicrobial zone (mm)		
	DPPH	ABTS[+]	*S.aureus*	*P.aeroginosa*	*E.coli*
F	89.7 ± 5.1a	79.6 ± 3.3a	20.1 ± 3.2a	13.8 ± 1.6a	4.5 ± 0.3a
G	85.4 ± 8.2ab	71.4 ± 2.9b	18.3 ± 1.5a	10.7 ± 0.4b	4.4 ± 0.1a
O	76.8 ± 4.3b	58.6 ± 1.2c	14.7 ± 0.7b	8.3 ± 1.1c	3.6 ± 0.2b
R	58.0 ± 7.9c	51.3 ± 5.0d	11.2 ± 1.4c	6.4 ± 0.2d	3.1 ± 0.1c

Different letters (a ~ e) indicate the significant difference ($p < 0.05$) between each treatment.

treated samples exhibited slower rates of decline in these attributes, demonstrating their efficacy in preserving product quality during storage.

The degradation of fish quality during storage is driven by a combination of enzymatic, oxidative, and microbial processes. Tea components, particularly catechins and theaflavins, exhibited potent antioxidant and antimicrobial properties, playing a key role in mitigating these processes. By inhibiting lipid oxidation and microbial activity, tea treatments effectively preserve the integrity of flavor compounds, contributing to fresher and more desirable sensory profiles.

Regarding flavor, fresh tea contributes pronounced astringency, while green tea, rich in catechins, imparts a mild bitterness. Semifermented oolong tea offers a balanced bitterness and sweetness, and fully fermented red tea introduces subtle malt-like notes. These distinct flavor profiles not only maintain more desirable freshness, but also enrich the sensory diversity of the fish.

In terms of texture, tea polyphenols interact with proteins through covalent bonding, modifying protein structure and improving water retention, which enhances the fish's firmness and springiness. Furthermore, the antioxidant properties of catechins and theaflavins prevent oxidative browning of proteins and lipids, thereby preserving both the texture and color of the fish. These combined effects highlight the efficacy of tea treatments in maintaining the overall quality of preserved fish during storage.

3.4. Basic metabolism the preserved fish

The k-value, a critical indicator of ATP degradation in fish muscle, provided additional insight into fish freshness (Du et al., 2023). As shown in Fig. 3D, the k-value progressively increased over time indicating declining freshness. However, tea treatments significantly showed this increase. This effect is attributed to tea polyphenols, which delay ATP breakdown by inhibiting ATPase and other related enzymes (He et al., 2018).

Similarly, Ca^{2+}-ATPase activity, a key biomarker for muscle function and oxidative damage, displayed consistent trends in response to tea treatments. Ca^{2+}-ATPase activity is sensitive to protein oxidation and cell membranes disruption. The antioxidant properties of catechins effectively mitigated oxidative damage, preserving enzymatic activity. Among the tested teas, fresh tea, with its high catechin content, maintained the highest Ca^{2+}-ATPase activity, followed by green tea, while oolong tea and red tea offered moderate protective effects.

3.5. Microbial counts in the preserved fish

The antimicrobial effects of tea further corroborate its role in preserving fish quality. As shown in Fig. 3E, both TBC and TAC were significantly reduced in tea-treated samples, particularly less processed teas. These results underscore the effectiveness of tea polyphenols in inhibiting microbial growth.

Common spoilage and pathogenic bacteria, such as *E. coli*, *S. aureus*, *P. aeruginosa*, and *Listeria monocytogenes*, are frequently found in fish and pose serious risks to storage quality and food safety (Mendes et al., 2023). Stringent regulatory limits exist for these species in commercial fish products. Tea treatments, leveraging their potent antimicrobial properties, effectively control microbial contamination, thereby ensuring both the safety and quality of the preserved fish products.

3.6. Lipid oxidation in preserved fish

Fish lipids, rich in unsaturated fatty acids, are highly vulnerable to oxidative damage caused by reactive oxygen species (ROS). PV measures primary oxidation products such as hydroperoxides, while TBARS quantify secondary products like malondialdehyde. As shown in Fig. 4A, tea extracts significantly reduced both PV and TBARS levels, indicating their robust antioxidant capacity, especially in low-fermentation tea.
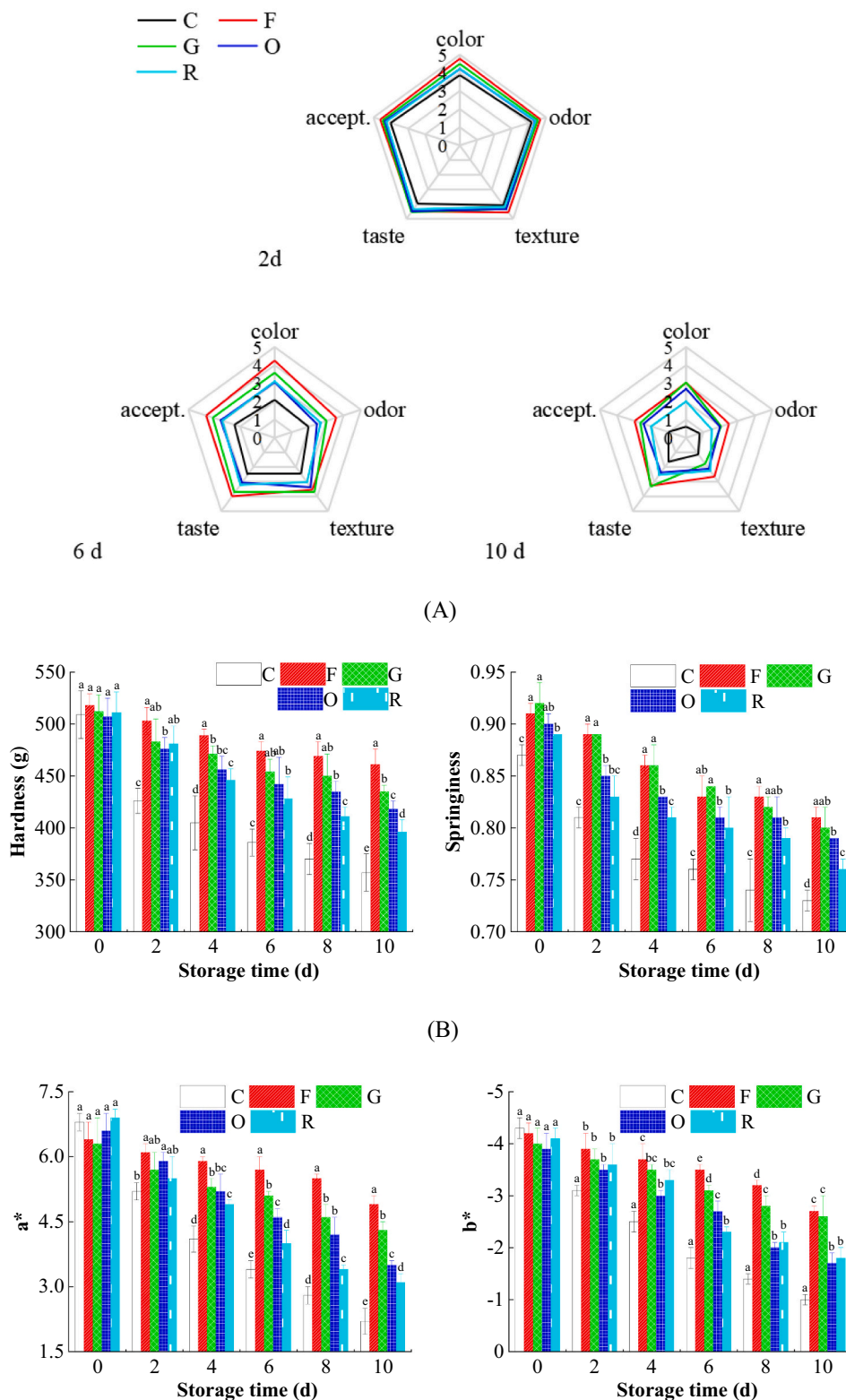
Fig. 3. The effects of the teas on the overall qualities of "tea flavored fish". (A) Sensory scores; (B) Texture; (C) Colorimetric parameter; (D) Basic metabolism; and (E) Microbial counts.
At least 5 independent replicates were conducted on different samples.
Different letters (a ~ e) indicate the significant difference ($p < 0.05$) between each treatment.

ROS in the fish is derived from both endogenous (e.g., metabolic reactions, enzymatic activity) and exogenous sources (e.g., microbial activity, UV radiation). These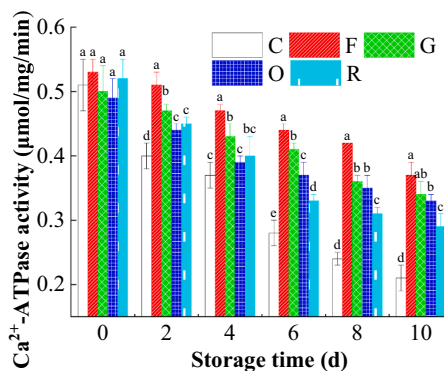 reactive species attack unsaturated lipids, initiating chain reactions that produce aldehydes, ketones, and alcohols — compounds associated with spoilage and off-flavors like 2,4-heptadienal and 2,4-decadienal. Catechins in teas counteracted these processes
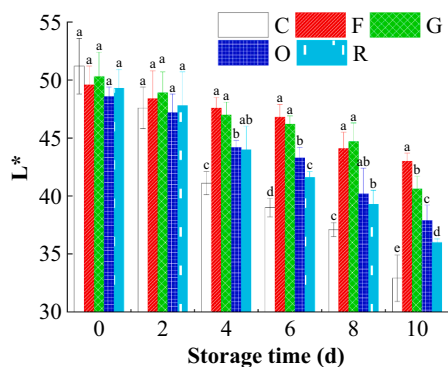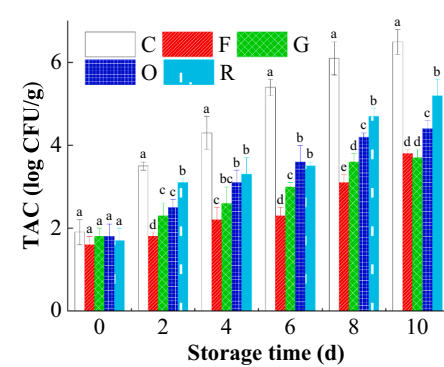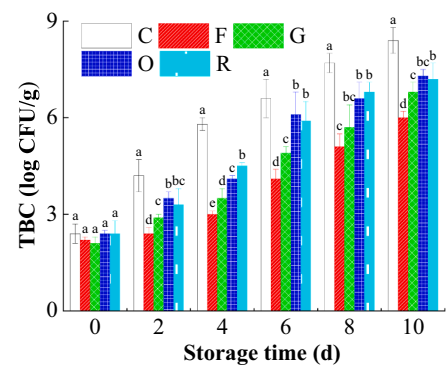
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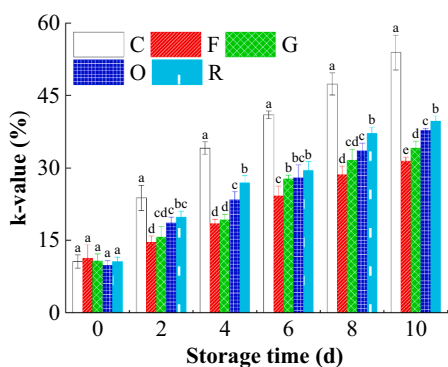
(D)

(E)

Fig. 3. (*continued*).

by scavenging ROS through hydrogen donation from hydroxyl groups, forming stable phenoxyl radicals (Truong & Jeong, 2021). Additionally, catechins rearranged unpaired electrons into resonance-stabilized quinones, further mitigating oxidative chain reactions. These mechanisms not only inhibited lipid oxidation but also contributed to maintaining the sensory quality and extending the shelf life of preserved fish.

### 3.7. Protein degradation of the preserved fish

TVB-N content is a widely recognized indicator of protein degradation, reflecting the enzymatic hydrolysis of fish proteins. As shown in Fig. 4B, tea treatment significantly reduced TVB-N accumulation, likely due to their inhibitory effects on proteolytic enzymes (Abedini et al.,

2023). A similar trend was observed in TCA-soluble peptide levels (Fig. 4B), reflecting the extent of protein hydrolysis during storage.

Protein degradation in fish involves the breakdown of myofibrillar and sarcoplasmic proteins into peptides and free amino acids, driven by endogenous proteolytic enzymes and microbial activity (Abedini et al., 2023). Tea extracts, particularly those rich in catechins, mitigated protein degradation through multiple mechanisms. (1) Enzyme inhibition. Catechins effectively inhibited the activity of both endogenous and microbial-derived proteolytic enzymes (Salman et al., 2022). (2) Antimicrobial action. Catechins not only reduced microbial proliferation, but also inhibited microbial metabolic activity, thereby minimizing the impact of microorganisms on fish protein (Ruengdech & Siripatrawan, 2021). (3) Antioxidant effects. Catechins protected proteins from
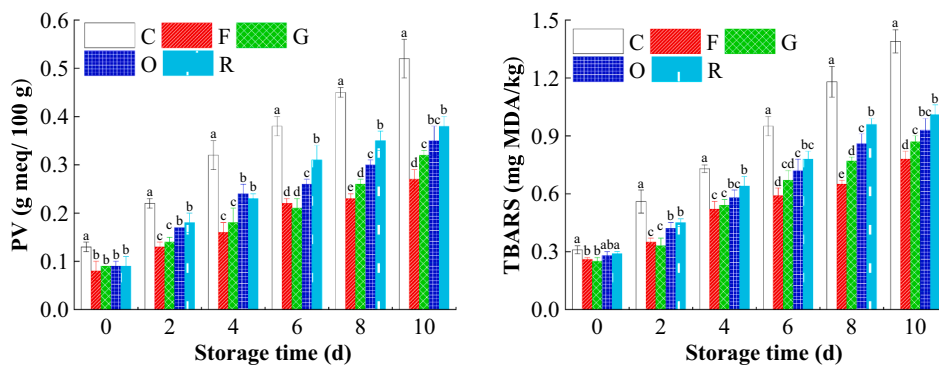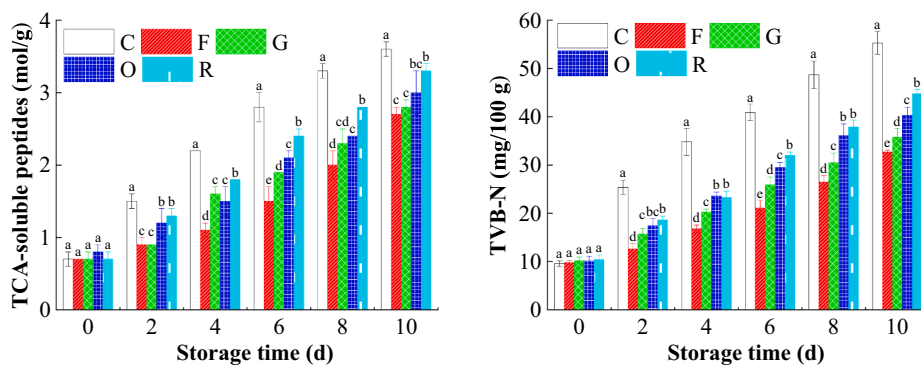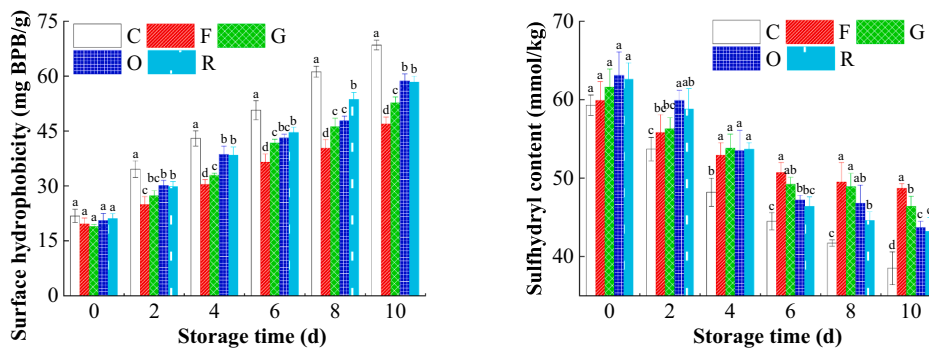
Fig. 4. The effects of the teas on variations in composition and microstructure of "tea flavored fish". (A) Liquid oxidation; (B) Protein degradation; and (C) Microstructure variations.

At least 5 independent replicates were conducted on different samples.

Different letters (a ~ e) indicate the significant difference (p < 0.05) between each treatment.

oxidative modifications, preserving the structural integrity of muscle proteins (Truong & Jeong, 2021). (4) Water retention. Catechins enhanced water retention in fish tissue, creating less favorable conditions for protein degradation reactions (Oliveira et al., 2022). Collectively, these effects highlight the ability of tea extracts to preserve the quality of fish during storage by mitigating protein degradation and inhibiting the factors that contribute to spoilage. This underscores the potential of tea treatments as an effective natural preservative.

3.8. Accumulation of biogenic amines in the preserved fish

Biogenic amines are nitrogenous compounds formed through microbial decarboxylation of amino acids, serving as key indicators of fish spoilage. As shown in Table 2, their accumulation patterns of change during storage can be categorized as follows: (1) Spoilage markers. Putrescine, cadaverine, and histamine, major spoilage indicators, increased significantly over time. Tea treatment markedly inhibited their formation. (2) Naturally occurring polyamines. Spermine and spermidine, initially abundant in fish tissues, exhibited an increase followed by a decline during storage. Tea treatments had minimal impact on their levels. (3) Stable amines. Tyramine and tryptamine remained at consistently low levels, showing negligible changes regardless of storage or treatment.

The formation of biogenic amines is driven by microbial activity and protein degradation, where amino acids serve as precursors (Jaguey Hernandez et al., 2021). Tea extracts, particularly those rich in catechins, reduced protein hydrolysis and the availability of free amino acids, thereby limiting biogenic amine synthesis (Wang et al., 2024). This effect contributed to improve safety and extended shelf life of the fish.

3.9. Microstructure of the preserved fish

During storage, the balance between hydrophilicity and hydrophobicity in fish tissue significantly influenced its quality. This balance was primarily determined by surface molecules charge, which shifted as the microscopic surface structure changed (Shi et al., 2022). As shown in Fig. 4C, tea treatment effectively preserved the surface structure of fish, stabilizing hydrophobicity and maintaining overall quality. The changes in hydrophilicity observed during fish storage are primarily driven by chemical alterations in proteins. The action of enzymes and microorganisms promotes the release of hydrophobic amino acids from proteins, increasing the fish's surface hydrophobicity (Fig. 4C). Additionally, lipid oxidation exposes hydrophobic residues, further modifying the fish's hydrophilic properties.

Functional group modifications were also observed, with carbonyl groups serving as indicators of the redox state of fish tissue. Initially, carbonyl group content showed no significant differences among the samples. However, as storage progressed, carbonyl group levels increased markedly, indicating the increase of oxidative stress degree. Tea treatments, particularly those involving low-fermentation teas, significantly inhibited this increase (Fig. 4C), highlighting their protective effects on redox balance.

Free -SH in fish proteins are critical for maintaining protein structure and function. During storage, oxidative stress converted these -SH into disulfide bonds (-S-S-), reducing the total -SH content (Fig. 4C) and destabilizing protein structures (Wei et al., 2021). ROS generated during lipid oxidation exacerbate this process.

3.10. Comprehensive analysis of tea's impact on tea-flavored fish

In summary, tea extracts, particularly those from low-fermented teas, significantly improved the storage quality of fish by mitigating quality deterioration across multiple dimensions. These effects were not only reflected in sensory evaluations, highlighting the enhancement of color, texture, and flavor, but also in biochemical analyses, revealing

Table 2
The effects of the teas on the levels of biogenic amines in the "tea flavored fish".

BAs	Groups	Concentration (mg/kg)					
		0 d	2 d	4 d	6 d	8 d	10 d
HIM	C	ND	2.1 ± 0.2a	6.8 ± 1.3a	11.8 ± 0.7a	17.5 ± 0.9a	21.4 ± 1.7a
	F	ND	0.4 ± 0.1c	0.6 ± 0.0e	1.1 ± 0.1d	1.5 ± 0.3d	1.7 ± 0.1e
	G	ND	0.5 ± 0.0c	0.9 ± 0.1d	1.5 ± 0.2c	2.0 ± 0.4 cd	2.3 ± 0.2d
	O	ND	0.7 ± 0.0b	1.2 ± 0.0c	1.9 ± 0.1b	2.4 ± 0.1c	2.7 ± 0.1c
	R	ND	0.8 ± 0.1b	1.5 ± 0.1b	2.1 ± 0.2b	2.9 ± 0.3b	3.2 ± 0.2b
PUT	C	0.2 ± 0.1a	1.4 ± 0.2a	4.7 ± 0.8a	10.9 ± 1.4a	18.7 ± 0.8a	31.0 ± 1.9a
	F	0.2 ± 0.0a	0.6 ± 0.0c	1.1 ± 0.2d	2.5 ± 0.2d	4.6 ± 0.2c	5.9 ± 0.5b
	G	0.2 ± 0.0a	0.7 ± 0.2bc	1.3 ± 0.0c	2.9 ± 0.1c	4.4 ± 0.1c	5.8 ± 0.1c
	O	0.2 ± 0.0a	1.0 ± 0.0b	2.0 ± 0.2b	3.1 ± 0.5bc	5.5 ± 0.5b	7.6 ± 0.4 cd
	R	0.2 ± 0.0a	0.9 ± 0.2b	2.2 ± 0.3b	3.8 ± 0.4b	6.0 ± 0.3b	8.7 ± 0.2d
CAD	C	0.1 ± 0.0a	1.7 ± 0.2a	3.6 ± 0.7a	7.5 ± 0.4a	11.6 ± 0.6a	14.6 ± 2.0a
	F	ND	ND	0.6 ± 0.1d	0.9 ± 0.2e	1.9 ± 0.3d	3.2 ± 0.5d
	G	ND	0.3 ± 0.1b	0.7 ± 0.0d	1.5 ± 0.1d	2.6 ± 0.5 cd	4.4 ± 0.3c
	O	ND	0.3 ± 0.0b	0.9 ± 0.0c	1.8 ± 0.2c	3.5 ± 0.4c	6.3 ± 0.5b
	R	ND	0.4 ± 0.1b	1.2 ± 0.1b	2.3 ± 0.3b	4.4 ± 0.5b	6.8 ± 0.2b
SPM	C	21.3 ± 1.7a	24.9 ± 2.3a	28.8 ± 1.7a	19.4 ± 0.5a	14.7 ± 0.6b	10.6 ± 1.3a
	F	19.8 ± 0.7a	21.5 ± 0.6b	22.6 ± 1.7c	18.1 ± 1.5ab	16.6 ± 0.8a	12.8 ± 1.2a
	G	20.8 ± 1.4a	22.7 ± 1.5ab	24.8 ± 1.4bc	18.8 ± 0.9a	18.0 ± 2.2a	10.7 ± 0.5a
	O	19.7 ± 2.2a	23.6 ± 3.8ab	25.6 ± 0.7b	16.4 ± 1.2b	16.8 ± 1.5a	11.9 ± 1.3a
	R	20.6 ± 1.4a	24.6 ± 0.6a	26.1 ± 1.9ab	17.4 ± 2.2ab	13.7 ± 1.6b	11.5 ± 0.7a
SPD	C	9.1 ± 0.6a	15.2 ± 0.8a	23.6 ± 1.3a	18.8 ± 0.7a	13.5 ± 1.2b	7.9 ± 0.5b
	F	8.4 ± 1.3a	9.2 ± 0.7c	14.7 ± 1.2e	11.9 ± 0.8b	10.3 ± 0.6c	8.8 ± 1.2ab
	G	8.8 ± 0.8a	11.6 ± 0.3b	16.1 ± 0.5d	16.7 ± 1.6a	13.6 ± 1.2b	10.4 ± 0.3a
	O	8.5 ± 1.4a	12.7 ± 0.5ab	17.6 ± 0.7c	18.9 ± 2.0a	15.3 ± 0.5a	9.4 ± 0.7a
	R	8.7 ± 1.6a	14.0 ± 1.3a	19.9 ± 1.2b	17.7 ± 0.5a	10.5 ± 1.3a	8.2 ± 0.3b
TYM	C	0.7 ± 0.1a	0.9 ± 0.1a	1.3 ± 0.1a	1.2 ± 0.1b	0.9 ± 0.2a	1.0 ± 0.1a
	F	0.6 ± 0.1a	0.7 ± 0.0b	0.7 ± 0.1c	0.7 ± 0.0d	0.7 ± 0.1b	0.6 ± 0.1b
	G	0.7 ± 0.0a	0.8 ± 0.2ab	0.9 ± 0.0b	0.9 ± 0.1c	0.7 ± 0.0b	0.6 ± 0.2b
	O	0.6 ± 0.1a	0.8 ± 0.1ab	0.9 ± 0.1b	1.0 ± 0.0c	0.8 ± 0.1ab	0.7 ± 0.0b
	R	0.7 ± 0.2a	0.9 ± 0.1ab	1.0 ± 0.0b	1.1 ± 0.0b	0.9 ± 0.1a	0.8 ± 0.2ab
TRM	C	ND	ND	0.1 ± 0.0a	0.4 ± 0.0a	0.3 ± 0.1a	0.7 ± 0.2a

(continued on next page)

Table 2 (*continued*)

BAs	Groups	Concentration (mg/kg)					
		0 d	2 d	4 d	6 d	8 d	10 d
	F	ND	ND	ND	ND	$0.1 \pm 0.0c$	$0.4 \pm 0.1b$
	G	ND	ND	ND	ND	$0.1 \pm 0.0c$	$0.4 \pm 0.0b$
	O	ND	ND	ND	$0.1 \pm 0c$	$0.2 \pm 0.0b$	$0.6 \pm 0.0a$
	R	ND	ND	ND	$0.2 \pm 0b$	$0.2 \pm 0.0b$	$0.6 \pm 0.1a$

BAs: biogenic amines; HIM: histamine; PUT: putrescine; CAD: cadaverine; SPM: spermine; SPD: spermidine; TYM: tyramine; TRM: tryptamine; ND: not detected. At least 5 independent replicates were conducted on different samples. Different letters (a ~ e) indicate the significant difference ($p < 0.05$) between each treatment.

delayed lipid oxidation, reduced protein degradation, and stabilized microbial community structures.

The influence of tea extract on the chemical composition of fish is worth noting, forming the basis for the distinct flavor, taste, and preservation characteristics of "tea-flavored fish." A primacy mechanism was the inhibition of lipid oxidation, as indicated by lower TBARS and PV, reduced carbonyl content, and higher levels of -SH groups. Additionally, tea extracts slowed protein degradation, as evidenced by reduced levels of peptides, polyamines, and nitrogen-containing small molecules during storage. Additionally, measurements of surface hydrophobicity further confirmed that tea-treated samples retained protein stability by minimizing the exposure of hydrophobic residues. These findings highlight the potential of tea-based processing methods as natural and efficient strategies for extending the shelf life of fish products while improving their quality and consumer appeal.

4. Conclusion

Processing and fermentation of teas significantly reduced catechin content, with EGCG showing the most pronounced decline, and partially transformed catechins into theaflavins. In contrast, caffeine content remained largely unaffected. These changes diminished the antioxidant and antimicrobial activities of teas, which influenced their efficacy in preserving fish. Using different teas, fish exhibited improved sensory scores, texture stability, and color retention, while metabolic activity, microbial growth, lipid oxidation and protein degradation were significantly suppressed. Biogenic amines such as HIM and PUT were maintained at relatively low levels, and microstructural deterioration in the fish was mitigated. Among the teas tested, low-processed teas demonstrated superior preservation effects, aligning with the preferences of traditional practices. These findings provide a scientific basis for the historical use of low-processed teas in preserving fish, offering valuable insights into the inheritance of traditional methods. The study underscores the potential of integrating traditional knowledge with modern scientific understanding to enhance food preservation practices.

CRediT authorship contribution statement

Wenxia Wang: Writing – original draft, Investigation. **Kun Liu:** Investigation. **Chunlong Liu:** Investigation. **Bei Yang:** Investigation, Writing – review & editing. **Hao Dong:** Writing – review & editing, Investigation. **Wenzhen Liao:** Writing – review & editing. **Xingfen Yang:** Supervision. **Qi He:** Writing – review & editing, Supervision, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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