





Review

Off-Flavors in Aquacultured Fish: Origins and Implications for Consumers

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Abstract: Off-flavors in fish and water are considered a worldwide problem. Several factors, such as the presence of phosphorus, micronutrients, and organic matter, contribute to phytoplankton proliferation and the production of off-flavors. Geosmin and 2-methylisoborneol are the most common off-flavors that confer the smell of earth or mold to water and fish. These metabolites are not considered toxic, but they can be easily transferred from water to living organisms and accumulate in the biota, up the trophic levels and to consumers, including fish species. Numerous processes have been studied to eliminate or reduce the presence of off-flavors in recirculating aquaculture systems. Managing off-flavors must be eco-friendly and consumer-friendly. Strategies against off-flavors must be efficient and low-cost. However, these solutions may be different for each fish production system. We review herein the main compounds produced by cyanobacteria that can accumulate in fish used in aquaculture that can affect the quality of food, as well as production costs and consumer preference.

Keywords: cyanobacteria; geosmin; 2-methylisoborneol; bioaccumulation



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1. Introduction

Aquaculture has grown worldwide annually; the sector has expanded significantly in recent years, and total production, trade, and consumption have reached all-time highs in recent years [1]. The world's aquaculture fish production inland was 47 million tons of live weight in 2018. The Asian continent has dominated the world's fish production, with an 89% share of aquaculture production in the last two decades. Among the main producing countries, China, India, Indonesia, Vietnam, Bangladesh, Egypt, Norway, Chile, and Brazil stand out [1,2].

Different aquaculture systems have been used for fish production, such as water-based systems (e.g., onshore/offshore), land-based systems (e.g., rainfed ponds, flow-through systems, tanks, and raceways), integrated farming systems (e.g., livestock-fish, agriculture, and fish dual-use aquaculture and irrigation ponds), recycling systems (e.g., high control enclosed systems, more open pond-based recirculation) [3].

However, recirculating aquaculture systems (RAS) have gained prominence, as they are indoor systems that permit fish farmers to manage environmental conditions year-round; they characterize an ideal alternative to open fish culture systems [4]. These systems may contribute to reducing environmental problems by minimizing water demand and managing effluent discharge [5]. However, several factors, such as the presence of phosphorus, micronutrients, and organic matter, can affect the quality of the water. Studies have shown that these compounds are associated with the heightened growth

of phytoplankton that can produce off-flavors as secondary metabolites [6–8]. These off-flavors are easily bioaccumulated by fish and reduce their market value [9].







Some microorganisms are responsible for synthesizing secondary metabolites that may alter the taste, odor, and color of foods, which are known as off-flavors and taste/odor compounds (TOCs). These metabolites are a major concern in a wide range of environments as they make end products undesirable [9–11]. Thus, it is important that the fish production system incorporates approaches that enable preventive actions, instead of having a large production of fish with off-flavor with reduced market value [12,13]. Therefore, the general objective of this review is to aggregate information about the main TOCs produced by cyanobacteria and other phytoplankton, how these compounds affect aquaculture, fish consumption and commercialization, and the main detection and purification methods.

2. Off-Flavor Compounds in the Environment: An Overview

Climate change and anthropogenic factors, such as nutrient enrichment, pollutant load, increased temperature, and exposure to sunlight, can lead to increased blooms of cyanobacteria and other phytoplanktonic species [14–16]. Usually, the blooms occur in summer and early autumn, a period with favorable conditions such as warmth, ample sunlight, and a stable or low water flow. These cyanobacterial blooms are generally responsible for the appearance of undesirable metabolites, are toxic in many cases or non-toxic as off-flavors [17] and are increasing annually worldwide [18,19].

The main derivatives of algae, fungi, cyanobacteria, and other microorganisms (*Actinomycetales* and *Myxococcales*) are commonly identified as terpenoids, carotenoid derivatives, fatty acids, and sulfur compounds [20–24]. These metabolites confer flavors and smell described as “earthy”, “muddy” or “moldy” [25]. Studies have described that the main metabolites that impart earthy, moldy and tobacco odor in water and food are the volatile compounds such as 2-methylisoborneol (MIB), geosmin (GEO), 2-isopropyl-3-methoxypyrazine (IPMP), 2-isobutyl-3-methoxypyrazine (IBMP), β -Cyclocitral, and β -Ionone [26–29]. The main physical-chemical properties of these compounds are presented in Table 1. Among the TOCs produced by cyanobacteria and other microorganisms, GEO, and MIB are the TOCs most commonly found in fish and water. They are also the most difficult to remove through oxidation, which is the process applied in water purification [6,30,31].

Table 1. Physico-chemical properties of main off-flavor TOCs.

Compound	Chemical Structure	Chemical Formula	Molecular Weight	CAS Number	Water Half-Life	Log Kow	Water Solubility (mg·cm ³)
MIB		C ₁₁ H ₂₀ O	168.3	2371-42-8	19.5 days	3.13	0.45
GEO		C ₁₂ H ₂₂ O	182.3	16423-19-1	24.5 days	3.7	0.0512
IPMP		C ₈ H ₁₂ N ₂ O	152.2	25773-40-4	n.a.	2.41	61.4
IBMP		C ₉ H ₁₄ N ₂ O	166.2	24683-00-9	n.a.	2.72	20.9
β -Ionone		C ₁₃ H ₂₀ O	192.2	14901-07-6	n.a.	2.9	0.104
β -Cyclocitral		C ₁₀ H ₁₆ O	152.2	432-25-7	n.a.	2.4	Insoluble

n.a. = not available.

Initially, GEO was isolated and identified as sesquiterpenoid alcohol degraded in cyanobacteria at the gills and skin, and are the main site of GEO and MIB on uptake due to contact with [32], while MIB was isolated as methyl monoterpene in actinomycetes [33]. *Anabaena* strains produce TOCs, and according to Oh et al. [34], this strain has shown that

the lowest MIB production was achieved at lower temperatures (<20 °C), while a lower production of GEO was achieved at high light intensity (>100 $\mu\text{mol}/\text{m}^2/\text{s}$) [34]. GEO is a semi-volatile metabolite that remains stored in vacuoles inside cells and its release to ambient water is due to the decomposition of cyanobacteria biomass or cell death [17]. Some researchers have shown that GEO is a residual metabolite that provides an energy benefit to bacteria production since more energy is required for the production of chlorophyll-a (Chl a) than for the production of GEO, and thus when cyanobacteria do not need Chl a, GEO production occurs. Although some studies are being carried out to understand the mechanisms of GEO production, its biological function in the cell has not yet been fully elucidated [35].

One of the first reports of MIB and GEO altering the flavor and quality of water and commercially farmed fish was in 1931, in the African lungfish *Protopterus aethiopicus*, and named by the Indians “mudfish” [36]. Since 1970, these episodes have been reported in the United States [37], the Netherlands [38], and Japan [39]. In addition, problems have been reported with changes in the taste and odor of water for human consumption in Asia, Australia, North America, and Europe [40]. Over the past two decades, the number of TOC episodes in treated water and customer complaints have increased [41]. Additionally, in some countries, consumer acceptance of off-flavors in water is mixed [42].

The production of fish, such as the rainbow trout (*Oncorhynchus mykiss*), tilapia (*Oreochromis niloticus* and *O. aureus*), Arctic charr (*Salvelinus alpinus*), largemouth bass (*Micropterus salmoides*), and Atlantic salmon (*Salmo salar*) in RAS have been affected by the presence of unpleasant flavors caused by GEO and MIB [9]. These metabolites have been found at high levels in fish reared in ponds, cages, and other farming systems, as well as in municipal water, causing off-flavor problems [43].

Humans are able to detect TOCs in water at concentrations of 10 ppt or less. Although several studies have shown that these metabolites are non-toxic and pose no risk to health or food safety [44,45], off-flavors have a major impact on taste and make consumers unwilling to buy or consume the final product. As a result, fish farmers must frequently analyze the quality of water and fish.

Studies have shown that in aquatic environments, the main producers of GEO and MIB are cyanobacteria of the genera *Anabaena*, *Aphanizomenon*, *Lyngbya*, *Oscillatoria*, *Phormidium*, *Planktothrix*, and *Pseudanabaena* [34], while in soil, the main producers of these metabolites are actinobacteria [24,46,47]. As cyanobacteria blooms are known to affect water and fish quality, the Australian government has initiated strategic management to prevent the occurrence of excess phytoplankton in drinking water through early analysis and monitoring of the number of cells and species present. Thus, it was possible to predict the magnitude of the problem and plan solution strategies [48]. Additionally, it is relevant to work to minimize the risks of having the bloom caused by the excess of cyanobacteria. Studies have shown that it is necessary to maintain constant monitoring of water nutrients, especially phosphorus and nitrogen [48,49], and to invest in a more advanced analysis that enables the prediction of the risk of blooming.

3. Off-Flavor Detection Methods

Sensory analyzes have been widely used in the assessment of fish and drinking water quality. According to Dietrich [50], standard methods include the use of tools, such as the odor threshold number (TON) and flavor profile analysis (FPA) for sensory analysis. These methods reflect the maximum level of dilution at which an odor is still perceptible. The revisions cited in [50] are based on gas chromatography coupled to mass spectrometry (GC/MS) with different strategies of extraction techniques that have been used to identify and quantify the types of several off-flavors [51,52]. Headspace solid-phase microextraction (HS-SPME) has been recommended as a suitable method for volatile compounds' quantitation in source water, due to its better selectivity towards target compounds [17,24]. Stir bar sorbent extraction (SBSE) is a technique that is highly sensitive to TOCs and has good

reproducibility [53,54]. In addition, several methods used to analyze TOCs more quickly and accurately are being developed [55,56].

Furthermore, molecular biology techniques have been studied to monitor and identify early microorganisms and genes involved in the production of TOCs in aquatic environments. In this sense, the *geoA* gene, which encodes the bi-functional enzyme GEO synthase, has been used as a molecular marker [20,23,56,57]. Additionally, the 16S rRNA gene is often used to identify prokaryotic microorganisms and cyanobacteria and has been combined with other markers, such as *geoA* for molecular analysis (Table 2). In addition, researchers have created a reference database in order to monitor the toxinogenic taxa that form blooms and act as an effective early warning system for the growth of potentially harmful blooms.

Genes involved in the synthesis of MIB were first identified in actinomycetes [58] and subsequently, these genes were also reported in cyanobacteria [20]. Phylogenetic analysis suggests that the MIB synthase gene was spread by horizontal transfer and that this gene has a common origin in cyanobacteria and actinomycetes. However, the organization of the genes was different in cyanobacteria, suggesting that recombination events may have occurred during evolution [59]. In any case, the biosynthetic mechanism of MIB occurs in two stages, first, a reaction occurs where geranyl diphosphate (GPP) is converted by methyltransferase into methyl-GPP, and then MIB synthase cyclizes methyl-GPP into MIB [58], while the GEO mechanism is related to the cyclization of the precursor sesquiterpene C15.

Table 2. Primer pairs were used for PCR and sequencing of *geoA*, MIB synthase, and 16S rRNA genes to assess concentrations of off-flavor compounds.

Target Gene	Primer	Sequence 5'-3'	Product Length	Reference
<i>geoA</i>	geo78F	GCATTCCAAAGCCTGGGCTTA	912 pb	[20]
	geo971R	CCCTYGTTCATGTARCGGC		
	geo982R	ATCGCATGTGCCACTCGTGAC	905 pb	
MIB synthase	MIB3313F	CTCTACTGCCCCATTACCGAGCGA	913 pb	[60]
	MIB4226R	GCCATTCAAACCCGCCGCCATCCA		
	MIB3324F	CATTACCGAGCGATTCAACGAGC	726 pb	
	MIB4050R	CCGCAATCTGTAGCACCATGTTGA		
16S rRNA	27F	AGAGTTTGATCMTGGCTCAG	850 pb	[61]
	1492R	TACGGYTACCTTGTTACGACTT		

Accurate diagnostic tools for detecting GEO and MIB producers are important in monitoring water reservoirs for quality purposes. The monitoring of microbial communities in aquaculture production can provide a tool for future microbial management in order to guarantee stability in fish production performance. In addition, biomolecular methods, such as conventional and quantitative PCR (qPCR), are widely used techniques. Furthermore, qPCR has been a great tool for the early detection and monitoring of cyanobacteria and toxins, especially when they are present in small quantities.

4. Transfer of Off-Flavor Compounds, Bioaccumulation in Fish, and Toxicity

Off-flavors in foods may derive from environmental pollutants, the growth of microorganisms or algae, oxidation of lipids, or endogenous enzymatic decomposition in foods. Additionally, these compounds can be absorbed and accumulated in fish tissues [61]. According to Aschner et al. [62], earthy flavors in fish grown in tanks with phytoplankton are common, suggesting that fish can absorb off-flavors, such as GEO and MIB not only by osmosis but also by feeding on the biomass of phytoplankton (cyanobacteria).

Recent studies have also shown that off-flavors were present in the stomach and intestinal mucous layer of fish, suggesting that fish can actively feed on potential off-flavor-producing organisms [23,31,63]. The accumulation of off-flavors may vary due to different feeding habitats. According to Papp et al. [64], insignificant levels of MIB were found

in five important species cultivated in Hungarian aquaculture: the planktivorous silver carp (*Hypophthalmichthys molitrix*), the herbivorous grass carp (*Ctenopharyngodon idella*), the omnivorous common carp (*Cyprinus carpio*), the omnivorous Nile tilapia (*Oreochromis niloticus*) and the carnivorous African catfish (*Clarias gariepinus*), however the highest concentrations of GSM were found in the bottom-feeding common carp fillet, being higher than in the silver carp or African catfish.

Furthermore, TOCs can be absorbed and accumulated in lipid-rich fish tissues, since GEO and MIB have lipophilic properties, and due to this characteristic, tend to accumulate in fishes with a higher fat content [65]. In fishes, it is assumed that the gills and skin are the main sites of GEO and MIB on uptake due to the contact with water with off-flavors [65]. The absorption of GEO through the skin, intestine, and stomach has also been proposed as an alternative source. Studies through sensory analysis have shown that the absorption and digestion of cyanobacteria containing GEO could result in the accumulation of GEO in fish flesh [63,66,67]. Lukassen et al. [23] described the high abundance of GEO-producing microorganisms in the intestinal mucous and also digesta, suggesting that the digestive system in fish is a relevant source of GEO and probably other off-flavours in fish that until now, has been neglected.

While GEO and MIB are absorbed and accumulate in fish quickly, compound clearance is a slow process that takes several days to reach a level below human perception; for example, sensory thresholds of 0.9 µg/kg for GEO and 0.7 µg/kg for MIB in rainbow trout have been suggested [67–69].

The toxicity of TOCs is frequently found in experiments with human cells and most results show low effects. According to Burgos et al. [70], only 2-MIB and GEO concentrations above 100 and 75 µg/mL, respectively, were cytotoxic to HepG2 cells (human liver cells). Additionally, the concentrations studied were not able to induce DNA damage.

Usually, when cytotoxicity is observed, the concentrations of these off-flavors are much higher than those that occur in aquatic environments and fish. Thus, environmentally relevant concentrations of GEO and MIB are not expected to exhibit cytotoxicity or genotoxicity to humans. Considering the low toxicity of GEO and MIB, there are a limited number of studies on the biological effects on human health of off-flavors.

5. Depuration of Off-Flavors in Fish

Numerous processes have been studied and tested to eliminate or reduce the formation of GEO, MIB, and other TOCs in RAS, as well as ozonation [71], advanced oxidation processes (AOPs) [72], algicides [73], adsorption, i.e., with activated carbon [69], zeolites [74], and ultrasonic methods. According to Nam-Koong et al. [75], ultrasound-induced cavitation significantly reduces TOCs in tap water and both freshwater RAS and saltwater RAS. However, it is still necessary to perform studies of this treatment in RAS to assess its economic and technical viability.

Photocatalysis-based methods, such as modified TiO₂ with sunlight and palladium-modified tungsten trioxide photocatalyst, have been studied [76,77]. This technique uses degradation by means of light (oxidation/reduction), which is caused by the activation of a catalyst resulting from ultraviolet (UV) or visible radiation to which it has been subjected. Currently, this method is considered promising, since it has been used to remove GEO and MIB in drinking water [78]. However, the implementation of this technique on a full scale in RAS is still unfeasible due to the impossibility of carrying out the process with a batch reactor and the high cost of the process [79].

Despite the diversity of methods presented, depurating using clean water is still the most effective process available to eliminate off-flavors [65,80]. This occurs because it is a relatively simple and highly effective method, based on the idea that with the circulating aqueous environment and a concentration gradient, the bioaccumulated compounds will be diffused freely out of the fish [68,81].

Depuration can take from days to weeks, depending on several factors, such as preliminary concentrations of GEO and MIB, the volume of water available in the process, the

species, and the size of the fish [69], in addition to other factors such as water temperature [81–84]. According to Lu [85], the concentration of MIB and GEO in the dorsal and ventral tissue of Japanese sea bass (*Lateolabrax japonicus*) decreased by 50% after 10 days of depuration. The lipid content and weight of fish are directly correlated with the ability to absorb off-flavor compounds such as GEO and MIB, since these compounds are lipophilic [81]. During the depuration process, fish are not fed, ensuring a good water quality and having the most effective depuration possible, which can lead to significant weight loss and generate financial losses [80]. Therefore, it is essential that the depuration is performed as quickly and efficiently as possible.

According to an experiment carried out by Lindholm-Lehto et al. [85], the feeding of European whitefish (*Coregonus lavaretus*) during the process of depuration of TOCs resulted in a significant increase in the rate of elimination of GEO from the ovary—this being a more rapid elimination compared to hungry fish. In addition, the retention of food during long periods of purification causes a reduction of fish weight, lipid content, and color of the fillet, resulting in lower quality products [69].

Lipophilic compounds such as off-flavors are eliminated from fish by passive diffusion through the gills and/or skin, or by metabolizing these compounds into more polar compounds that are excreted in the urine (via the kidneys) or the feces (secreted in bile—gallbladder) [86,87]. Pharmacokinetic studies of MIB in catfish have shown a rapid total clearance of the compound [82,83], suggesting that urinary excretion is responsible for only a minor portion of total loss and elimination through the gills or rapid biotransformation with subsequent clearance of metabolites.

Sensory analyzes showed that approximately 6 days of purification in clean water were required for the GEO concentrations to decrease below the concentration of the sensory threshold, going from 90 µg/kg to 8 µg/kg in channel catfish [83,88]. GEO appears to be eliminated a little more slowly from rainbow trout than from channel catfish [89], probably because the low water temperatures used in trout culture reduce the rate at which the compound is eliminated from the fish. Studies have shown that water temperature is an important variable for clearance, and the higher the temperature, the greater the elimination of these compounds due to a decreased oxygen solubility and increased branchial ventilation [68,81].

Fish may eliminate MIB more quickly than GEO. Studies have indicated that depuration rates are affected by fish lipid content and water temperature [83,88,90], and that extremely fatty fish kept in cold water (<10 °C) may require a week or more to eliminate the unpleasant taste. Under depuration conditions (lean fish temperatures and hot water), the fish can be purified from the TOCs in less than 60 h. However, Lindholm-Lehto et al. [65] described that it takes up to 16 days to eliminate MIB in European whitefish, but a shorter time could be sufficient to eliminate GEO. In this study, the authors mixed clean water into the circulating water, which would consequently wash away off-flavor compounds over a longer depuration time. Additionally, the GEO decrease in compounds occurred in a very similar way in all parts of the body of the fish, even though the initial concentrations were different [65]. In addition, the fat content decreased by up to 50% compared to the original values during clearance and showed the effect of fasting. However, optimizing the depuration time is crucial to reduce production costs while still producing high-quality fish products.

Thus, several studies are being developed in order to reduce RAS depuration time [80]. In this sense, Davidson et al. [89] tested different operational cleaning methods and according to their results, cleaning systems without water aeration in the gas transfer columns resulted in a greater and faster reduction of the TOCs in Atlantic salmon (*Salmo salar*) in RAS.

6. Effects of Off-Flavors and Consequences for Producer and Consumer

Several studies have analyzed consumer behavior and the acceptability of food based on sensory (taste, flavor, texture, color, appearance), safety, and nutritional properties [91–94].

In recent decades, healthy eating habits have received greater attention, and it is widely recognized that the regular consumption of fish is a possible practice that improves health [95,96]. Due to its nutritional properties and an awareness of healthy eating, fish consumption has increased worldwide [1,97]. Therefore, it is necessary to produce high-quality food that is more attractive to consumers [97].

The 2020 edition of the State of The World Fisheries and Aquaculture of the United Nations Food and Agriculture Organization (FAO/UN) showed that world aquaculture production grew approximately 5.3% per year in the period from 2001 to 2018 [1]. In addition, aquaculture for human consumption, totaling 57 million tons, surpassed aquaculture for non-food purposes, which was responsible for 30.5% of the total production in 2018 [98].

Furthermore, flavor changes in fish flesh are characterized as low product quality and are generally not appreciated by consumers. Consequently, this results in a large reduction in fish consumption and negatively affects the marketing of aquaculture products [8], representing one of the most significant economic problems in aquaculture [8,69]. According to Petersen et al. [67], sales of channel catfish in the United States decreased by about 30% due to off-flavors in fish. Similarly, in Europe, there was also an incidence of off-flavors in fish, which resulted in losses of up to 20% for UK trout farmers. In France, one in four rainbow trout had severe concentrations of TOCs, which also resulted in losses for farmers.

Due to the high cost of fish production, producers have been looking for alternatives to improve fish quality and reduce production costs. Nevertheless, in these attempts, some producers can raise the cost and reduce the quality. In Thailand, for example, fertilizers are added to tilapia culture water to induce the natural growth of algae, which are used as natural food for fish, thus reducing capital investment, however, the depuration process is expensive [43,99]. In addition, a loss of fish weight during depuration and the death of some fish due to moving to new tanks can generate additional costs. Some evaluations point out that the removal of off-flavors raises the annual costs of 10–60 million US dollars for catfish producers, while others have assessed an increase of 0.25 US dollars per kg of fish [100,101].

Studies have compared the production and economic performance of fish in different management systems. According to Whangchai et al. [43] significantly higher amounts of chlorophyll-a and off-flavor were found in terrestrial lagoons compared to the cage culture, suggesting that cultivation in lakes may be more expensive due to the cost of the purification process. As previously mentioned, unfortunately, depuration is a laborious process that requires a large volume of water and can generally take days to weeks. Thus, the removal of off-flavors can inflict a significant economic loss, due to delays in harvesting and the high cost of drinking clean water [17,25,69,101].

7. Conclusions

The production and consumption of fish as human food has grown in recent decades; however, intensive fish production and high food supply can favor the development of phytoplankton, especially cyanobacteria. The occurrence of cyanobacterial blooms can cause serious consequences from aquaculture, as cyanobacteria produce secondary metabolites capable of altering the taste and odor of water and the quality of fish. Although these substances (GEO and MIB, mainly) are not toxic, they are not appreciated by consumers and negatively affect the marketing of aquaculture products. Based on toxicity data, off-flavors in freshwater fish present a low risk to consumers; however, it may indicate fish were cultivated in the presence of cyanobacteria and eutrophic conditions.

Additionally, the lipid content and weight of the fish are directly correlated with the ability to absorb compounds with a strange taste, such as GEO and MIB, since these compounds are lipophilic. In this context, the elimination of these compounds is an expensive and slow process, in addition to requiring large amounts of water to reach a level below human perception. Therefore, it is considered of great importance to use accurate tools for the monitoring and early detection of the presence of microorganism producing TOCs or TOCs even in low concentrations, such as highly sensitive molecular biology and

analytical chemistry techniques to avoid expenses associated with the purification process to eliminate undesirable flavors. For all these aspects, this review synthesizes information regarding the main TOCs produced by cyanobacteria and other phytoplankton, how these compounds affect the consumption and commercialization of fish, and the main detection and purification methods.

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