

**Research Article**

## Systematic review on off-flavors caused by geosmin and 2-methylisoborneol in aquatic products

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**ABSTRACT.** This systematic review examines off-flavors in farmed freshwater fish, which compromise sensory quality and consumer acceptance, resulting in financial losses. Using the PRISMA method, 7,576 documents from the Scopus and Web of Science databases were analyzed, resulting in the selection of 44 studies published within the last six years. The articles were examined for their objectives, studied species, farming systems, main findings, gaps, and suggestions for future research. The studies highlight the influence of water quality, climatic conditions, management practices, and feeding, with an emphasis on the presence of cyanobacteria, algal blooms, fungi, and metabolic compounds, particularly geosmin and 2-methylisoborneol, which are the main contributors to unpleasant tastes and odors. The review highlights the need to enhance management practices and control of these compounds, while also suggesting new research to develop more effective and accessible mitigation methods. The importance of continuous water quality monitoring is emphasized as an essential strategy to prevent the formation of off-flavors. In summary, the review provides a comprehensive overview of undesirable tastes and odors in freshwater fish, identifies knowledge gaps, and proposes directions for future investigations, which are crucial for the sustainability and quality of aquaculture production.

**Keywords:** Cyanobacteria; economic impact; freshwater fish; water quality; sensory quality; water quality management

### INTRODUCTION

Freshwater aquaculture has been increasingly established as a strategic solution to meet the growing global demand for sustainable animal proteins (Silva & Piana 2020, Lopes et al. 2022, Silva et al. 2024), emerging as one of the world's leading methods for protein production (Pettersson et al. 2022). According to the FAO (2024) report, global fish production reached a historic milestone in 2022, with aquaculture surpassing capture fisheries for the first time, accounting for 51% of total protein production. This growth highlights the increasing importance of aquaculture in achieving global food security, particularly

given that freshwater ecosystems, which cover less than 1% of the Earth's surface, harbor approximately half of the planet's fish diversity (Barbarossa et al. 2021).

Among economically valuable freshwater species, the Nile tilapia (*Oreochromis niloticus*) stands out as one of the most widely farmed fish in Brazil and globally (Arumugam et al. 2023), accounting for approximately 75% of global tilapia production and about 8.3% of total aquaculture output (FAO 2024). Tilapia is highly valued for its adaptability to different farming systems and the quality of its meat. However, the increase in production has led to challenges related to the sensory quality of fish, primarily due to the formation of compounds responsible for off-flavors,

unpleasant tastes, and odors (Colonia et al. 2023). Compounds such as geosmin (GSM) and 2-methylisoborneol (MIB), produced by certain bacteria and algae present in freshwater environments and aquaculture systems, are frequently responsible for these sensory alterations. When accumulated in fish tissues, these compounds alter the flavor of the product, often resulting in an undesirable taste commonly described as earthy or musty, which affects consumer acceptance and, consequently, the industry's profitability (Sun et al. 2023, Cheatham et al. 2024).

The objective of this study was to conduct a systematic review on off-flavors in farmed fish, focusing on the causes, detection methods, mitigation strategies, and commercial impacts of GSM and MIB compounds. These compounds pose a significant concern for the aquaculture industry, as they not only impact sensory quality but can also lead to substantial economic losses (Imsland et al. 2020). The detection and quantification of these substances in water and fish samples have been essential for understanding the extent of contamination and its sources (Lindholm-Lehto et al. 2019a). Additionally, various approaches, such as dietary modifications for fish, water purification treatments, and advanced oxidation techniques, have been explored as mitigation strategies to reduce the formation of these compounds and improve the sensory quality of farmed fish (Zorzi et al. 2023).

Thus, this study is justified by the need for a deeper understanding of the factors influencing the formation of off-flavors in farmed fish and the strategies that can be implemented to minimize their impact. The implementation of effective off-flavor control practices is crucial for ensuring the competitiveness and sustainability of aquaculture, thereby contributing to the production of high-quality fish that meet the demands of the global consumer market.

This review will examine the primary causes, detection methodologies, and proposed solutions to mitigate the effects of these compounds, as well as the commercial implications for the aquaculture industry, providing a comprehensive overview of the challenges and advancements in off-flavor control.

## MATERIALS AND METHODS

This systematic review was conducted under the PRISMA 2020 (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines, ensuring transparency, reproducibility, and methodological rigor, as outlined by Page et al. (2021). By

adhering to the PRISMA 2020 framework, the flowchart ensures transparency, traceability, and methodological rigor, thereby facilitating both comprehension and reproducibility of the systematic review process.

The literature search was performed using the Scopus and Web of Science databases. The search covered peer-reviewed articles published between 2019 and 2024, in English, with a specific focus on off-flavor issues in fish species raised in freshwater aquaculture systems, particularly in fish farming contexts. The selection of this time frame reflects the intent to identify the most recent developments and innovations related to off-flavor control strategies in response to intensified aquaculture practices, higher stocking densities, and increasing occurrence of undesirable compounds in aquatic environments.

The search strategy was structured using the descriptors: "off-flavor," "geosmin," "2-methylisoborneol," "freshwater," "aquaculture," "fish farm," and "water quality." Initially, 7,576 documents were identified. Filters were then applied sequentially to select articles relevant to aquaculture, freshwater systems, fish farms, and article type (research articles only), reducing the pool to 83 articles. Through further refinement, incorporating terms related to volatile compounds and water quality, 44 studies were identified as highly relevant. Review articles, editorials, and letters to the editor were excluded, resulting in the removal of a total of 39 articles.

The data extraction process was standardized and included key elements such as:

- a) Specific compounds causing off-flavor.
- b) Methods used for detection (physical, chemical, genetic, sensory).
- c) Strategies proposed for mitigation (technological, dietary, environmental).
- d) Commercial and sensory impacts on production and the market.
- e) Types of cultivation systems employed.

To facilitate data interpretation, the 44 selected studies were categorized into four analytical groups:

- 1) Causes: environmental, microbiological, and nutritional factors contributing to off-flavor formation (14 studies).
- 2) Impacts: sensory perceptions and economic repercussions within the production chain (9 studies).
- 3) Detection: identification techniques for undesirable compounds (5 studies).
- 4) Mitigation: strategies for control and removal of off-flavor compounds (16 studies).

Additionally, a year-by-year analysis of publications and citations from 2019 to 2024 was conducted. The Table 1 was developed to present the number of studies published per year, total citations, and the average impact factor (IF), calculated as the ratio of total citations to the number of publications ( $IF = \text{total citations} / \text{total publications}$ ). This analysis illustrates trends in scientific output, with particular attention to the period between 2019 and 2022, which was notably affected by the COVID-19 pandemic, resulting in global disruptions to research activities.

The evaluation of methodological quality across the included studies considered the clarity and rigor of methodological descriptions, the transparency of reported results, and the practical applicability of proposed solutions. This approach enabled a qualitative synthesis of current knowledge and trends, offering insights into the challenges and innovations surrounding off-flavor control in freshwater aquaculture.

## RESULTS

Table 1 presents quantitative analysis of the scientific production related to off-flavor in fish raised in freshwater aquaculture systems, covering the period from 2019 to August 2024. The data were obtained from the Scopus and Web of Science databases and demonstrate a trend of growth in both the volume of publications and the number of citations over the considered period. It is observed that the period from 2019 to 2022 was significantly impacted by the COVID-19 pandemic, during which lockdown measures resulted in the disruption of research activities worldwide. Despite this, the health crisis also fostered increased interest in the resilience of food production, including aquaculture, which contributed to a notable resurgence in scientific output and citations starting from 2022. These data reflect the growing scientific and practical relevance of the topic, evidenced by the increase in impact metrics over recent years.

Figure 1 illustrates the sequential steps involved in selecting the studies, from initial identification to final inclusion based on eligibility criteria. The process encompasses the stages of searching, screening, selecting, data extraction, and critical analysis, offering a comprehensive overview of the methodological decisions made throughout the systematic review.

The continuous growth in the number of publications over the years, accompanied by a notable increase in citations, particularly since 2022 is shown (Fig. 2).

**Table 1.** Number of publications and citations per year based on search results from Scopus and Web of Science databases.

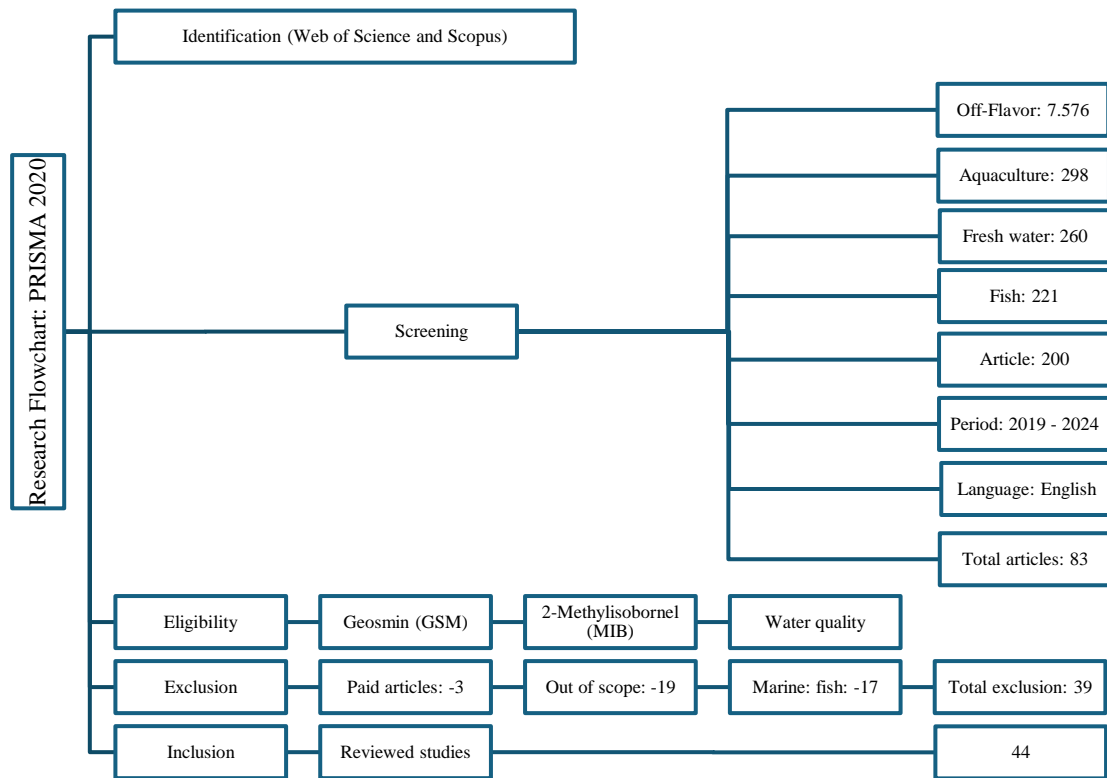
Year	Number of publications	Number of citations	Impact factor	Included in the final analysis
2019	16	5	0.31	8
2020	11	50	4.55	5
2021	17	97	5.71	6
2022	15	162	10.80	6
2023	16	243	15.19	13
2024	8	202	25.25	6
<b>Total</b>	<b>83</b>	<b>642</b>	<b>17.83</b>	<b>44</b>

It presents the number of articles published each year, along with their respective citation counts. The relationship between these data reveals the average citation rate per publication, providing insights into the visibility and impact of the research. Despite fluctuations in publication volume, the overall trend of increasing citations highlights the growing importance and recognition of studies investigating compounds with unpleasant tastes in freshwater aquaculture. This trend can be attributed not only to the effects of the pandemic but also to the rising relevance of aquaculture in global food production.

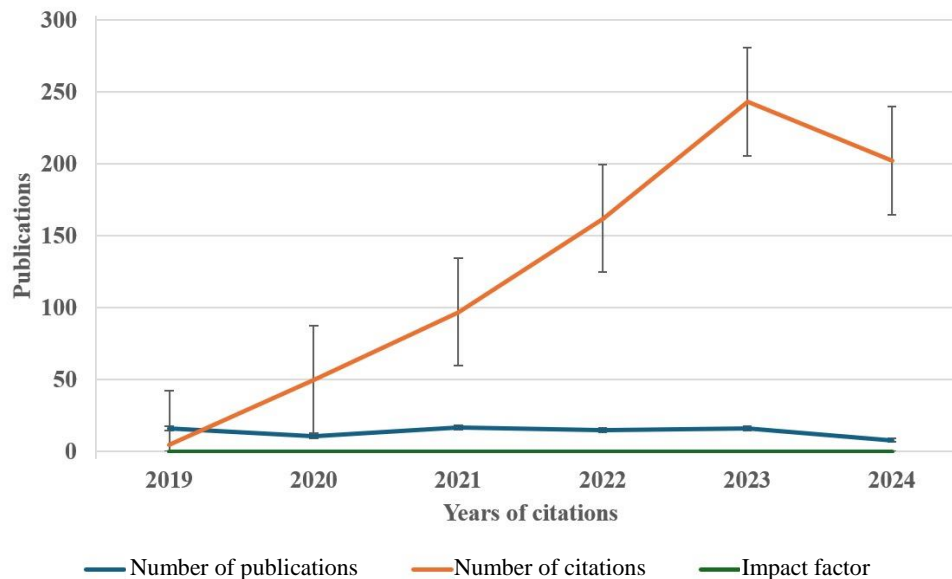
Among the 83 publications initially identified, a total of 642 citations were recorded, resulting in an average of approximately 7.73 citations per article and an h-index of 14, which indicates that at least 14 of the 83 articles were cited 14 times or more, suggesting a strong and consistent research impact. After the screening and selection phases, 44 publications, published between January 2019 and August 2024, met the inclusion criteria and were considered for an in-depth qualitative synthesis.

The citation analysis showed an upward trend, indicating the increasing importance of the selected studies. In 2019, 16 articles were published, resulting in a total of just 5 citations, with an average of approximately 0.31 citations per article, indicating a limited initial impact. In 2020, despite a decrease in the number of publications to 11, these articles were cited 50 times, resulting in an average of approximately 4.55 citations per article. This upward trend continued in the following years, highlighting the growing academic interest in the topic.

The number of articles was included in the final set of 44 studies. In comparison, 39 studies were excluded due to reasons such as insufficient relevance, inadequate methodological description, or failure to meet predefined criteria (including publication type, language, period, or focus on freshwater aquaculture). This filtering process helps clarify the methodology and



**Figure 1.** Search and exclusion criteria - PRISMA 2020, in the Scopus and Web of Science databases.



**Figure 2.** Evolution of articles and citations from January 2019 to August 2024.

reinforces the rigor of the review, ensuring that the selected studies are the most relevant and reliable for the analysis.

In 2021, the number of publications increased to 17, with a total of 97 citations, resulting in an average of approximately 5.71 citations per article, indicating a

growing impact. In 2022, despite a decrease in the number of publications to 15, the number of citations rose significantly to 162, resulting in an average of approximately 10.80 citations per article. By 2023, 16 articles were published and received a total of 243 citations, with an average of approximately 15.19 citations per article. As of August 2024, 8 articles have accumulated 202 citations, corresponding to an average of about 25.25 citations per article. The number of citations exceeding the number of publications reflects the exceptional influence of recent research.

In 2024, despite a smaller number of articles published, the average number of citations per article reached its highest point, reinforcing the growing recognition of the quality and relevance of recent studies. Overall, the trend indicates a sustained increase in the impact and visibility of publications addressing compounds with unpleasant taste in freshwater aquaculture.

When analyzing publication data by country from 2019 to 2024, significant disparities in research output across regions are evident. Table 2 provides a clear overview of the distribution of the 83 selected studies by country, highlighting the dominance of specific nations. The USA led with 36.14% of the publications, indicating strong research activity. Following that, China accounted for 21.69%, while Finland contributed 12.69%. Denmark and Brazil had shares of 8.64 and 6.2%, respectively. Other countries represented less than 5% each, reflecting more modest and dispersed international contributions.

This distribution reflects a concentration of scientific production in specific countries, which may be influenced by factors such as research infrastructure, funding availability, and national research priorities. The dominance of the USA, China, Finland, Denmark, and Brazil suggests that these nations have established robust research environments that facilitate higher publication outputs. Understanding these patterns is crucial for identifying opportunities to promote international collaboration, particularly with countries that contribute less to the global research landscape. Addressing these disparities can help promote a more equitable distribution of knowledge and encourage broader global engagement in research activities. Recognizing the underlying factors behind this uneven distribution also highlights the importance of investing in research capacity-building in underrepresented regions to diversify and strengthen the international scientific community.

Table 3 presents the list of the 44 articles selected for the final analysis, organized into four main categories:

**Table 2.** Distribution of publications by country.

Country	Number of publications	%
USA	30	36.14
China	18	21.69
Finland	10	12.05
Denmark	8	9.64
Brazil	5	6.02

causes, impacts, detection, and mitigation. These categories represent the different aspects addressed by the studies concerning the central theme of the research. Table 4 presents the number of articles categorized into each category, providing an overview of the thematic distribution among the analyzed works. These thematic classifications will be explored in more detail in the upcoming sections of the paper, where each group will be examined more thoroughly to gain a deeper understanding of their approaches, findings, and contributions within the context of the study.

## DISCUSSION

The analysis of studies on off-flavors in modern aquaculture reveals that undesirable compounds, such as GSM and MIB, are frequently identified as the primary contributors to earthy or musty flavors, which negatively impact both the sensory quality and commercial value of aquatic products. These volatile compounds, classified as sesquiterpenoids, are commonly associated with organisms such as algae (*Aphanizomenon*, *Oscillatoria*, *Nostoc*, and *Anabaena*) and bacteria from the genus *Streptomyces*, including *S. griseus* and *S. coelicolor*.

Additionally, environmental factors, management practices, and nutritional strategies play a significant role in the formation of these compounds. However, the accurate detection of GSM and MIB poses challenges for producers, requiring specialized labor and advanced analytical techniques, such as chromatography and mass spectrometry.

Various approaches for mitigating or eliminating off-flavors have been discussed in the literature, including strict control of farming conditions and post-harvest treatments such as filtration and ozonation. The economic and commercial impacts associated with these compounds are substantial, resulting in significant losses for the industry, including both mitigation costs and reduced consumer acceptance. Studies highlight the need for integrated management and the implementation of cost-effective technological

**Table 3.** Quantitative analysis of articles reviewed and classified according to their respective categories.

Category	Number	Relevance
Identification of causes	14	Fundamental for understanding the factors contributing to the formation of off-flavors.
Detection methods	5	Essential for the effective monitoring of odor-causing compounds.
Mitigation	16	Highlights the efforts to develop control strategies for off-flavors.
Impacts on aquaculture and the market	9	Emphasizes the practical relevance of the topic in aquaculture and the market.
<b>Total</b>	<b>44</b>	The analysis encompasses a diverse range of studies on off-flavors.

**Table 4.** Articles analyzed in the review are classified according to their respective categories.

Author(s)	Article title	Category
Azaria et al. (2020)	Changes in the bacterial community structure of denitrifying sludge from a recirculating aquaculture system (RAS) after GSM and MIB enrichment.	Causes
Davidson et al. (2018)	Evaluating the microbial effects of stocking freshwater snails ( <i>Physa gyrina</i> ) in water re-use systems culturing rainbow trout ( <i>Oncorhynchus mykiss</i> ).	Causes
Dupre et al. (2023)	Dietary uptake of geosmin in rainbow trout ( <i>Oncorhynchus mykiss</i> ).	Causes
Green et al. (2019)	Effects of dietary protein content on hybrid tilapia ( <i>Oreochromis aureus</i> × <i>O. niloticus</i> ) performance, common microbial off-flavor compounds, and water quality dynamics in an outdoor biofloc technology production system.	Causes
Green et al. (2021)	Impact of dietary phytase on tilapia performance and biofloc water quality.	Causes
Li et al. (2024)	Fugacity and kinetic models reveal specific-fate of geosmin in air-water-fish microcosm and channel catfish ( <i>Ictalurus punctatus</i> ).	Causes
Li et al. (2023)	Shift of phytoplankton and microbial communities cause seasonal dynamics of odor compounds in <i>Oncorhynchus mykiss</i> cultured in a freshwater reservoir.	Causes
Lindholm-Lehto et al. (2020)	Accumulation of geosmin and 2-methylisoborneol in European whitefish <i>Coregonus lavaretus</i> and rainbow trout <i>Oncorhynchus mykiss</i> in RAS.	Causes
Lindholm-Lehto et al. (2022)	Off-flavors and lipid components in rainbow trout ( <i>Oncorhynchus mykiss</i> ) reared in RAS: Differences in families of low and high lipid contents.	Causes
Lukassen et al. (2019)	Microbial production of the off-flavor geosmin in tilapia production in Brazilian water reservoirs: importance of bacteria in the intestine and other fish-associated environments.	Causes
Lukassen et al. (2022)	Impact of water quality parameters on geosmin levels and geosmin producers in European recirculating aquaculture systems.	Causes
Mahmoud & Magdy (2021)	Metabarcoding profiling of microbial diversity associated with trout fish farming.	Causes
Podduturi et al. (2023)	Characterization and finding the origin of off-flavor compounds in Nile tilapia cultured in net cages in hydroelectric reservoirs, São Paulo State, Brazil.	Causes
Schrader (2019)	Effects of relevant ammonium chloride concentrations on biomass and off-flavor compound production by <i>Streptomyces luridiscabiei</i> originating from a recirculating aquaculture system.	Causes
Silva et al. (2024)	Identification of odor-active compounds in Nile tilapia ( <i>Oreochromis niloticus</i> ) from recirculated aquaculture systems: A case study with different depuration procedures.	Detection
Lopes et al. (2022)	Off-flavor detection in tilapia reared in cages in tropical lakes.	Detection
Schrader (2022)	Flavor wheel for sensory analysis of fish raised in recirculating aquaculture systems.	Detection
Sun et al. (2023)	Off-flavor profiling of cultured salmonids using hyperspectral imaging combined with machine learning.	Detection
Tian et al. (2021)	An effective and efficient sample preparation method for 2-methyl-isoborneol and geosmin in fish and their analysis by gas chromatography-mass spectrometry.	Detection

Continuation

Author(s)	Article title	Category
Baten et al. (2020)	Effect of hot smoking treatment in improving sensory and physicochemical properties of processed Japanese Spanish mackerel <i>Scomberomorus niphonius</i> .	Mitigation
Buley et al. (2021)	Field evaluation of seven products to control cyanobacterial blooms in aquaculture.	Mitigation
Davidson et al. (2020)	Depuration system flushing rate affects geosmin removal from market-size Atlantic salmon, <i>Salmo salar</i> .	Mitigation
Davidson et al. (2021)	Effects of swimming speed and dissolved oxygen on geosmin depuration from market-size Atlantic salmon, <i>Salmo salar</i> .	Mitigation
Davidson et al. (2024)	Evaluating the feasibility of feeding RAS-produced Atlantic salmon ( <i>Salmo salar</i> ) during the depuration process: effects on fish weight loss and off-flavor remediation.	Mitigation
Kropp et al. (2022)	A novel advanced oxidation process (AOP) that rapidly removes geosmin and 2-methylisoborneol (MIB) from water and significantly reduces depuration times in Atlantic salmon <i>Salmo salar</i> RAS aquaculture.	Mitigation
Lindholm-Lehto et al. (2019a)	Depuration of geosmin-and 2-methylisoborneol-induced off-flavors in recirculating aquaculture system (RAS) farmed European whitefish <i>Coregonus lavaretus</i> .	Mitigation
Lindholm-Lehto et al. (2019b)	Effect of peracetic acid on levels of geosmin, 2-methylisoborneol, and their potential producers in a recirculating aquaculture system for rearing rainbow trout ( <i>Oncorhynchus mykiss</i> ).	Mitigation
Pettersson et al. (2022)	Effect of ozone and hydrogen peroxide on off-flavor compounds and water quality in a recirculating aquaculture system.	Mitigation
Podduturi et al. (2021)	Case study on depuration of RAS-produced pikeperch ( <i>Sander lucioperca</i> ) for removal of geosmin and other volatile organic compounds (VOCs) and its impact on sensory quality.	Mitigation
Rodriguez-Gonzalez et al. (2018)	Oxidation of off-flavor compounds in recirculating aquaculture systems using UV-TiO <sub>2</sub> photocatalysis.	Mitigation
Schram et al. (2021)	Effect of feeding during off-flavour depuration on geosmin excretion by Nile tilapia ( <i>Oreochromis niloticus</i> ).	Mitigation
Zhang et al. (2023)	Fishy odorants in pre-processed fish fillet and surimi products made from freshwater fish: Formation mechanism and control methods.	Mitigation
Zhou et al. (2023)	Depuration and starvation regulate metabolism and improve flesh quality of yellow catfish ( <i>Pelteobagrus fulvidraco</i> ).	Mitigation
Zorzi et al. (2023)	The application of advanced oxidation processes including photocatalysis-based ones for the off-flavours removal (GSM and MIB) in recirculating aquaculture systems.	Mitigation
Zou et al. (2023)	Starvation alters gut microbiome and mitigates off-flavors in largemouth bass ( <i>Micropterus salmoides</i> ).	Mitigation
Cheatham et al. (2024)	Cost and impact of off-flavor on U.S. catfish farms.	Impacts
Davidson et al. (2023)	Water quality, waste production, and off-flavor characterization in a depuration system stocked with market-size Atlantic salmon, <i>Salmo salar</i> .	Impacts
FAO (2024)	The state of the world fisheries and aquaculture (SOFIA 2024)	Impacts
Gharti et al. (2023)	Growth and muscle quality of grass carp ( <i>Ctenopharyngodon idella</i> ) in in-pond raceway aquaculture and traditional pond culture.	Impacts
Han et al. (2024)	Histology and transcriptomic analysis reveal the inflammation and affected pathways in grass carp following exposure to 2-methylisoborneol (2-MIB).	Impacts
Imsland et al. (2020)	Effect of rearing temperature on flesh quality in Arctic charr ( <i>Salvelinus alpinus</i> ).	Impacts
Lindholm-Lehto et al. (2023)	Quality of rainbow trout ( <i>Oncorhynchus mykiss</i> ) reared in recirculating aquaculture system and during depuration based on chemical and sensory analysis.	Impacts
Silva & Piana (2020)	Production of tilapia in biofloc with different salt conditions: An evaluation of body composition and organoleptic properties.	Impacts
Zhang et al. (2024)	Comprehensive mRNA and microRNA analysis revealed the effect and response strategy of freshwater fish, grass carp ( <i>Ctenopharyngodon idella</i> ) under geosmin exposure.	Impacts

solutions to ensure the quality and competitiveness of aquatic products in the global market.

### Causes

The sensory quality of aquatic products, particularly in terms of flavor and aroma, is a crucial factor for consumer acceptance in the market. Undesirable compounds, which are known for imparting unpleasant flavors, such as GSM and MIB, are frequently found in fish farmed in aquaculture systems. These compounds are associated with various biological, environmental, dietary, and management factors.

Several studies highlight the relationship between microbial communities and the formation of odorant compounds in aquaculture systems. Cyanobacteria such as *Aphanizomenon*, *Oscillatoria*, and *Anabaena* are responsible for producing volatile compounds like GSM and MIB, particularly under specific environmental conditions, such as high phosphorus concentrations and elevated temperatures. Li et al. (2023) observed that the concentrations of these compounds peak during summer when cyanobacteria proliferate. Additionally, water quality control measures, such as phosphorus reduction, can be an effective strategy to limit the production of odorant compounds.

Microbiological studies, such as those by Davidson et al. (2018) and Azaria et al. (2020), emphasize that the presence of *Streptomyces* bacteria, as well as interactions between microorganisms and odorant compounds, plays a crucial role in off-flavor formation. The microbial diversity in water can influence the formation of these compounds both positively and negatively, making the management of aquatic microbiota a strategic approach in recirculating aquaculture systems.

The microbiota in aquaculture farms also has a significant impact on the formation of off-flavor compounds. Mohamoud & Magdy (2021) highlighted that microbial diversity in water affects both the sensory quality of fish and the overall health of the aquatic environment. Zhou et al. (2023) investigated how fasting affects the gut microbiota of black bass and reduces the formation of odorant compounds, suggesting that dietary interventions could be an additional effective strategy for improving fish quality and minimizing negative sensory impacts.

Additionally, Mohamoud & Magdy (2021) discussed the impact of external agricultural and industrial practices on aquaculture areas, identifying that microbiological imbalances caused by these factors could intensify the production of undesirable compounds in aquaculture systems.

Another critical factor in off-flavor formation is fish feeding and dietary management. Studies such as those by Green et al. (2021) and Dupre et al. (2023) demonstrate that diet plays a predominant role in the accumulation of compounds like GSM and MIB. GSM, for instance, is primarily absorbed through feeding, meaning that the selection of feed sources can directly impact the levels of odorant compounds in fish tissues.

Lukassen et al. (2022) observed that fish with higher lipid content tend to accumulate greater concentrations of lipophilic compounds, such as GSM. Therefore, controlling the lipid profile of fish through dietary adjustments may be an effective approach to mitigating the formation of off-flavors in fish. Similarly, Li et al. (2024) indicated that diet management aimed at reducing lipid accumulation or controlling lipid composition could serve as a strategy to minimize the effects of odorant compounds in fish.

Likewise, Lopes et al. (2022) discussed how diet and nutritional management can be used to regulate the accumulation of odorant compounds, particularly through the modulation of the protein-to-energy ratio in fish feed. However, as noted by the same authors, this approach is not universally applicable and depends on environmental and genetic factors, making standardization challenging.

Beyond dietary and microbiological factors, environmental conditions such as water temperature play a significant role in the formation of odorant compounds. Imsland et al. (2020) investigated the impact of temperature on the sensory quality of Arctic char (*Salvelinus alpinus*), demonstrating that manipulating environmental factors, such as lowering rearing temperatures, can enhance fish quality. While the study did not specifically focus on off-flavor compounds, it suggests that optimizing farming conditions may positively impact texture, appearance, and overall sensory acceptance, complementing existing off-flavor control strategies.

The choice of farming system also influences the formation of off-flavors. Gharti et al. (2023) compared intensive pond recirculating aquaculture (IPRA) and total pond culture (TPC) systems, finding that while IPRA is more efficient in promoting fish growth and lipid quality, it is associated with higher levels of odorant compounds, highlighting a classic dilemma in aquaculture, where increased productivity does not always translate into improved sensory quality. Intensive farming systems, such as IPRA, require strict control of water quality and dietary management to prevent the formation of off-flavors. On the other hand, TPC, with lower stocking density, demonstrated lower



concentrations of these compounds but was less efficient in terms of growth and lipid quality.

### Impacts

The accumulation of odorant compounds such as GSM and MIB in farmed fish has raised significant concerns regarding consumer sensory acceptance, in addition to causing substantial economic impacts on the aquaculture industry. Several studies have shown that these compounds, often associated with earthy and musty flavors, directly affect fish quality and undermine their competitiveness in the market.

Gharti et al. (2023) analyzed the impact of the raceway aquaculture system on carp farming. They observed that, although this system yielded the best results in terms of weight gain and lipid quality, it also led to a higher concentration of MIB, compromising the sensory acceptance of the product. These findings align with those of Lindholm-Lehto et al. (2020, 2022), who reported the accumulation of GSM and MIB in various fish species, including tilapia, catfish, trout, and salmon, farmed in recirculating aquaculture systems, confirming the persistence of this issue despite productivity improvements.

The economic losses associated with the formation of these odorant compounds are considerable. Cheatham et al. (2024) estimated the annual management costs of off-flavors in the USA catfish aquaculture industry at US\$40 million, with total losses reaching approximately US\$73.9 million. These figures are consistent with the findings of Buley et al. (2021), who estimated annual losses of US\$23 million due to the effects of substances such as *Microcystis* and undesirable flavor compounds like GSM and MIB. A comparison between these studies reveals a substantial increase in economic losses, with Cheatham et al. (2024) reporting a significant rise, amounting to an additional US\$13 million in the year following their study.

Beyond economic losses, off-flavor compounds directly impact consumer acceptance of the product. The literature highlights the difficulty in detecting these compounds through sensory means at low concentrations, making control even more challenging. Despite technological innovations and management strategies, the economic impact remains a central issue. As emphasized by several studies, the costs associated with mitigating odorant compounds are substantial, and the financial viability of aquaculture operations depends on implementing solutions that strike a balance between technical effectiveness, environmental sustainability, and economic feasibility.

### Detections

The detection and monitoring of off-flavor compounds, such as GSM and MIB, in farmed fish have proven to be a complex and multidisciplinary challenge, involving sensory, chemical, microbiological, and technological approaches. The impact of these compounds on the sensory quality of fish, and consequently, on consumer acceptance, is a primary concern for the aquaculture industry. Several studies have addressed the detection and mitigation strategies for these compounds, providing crucial insights into improving the quality of the final product.

Several studies emphasize the significance of sensory and physicochemical methods in evaluating fish quality. Baten et al. (2020) conducted a comprehensive analysis of the sensory characteristics of fish, including appearance, odor, flavor, texture, and color, while also evaluating physicochemical and microbiological properties. Their research demonstrated how the presence of off-flavor compounds alters the sensory properties of fish, negatively affecting consumer acceptance. Similarly, Lindholm-Lehto et al. (2023) quantified odorant compounds during fish cultivation and the depuration process in RAS, observing a significant reduction in GSM and MIB during depuration, which led to improvements in sensory quality. The comparison between these approaches highlights the importance of understanding how off-flavor compounds are formed and removed during the cultivation and treatment processes.

Lopes et al. (2022) expanded the analysis of odorant compound concentrations, emphasizing the importance of continuous monitoring in both water and fish tissues. Their study highlighted the impact of depuration on reducing these compounds and emphasized the necessity of regular monitoring to ensure the final product's quality. Regarding fish lipid composition, Liu et al. (2022) observed that the distribution of off-flavor compounds in ventral and dorsal tissues can be influenced by lipid concentration. Diets with higher lipid content resulted in lower levels of polyunsaturated fatty acids (PUFAs), such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). In contrast, lower-lipid diets were associated with higher concentrations of these beneficial acids and greater accumulation of off-flavor compounds. These findings suggest that dietary manipulation may be an effective strategy for reducing undesirable sensory effects.

In addition to physicochemical and sensory approaches, microbiology and genetics have emerged as powerful tools for understanding the origins of off-flavor compounds. Mohamoud & Magdy (2021) used

genetic sequencing to characterize the microbiota in trout farming waters, identifying microorganisms associated with the production of odorant compounds. Molecular analysis provided a detailed understanding of how certain microorganisms contribute to the formation of these compounds, enabling more targeted microbiological control strategies in aquaculture systems.

Pettersson et al. (2022) and Podduturi et al. (2023) expanded on this research by exploring the use of oxidative treatments to reduce GSM and MIB concentrations in aquaculture waters. The combination of physicochemical treatments and microbiological monitoring has shown promising results, although its effectiveness depends on implementing integrated strategies that address both water quality and microbial management.

Recent technological advances have enabled faster and more precise detection of off-flavor compounds. Near-infrared hyperspectral imaging (NIR-HSI) combined with machine learning, as demonstrated by Sun et al. (2023), offers an innovative solution for real-time monitoring of fish sensory quality. This technology enables the detection of undesirable compounds with high accuracy, eliminating the need for sample destruction and representing a significant advancement for the industry. Zou et al. (2023) and Zhang et al. (2024) also employed genetic sequencing to investigate how organisms respond to GSM exposure, examining metabolic and bacterial changes associated with the formation of off-flavor compounds. These genetic and molecular approaches provide deeper insights into the biological processes influencing odorant compound production, offering new strategies for their mitigation.

The detection of off-flavored compounds in aquaculture is a multidisciplinary research field that combines sensory, chemical, microbiological, and technological approaches. Advances in monitoring methodologies, such as the use of NIR-HSI and genetic sequencing, have provided new opportunities for the rapid and non-destructive detection of off-flavor compounds. The application of oxidative treatments and the regulation of lipid composition in fish diets have also proven to be effective strategies for mitigating the sensory impacts of these compounds.

However, the effectiveness of these approaches still depends on the implementation of integrated management systems that consider water quality, microbiological control, fish diet, and depuration technologies. The combination of these strategies, along with the use of advanced monitoring and

detection technologies, has the potential to significantly improve the sensory quality of fish and ensure consumer acceptance. Furthermore, these solutions must be tailored to various farming conditions and the specific needs of the industry, promoting both sustainability and efficiency in aquaculture.

### Mitigations

The mitigation of odorant compounds such as GSM and MIB has been a critical area of aquaculture research, particularly in intensive farming systems, due to the negative impact these compounds have on fish sensory quality and, consequently, consumer acceptance. A multidisciplinary approach, as highlighted by the selected studies, suggests that no single solution exists; instead, an effective reduction of these compounds requires a combination of dietary strategies, microbiological control, management of the aquatic environment, and technological innovations. An integrated analysis of these strategies is essential to overcoming quality and sustainability challenges in fish production.

Several studies have highlighted the crucial role of dietary management as an effective strategy for mitigating off-flavor compounds. Green et al. (2019) and Lopes et al. (2022) explored the relationship between diet composition and odorant compound formation, suggesting that reducing digestible protein in tilapia diets can lower GSM production without compromising productivity. Green et al. (2021) also proposed the use of phytase to reduce phosphorus load in water, which helps minimize the negative effects of off-flavor compounds by improving nutrient efficiency and reducing the environmental impact of RAS systems.

Lopes et al. (2022) further investigated the relationship between digestible protein and digestible energy (DP/DE), emphasizing that balanced diets can not only enhance sensory quality but also reduce environmental impact by lowering nutrient loads in water. These approaches are essential, as they optimize productivity while directly addressing both sensory and environmental challenges.

Microbiological control is another key strategy for mitigating off-flavors, as evidenced by studies conducted by Lindholm-Lehto et al. (2019a,b) and Azaria et al. (2020). Azaria et al. (2020) demonstrated that the presence of odorant compounds, such as GSM and MIB, alters bacterial communities in RAS systems, favoring the growth of bacteria like *Thauera* and *Comamonas*, which are capable of metabolizing these compounds. These findings underscore the importance

of biofilters and biological processes in water purification, which must be optimized to eliminate odorant compounds effectively.

On the other hand, Lindholm-Lehto et al. (2019b) investigated the use of peracetic acid (PAA) as an alternative for reducing odorant compounds. However, they acknowledged that PAA alone is insufficient to eliminate the problem completely. Therefore, it is suggested that the effectiveness of depuration depends on a combination of biological and chemical factors to efficiently remove compounds such as GSM and MIB.

Technological innovations have also shown great potential in mitigating off-flavor compounds. The use of advanced oxidation processes (AOPs), such as UV-TiO<sub>2</sub> photocatalysis and ozone treatment, has been explored as an effective method for removing odorant compounds from water, as highlighted by Pettersson et al. (2022) and Zorzi et al. (2023). Although photocatalysis is efficient in batch mode, it faces limitations in continuous-flow systems due to the speed of water circulation, highlighting the need for optimization in dynamic RAS environments.

Baten et al. (2020) explored fish smoking as a technique to reduce off-flavor compounds, presenting an interesting application of a traditional method. Smoking not only helps decrease odorant compounds but also preserves beneficial fatty acids such as DHA and EPA, which are essential for the nutritional quality of fish. Additionally, this process extends the product's shelf life, making it more competitive in the market.

Beyond dietary and technological strategies, environmental factors also play a crucial role in fish sensory quality. Imsland et al. (2020) observed that temperature directly influences fish texture and sensory attributes, with lower temperatures leading to improved sensory quality. This factor, combined with careful management of environmental conditions such as water renewal and oxygenation, can be utilized to optimize depuration processes and enhance fish quality.

In the context of depuration, Davidson et al. (2020, 2021) investigated the influence of variables such as swimming speed and dissolved oxygen concentration. Although these factors did not show a substantial impact on GSM depuration, the results suggest that balancing environmental conditions with fish physiology is necessary to optimize depuration processes.

Gut microbiota modulation has also emerged as a promising strategy, particularly in light of the findings of Lukassen et al. (2019), which suggest that the intestine, rather than the gills, plays a central role in the production and absorption of GSM. The use of

probiotics to manipulate gut microbiota could be an innovative approach to reducing the formation of off-flavor compounds, offering a natural and effective solution to improve fish sensory quality. Additionally, Zhou et al. (2023) demonstrated that fasting can alter gut microbiota and reduce odorant compounds, highlighting the potential of microbiome management to optimize fish quality.

Mitigating off-flavor compounds is a multifaceted challenge that necessitates an integrated approach. While studies by Buley et al. (2021) on cyanobacterial bloom control and Schrader (2022) on feeding during depuration highlight the importance of environmental and dietary management, the most effective solution for removing compounds such as GSM and MIB may lie in combining multiple strategies. The use of advanced oxidative treatments, microbiological control, water depuration, and dietary adjustments can work synergistically to improve sensory quality and enhance the sustainability of RAS systems.

In summary, mitigating off-flavor compounds in aquaculture requires a holistic and multidisciplinary approach. Dietary strategies, microbiological control, environmental optimization, and technological innovations -such as photocatalysis and advanced oxidation-have shown potential to improve the sensory quality of fish cultivated in RAS systems. However, integrating these approaches, considering technical, economic, and environmental factors, is essential to achieving effective and sustainable solutions. Implementing more efficient and environmentally friendly strategies will be crucial to ensuring the competitiveness and sustainability of aquaculture in the future.

## CONCLUSIONS

The systematic review on off-flavors in aquaculture revealed that the generation and accumulation of odorant compounds, such as GSM and MIB (the main identified odor-causing compounds), are influenced by several interconnected factors. These factors include climatic conditions, water quality, stocking density, management practices, and the type of farming systems used. These compounds directly compromise the sensory quality of fish, impacting consumer acceptance and the industry's competitiveness in the global market.

While there are several strategies to mitigate the formation of off-flavors (such as purification, advanced oxidation processes, the use of algacides, or dietary adjustments), all of these approaches involve additional operational or technological costs. Thus, the key to

effective and sustainable management of odorant compounds lies in integrating different methods, which must be adapted to the specific characteristics of each farming system and local environmental conditions.

In conclusion, advancing high-quality and sustainable aquaculture depends on carefully balancing technical effectiveness, economic feasibility, and environmental impact. The combination of these strategies can not only enhance fish sensory quality but also contribute to reducing the environmental footprint of aquaculture, making it more competitive and responsible. The continuous development of innovative technologies, combined with enhanced management practices, will be crucial in addressing off-flavor challenges and promoting a more sustainable future for the industry.

#### Credit the author's contribution

Oswaldo Gois Santos: methodology, formal analysis, investigation, data curation, writing-original draft; Adriana Jornooki: formal analysis, investigation, writing-review & editing; Eduardo Luis Cupertino Ballester: conceptualization, validation, supervision, project administration, writing-review and editing.

#### Conflict of interest

The authors declare that they have no conflict of interest.

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#### REFERENCES

- Arumugam, M., Jayaraman, S., Sridhar, A., et al. 2023. Recent advances in tilapia production for sustainable development in Indian aquaculture and its economic benefits. *Fishes*, 8: 176. doi: 10.3390/fishes8040176
- Azaria, S., Post, A.F. & van Rijn, J. 2020. Changes in the bacterial community structure of denitrifying sludge from a recirculating aquaculture system (RAS) after geosmin and 2-methylisoborneol enrichment. *Current Microbiology*, 77: 353-360. doi: 10.1007/s00284-019-01844-z
- Barbarossa, V., Bosmans, J., Wanders, N. et al. 2021. Threats of global warming to the world's freshwater fishes. *Nature Communications*, 12: 1701. doi: 10.1038/s41467-021-21655-w
- Baten, M.A., Won, N.E., Mohibullah, M., et al. 2020. Effect of hot smoking treatment in improving sensory and physicochemical properties of processed Japanese Spanish mackerel *Scomberomorus niphonius*. *Food Science & Nutrition*, 8: 3957-3968. doi: 10.1002/fsn3.1715
- Buley, R.P., Adams, C., Belfiore, A.P., et al. 2021. Field evaluation of seven products to control cyanobacterial blooms in aquaculture. *Environmental Science and Pollution Research International*, 28: 29971-29983. doi: 10.1007/s11356-021-12708-0
- Cheatham, M., Kumar, G., Tucker, C.S., et al. 2024. Cost and impact of off-flavor on U.S. catfish farms. *North American Journal of Aquaculture*, 86: 267-276. doi: 10.1002/naaq.10342
- Colonia, B.S.O., Pereira, G.V.M., Carvalho, J.C., et al. 2023. Deodorization of algae biomass to overcome off-flavors and odor issues for developing new food products: Innovations, trends, and applications. *Food Chemistry Advances*, 2: 100270. doi: 10.1016/j.focha.2023.100270
- Davidson, J., Grimm, C., Summerfelt, S., et al. 2020. Depuration system flushing rate affects geosmin removal from market-size Atlantic salmon (*Salmo salar*). *Aquacultural Engineering*, 90: 102104. doi: 10.1016/j.aquaeng.2020.102104
- Davidson, J., Plautz, C.Z., Grimm, C., et al. 2018. Evaluating the microbial effects of stocking freshwater snails (*Physa gyrina*) in water reuse systems culturing rainbow trout (*Oncorhynchus mykiss*). *Journal of Applied Aquaculture*, 31: 97-120. doi: 10.1080/10454438.2018.1541771
- Davidson, J., Redman, N., Crouse, C., et al. 2023. Water quality, waste production, and off-flavor characterization in a depuration system stocked with market-size Atlantic salmon (*Salmo salar*). *Journal of the World Aquaculture Society*, 54: 96-112. doi: 10.1111/jwas.12920
- Davidson, J., Schrader, K., May, T., et al. 2024. Evaluating the feasibility of feeding RAS-produced Atlantic salmon (*Salmo salar*) during the depuration process: effects on fish weight loss and off-flavor remediation. *Journal of Applied Aquaculture*, 36: 436-456. doi: 10.1080/10454438.2023.2259892
- Davidson, J., Summerfelt, S., Grimm, C., et al. 2021. Effects of swimming speed and dissolved oxygen on geosmin depuration from market-size Atlantic salmon (*Salmo salar*). *Aquacultural Engineering*, 95: 102201. doi: 10.1016/j.aquaeng.2021.102201
- Dupre, R.A., Ardoin, R., Trushenski, J., et al. 2023. Dietary uptake of geosmin in rainbow trout

- (*Oncorhynchus mykiss*). *Aquaculture*, 571: 739458. doi: 10.1016/j.aquaculture.2023.739458
- Food and Agriculture Organization (FAO). 2024. The state of the world fisheries and aquaculture. FAO, Rome.
- Gharti, K., Yan, L., Li, K., et al. 2023. Growth and muscle quality of grass carp (*Ctenopharyngodon idella*) in in-pond raceway aquaculture and traditional pond culture. *Water*, 15: 1771. doi: 10.3390/w15091771
- Green, B.W., Rawles, S.D., Schrader, K.K., et al. 2019. Effects of dietary protein content on hybrid tilapia (*Oreochromis aureus* × *O. niloticus*) performance, common microbial off-flavor compounds, and water quality dynamics in an outdoor biofloc technology production system. *Aquaculture*, 503: 571-582. doi: 10.1016/j.aquaculture.2019.01.034
- Green, B.W., Rawles, S.D., Schrader, K.K. et al. 2021. Impact of dietary phytase on tilapia performance and biofloc water quality. *Aquaculture*, 541: 736845, 2021. doi: 10.1016/j.aquaculture.2021.736845
- Han, H., Zhang, J.M., Ji, S., et al. 2024. Histology and transcriptomic analysis reveal the inflammation and affected pathways under 2-methylisoborneol (2-MIB) exposure on grass carp. *Science of The Total Environment*, 938: 173233. doi: 10.1016/j.scitotenv.2024.173233
- Imsland, A.K.D., Ólafsdóttir, A., Árnason, J., et al. 2020. Effect of rearing temperature on flesh quality in Arctic charr (*Salvelinus alpinus*). *Aquaculture Research*, 52: 1063-1070. doi: 10.1111/are.14961
- Kropp, R., Summerfelt, S.T., Woolever, K., et al. 2022. A novel advanced oxidation process (AOP) that rapidly removes geosmin and 2-methylisoborneol (MIB) from water and significantly reduces depuration times in Atlantic salmon (*Salmo salar*) RAS aquaculture. *Aquacultural Engineering*, 97: 102240. doi: 10.1016/j.aquaeng.2022.102240
- Li, S., Fayi, W., Dong, X., et al. 2023. Shift of phytoplankton and microbial communities cause seasonal dynamics of odor compounds in *Oncorhynchus mykiss* cultured in a freshwater reservoir. *Aquaculture*, 570: 739422. doi: 10.1016/j.aquaculture.2023.739422
- Li, Z., Zhong, L., Chen, X., et al. 2024. Fugacity and kinetic models reveal specific fate of geosmin in air-water-fish microcosm and channel catfish (*Ictalurus punctatus*). *Aquaculture Reports*, 38: 102290. doi: 10.1016/j.aqrep.2024.102290
- Lindholm-Lehto, P., Koskela, J., Kaseva, J., et al. 2020. Accumulation of geosmin and 2-methylisoborneol in European whitefish (*Coregonus lavaretus*) and rainbow trout (*Oncorhynchus mykiss*) in RAS. *Fishes*, 5: 13. doi: 10.3390/fishes5020013
- Lindholm-Lehto, P.C., Koskela, J., Leskinen, H., et al. 2022. Off-flavors and lipid components in rainbow trout (*Oncorhynchus mykiss*) reared in RAS: Differences in families of low and high lipid contents. *Aquaculture*, 559: 738418. doi: 10.1016/j.aquaculture.2022.738418
- Lindholm-Lehto, P.C., Logrén, N., Mattila, S., et al. 2023. Quality of rainbow trout (*Oncorhynchus mykiss*) reared in recirculating aquaculture system and during depuration based on chemical and sensory analysis. *Aquaculture Research*, 1: 3537294. doi: 10.1155/2023/3537294
- Lindholm-Lehto, P.C., Suurnäkki, S., Pulkkinen, J.T., et al. 2019b. Effect of peracetic acid on levels of geosmin, 2-methylisoborneol, and their potential producers in a recirculating aquaculture system for rearing rainbow trout (*Oncorhynchus mykiss*). *Aquacultural Engineering*, 85: 56-64. doi: 10.1016/j.aquaeng.2019.02.002
- Lindholm-Lehto, P.C., Vielma, J., Pakkanen, H., et al. 2019a. Depuration of geosmin- and 2-methylisoborneol-induced off-flavors in recirculating aquaculture system (RAS) farmed European whitefish (*Coregonus lavaretus*). *Journal of Food Science and Technology*, 56: 4585-4594. doi: 10.1007/s13197-019-03910-7
- Liu, J., Izquierdo, M.S., Caballero, M.J., et al. 2022. Necessity of dietary lecithin and eicosapentaenoic acid for growth, survival, stress resistance and lipoprotein formation in gilthead sea bream *Sparus aurata*. *Fisheries Science*, 68: 6. doi: 10.1046/j.1444-2906.2002.00551.x
- Lopes, T.O.M., Pinto, E., Passos, L.S., et al. 2022. Off-flavor detection in tilapia reared in cages in tropical lakes. *Aquaculture*, 555: 738215. doi: 10.1016/j.aquaculture.2022.738215
- Lukassen, M.B., Jonge, N., Bjerregaard, S.M., et al. 2019. Microbial production of the off-flavor geosmin in tilapia production in Brazilian water reservoirs: Importance of bacteria in the intestine and other fish-associated environments. *Frontiers in Microbiology*, 10: 2447. doi: 10.3389/fmicb.2019.02447
- Lukassen, M.B., Menanteau-Ledouble, S., Jonge, N., et al. 2022. Impact of water quality parameters on geosmin levels and geosmin producers in European recirculating aquaculture systems. *Journal of Applied Microbiology*, 132: 2475-2487. doi: 10.1111/jam.15358

- Mahmoud, M.A.A. & Magdy, M. 2021. Metabarcoding profiling of microbial diversity associated with trout fish farming. *Scientific Reports*, 11: 421. doi: 10.1038/s41598-020-80236-x
- Page, M.J., McKenzie, J.E., Bossuyt, P.M., et al. 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *British Medical Journal*, 372: 71. doi: 10.1136/bmj.n71
- Pettersson, S.J., Lindholm-Lehto, P.C., Pulkkinen, J.T., et al. 2022. Effect of ozone and hydrogen peroxide on off-flavor compounds and water quality in a recirculating aquaculture system. *Aquacultural Engineering*, 98: 102277. doi: 10.1016/j.aquaeng.2022.102277
- Podduturi, R., Petersen, M.A., Vestergaard, M., et al. 2021. Case study on depuration of RAS-produced pikeperch (*Sander lucioperca*) for removal of geosmin and other volatile organic compounds (VOCs) and its impact on sensory quality. *Aquaculture*, 530: 735754. doi: 10.1016/j.aquaculture.2020.735754
- Podduturi, R., Silva-David, G., Silva, R.J., et al. 2023. Characterization and finding the origin of off-flavor compounds in Nile tilapia cultured in net cages in hydroelectric reservoirs, São Paulo State, Brazil. *Food Research International*, 173: 113375. doi: 10.1016/j.foodres.2023.113375
- Rodriguez-Gonzalez, L., Pettit, S.L., Zhao, W., et al. 2018. Oxidation of off-flavor compounds in recirculating aquaculture systems using UV-TiO<sub>2</sub> photocatalysis. *Aquaculture*, 502: 10. doi: 10.1016/j.aquaculture.2018.12.022
- Schrader, K.K. 2019. Effects of relevant ammonium chloride concentrations on biomass and off-flavor compound production by *Streptomyces luridiscabiei* originating from a recirculating aquaculture system. *Journal of Applied Aquaculture*, 32: 1-6. doi: 10.1080/10454438.2019.1610540
- Schrader, K.K. 2022. Flavor wheel for sensory analysis of fish raised in recirculating aquaculture systems. *North American Journal of Aquaculture*, 85: 87-91. doi: 10.1002/naaq.10275
- Schram, E., Kwadijk, C., Hofman, A., et al. 2021. Effect of feeding during off-flavour depuration on geosmin excretion by Nile tilapia (*Oreochromis niloticus*). *Aquaculture*, 531: 735883. doi: 10.1016/j.aquaculture.2020.735883
- Silva, T.S. & Piana, P.A. 2020. Production of tilapia in biofloc with different salt conditions: An evaluation of body composition and organoleptic properties. *Boletim do Instituto de Pesca*, 46: 537. doi: 10.20950/1678-2305.2020.46.1.537
- Silva, M.R., Loos, H.M. & Buettner, A. 2024. Identification of odor-active compounds in Nile tilapia (*Oreochromis niloticus*) from recirculated aquaculture systems: A case study with different depuration procedures. *Food Research International*, 192: 114755. doi: 10.1016/j.foodres.2024.114755
- Sun, D., Zhou, C., Hu, J., et al. 2023. Off-flavor profiling of cultured salmonids using hyperspectral imaging combined with machine learning. *Food Chemistry*, 408: 135166. doi: 10.1016/j.foodchem.2022.135166
- Tian, L.L., Han, F., Fodjo, E.K., et al. 2021. An effective and efficient sample preparation method for 2-methyl-isoborneol and geosmin in fish and their analysis by gas chromatography-mass spectrometry. *International Journal of Analytical Chemistry*, 2021: 9980212. doi: 10.1155/2021/9980212
- Zhang, J.-M., Han, H., Li, Y.-C., et al. 2024. Comprehensive mRNA and microRNA analysis revealed the effect and response strategy of freshwater fish, grass carp (*Ctenopharyngodon idella*) under geosmin exposure. *Ecotoxicology and Environmental Safety*, 269: 115775. doi: 10.1016/j.ecoenv.2023.115775
- Zhang, H., Xiong, S., Yu, X., et al. 2023. Fishy odorants in pre-processed fish fillet and surimi products made from freshwater fish: Formation mechanism and control methods. *Trends in Food Science & Technology*, 142: 104212. doi: 10.1016/j.tifs.2023.104212
- Zhou, Y., Xiong, Y., He, X., et al. 2023. Depuration and starvation regulate metabolism and improve flesh quality of yellow catfish (*Pelteobagrus fulvidraco*). *Metabolites*, 13: 1137. doi: 10.3390/metabo13111137
- Zorzi, V., Bertini, A., Robertson, A., et al. 2023. The application of advanced oxidation processes including photocatalysis-based ones for the off-flavours removal (GSM and MIB) in recirculating aquaculture systems. *Molecular Catalysis*, 551: 113616. doi: 10.1016/j.mcat.2023.113616
- Zou, S., Ni, M., Liu, M., et al. 2023. Starvation alters gut microbiome and mitigates off-flavors in largemouth bass (*Micropterus salmoides*). *Folia Microbiologica*, 68: 547-558. doi: 10.1007/s12223-022-01027-7

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