Journal of Agriculture and Food Research 26 (2026) 102615

Contents lists available at ScienceDirect

Journal of Agriculture and Food Research

journal homepage: www.sciencedirect.com/journal/journal-of-agriculture-and-food-research

# Feeding during off-flavour purging in recirculating aquaculture systems? An exploratory characterisation of waterborne and feedborne odour-active compounds in Russian sturgeon (*Acipenser gueldenstaedtii)*

Matteo Egiddi [a,b], Mariana Rodrigues da Silva [b], Eva Ortner [a], Bastien Debeuf [c], Helene M. Loos [a,b,d], Andrea Buettner [a,b], Jonathan Beauchamp [a,*]

[a] *Fraunhofer-Institute for Process Engineering and Packaging IVV, Giggenhauser Str. 35, 85354, Freising, Germany*
[b] *Chair of Aroma and Smell Research, Department of Chemistry and Pharmacy, Friedrich-Alexander Universität Erlangen-Nürnberg, Henkestraße 9, 91054, Erlangen, Germany*
[c] *SCEA Sturgeon, 29 Rue du Carillon, 17240, Saint Fort sur Gironde, France*
[d] *Institute of Nutritional and Food Sciences, Rheinische Friedrich-Wilhelms-Universität Bonn, Käthe-Kümmel-Str. 1, 53115, Bonn, Germany*

ARTICLE INFO

*Keywords:*
Geosmin
Depuration
Off-odours
RAS
Diet
Absorption
Feed

ABSTRACT

Off-flavours are a major challenge in recirculating aquaculture systems (RAS), with geosmin and 2-methylisoborneol (2-MIB) among key contributors to *earthy* taints. Purging unfed fish in flow-through (FT) water is a standard strategy for off-flavour removal, yet it entails high costs. This descriptive study examined off-flavour development in Russian sturgeon (*Acipenser gueldenstaedtii*) reared in two systems (RAS and FT depuration) under fed or unfed conditions. Sturgeon fillets, water of both systems, and the commercial feed were analysed via gas chromatography–mass spectrometry/olfactometry (GC–MS/O) combined with aroma extract dilution analysis (AEDA), leading to the identification of 85 odour-active compounds. Water and fillets from RAS showed greater off-odour diversity and potency in terms of their flavour dilution (FD) factors, including geosmin, 2-MIB, 1,3-benzothiazole and pyrazines. In contrast, water and fillets from depuration exhibited fewer off-odours and more desirable notes, such as *green*, *fruity* and *popcorn-like* attributes. The influence of feeding was system-dependent: in depuration, fed animals exhibited lower FD values of key compounds (e.g., geosmin) but higher odour diversity, including both pleasant (e.g., *mushroom-like, citrus-like*) and unpleasant (e.g., *ink-like, sweaty, pungent*) notes, whereas in RAS, lower compound diversity and minor odour profile differences were detected in fed sturgeons. Although not statistically relevant, observed differences between groups arose from shifts in relative odour attribute frequencies, compound diversity and FD values across water types and between feeding groups. Overall, sturgeon fed during depuration exhibited a preferable odour profile and a lower geosmin level, but new feedborne odorants were also introduced. The hypotheses generated in this study warrant future targeted sensory assessments and suggest formulation of finishing feeds that can mitigate off-odours and improve the marketability of RAS-reared fish.

## 1. Introduction

Aquaculture products, particularly those from recirculating aquaculture systems (RAS), often face challenges in meeting consumer sensory expectations due to the accumulation of exogenous odour-active compounds that lead to off-flavours [1–3]. These volatile organic compounds (VOCs) are absorbed via both water respiration and dietary intake, impairing seafood palatability and leading to consumer rejection and decreased market demand [4,5]. Most research on the undesirable sensory characteristics of RAS-grown seafood hitherto has focused on geosmin ((*4S,4aS,8aR*)-4,8a-dimethyloctahydronaphthalen-4a(2*H*)-ol), a sesquiterpenoid derivative with a strong *earthy, mouldy* odour, and 2-methylisoborneol (2-MIB; 1,2,7,7-tetramethylbicyclo[2.2.1]heptan-2-ol), a monoterpene derivative eliciting a strong *musty, wet soil* odour [3]. Other potent waterborne off-odours include various other terpenoids, sulphurous compounds, and pyrazines, although these are scarcely reported in the literature due to the paucity of untargeted sensory studies [6]. Off-odour compounds are often secondary

* Corresponding author.
*E-mail address:* jonathan.beauchamp@ivv.fraunhofer.de (J. Beauchamp).

https://doi.org/10.1016/j.jafr.2025.102615
Received 23 September 2025; Received in revised form 19 December 2025; Accepted 24 December 2025
Available online 10 January 2026
2666-1543/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

metabolites produced by microorganisms that are readily accumulated in fish tissue during water recirculation due to their lipophilic nature [7–9].

While some waterborne malodours are well-documented, the role of feed as a source of off-odours has received limited attention, to date. Recent comprehensive reviews have highlighted the dietary bioaccumulation of multiple odorants in aquaculture seafood, such as sulphurous and brominated compounds, as well as oxidation products of fatty acids [6,10]. Additionally, several feed-derived odorants, such as β-ionone, butanoic acid, or indole and geosmin itself [11–13], have been observed to be absorbed from raw feed ingredients extracted from fish, terrestrial animals, or plants, or originate due to post-extrusion oxidation of feed pellets during storage [6,10]. Moreover, the dietary uptake of feedborne odorants may represent an opportunity to positively modulate fish flavour, for instance by masking the presence of off-odours or introducing palatable aromas in fish flesh. Nevertheless, the complex interplay of oxidative processes and the combinatory absorption of compounds from multiple sources remains insufficiently characterised, to date.

The removal of off-odours in recirculating systems typically relies on 'purging' the fish at the end of production cycles prior to harvesting, a technique which often involves starvation in flow-through (FT) water systems for extended periods [4]. This common approach initially induces metabolic changes associated with the oxidation of fatty acids, causing a reduction in lipid reserves, and can subsequently generate metabolic shifts towards protein catabolism as a primary energy source [14]. Ultimately, such processes represent fish welfare imposition and result in significant losses of valuable biomass and a greater consumption of water. While alternative strategies, such as advanced oxidation processes (AOPs) or ultraviolet (UV) light treatments, have been tested, these have proven largely ineffective at scale due to increased costs and associated environmental implications [3,15]. Financial evaluations of the impact of off-odours are scarce, but significant costs due to sensory defects have been reported, including a total economic loss to the industry in 2022 of an estimated $74 million, a 15 % revenue decline in North American catfish production, and € 8 million annual loss in the European Union [5,6,16–18]. These values are likely underestimated due to the ongoing expansion of RAS production coupled with minimal progress in mitigating the off-odour issue, thus current economic costs may be substantially greater. In general, such reported losses primarily account for direct costs associated with depuration processes and fish weight loss during purging, but fail to include the substantial indirect costs, such as depuration labour and facilities, delays in harvesting, as well as implications from reputational damage [19,20].

Recent studies have suggested that feeding during depuration may support the elimination of off-odours, but the underlying mechanisms are not fully understood, with evidence remaining limited. In Nile Tilapia, for instance, feeding was found to accelerate the rate of geosmin elimination [21], an effect hypothesised to result from increased ventilation and elevated concentrations of lipids in blood. Higher blood lipid levels may promote the displacement of geosmin, and potentially other semi-lipophilic compounds, from lipid-rich tissues, such as fillets and ovaries, thereby accelerating their excretion and metabolism. Such findings suggest possible improvements in mitigating the drawbacks of traditional purging, yet it is essential to isolate the sources of absorption of VOCs and assess their individual influence in fish flesh to fully understand the effect of feeding on aroma quality during depuration.

Amongst the many RAS-reared fish species affected by off-odours, sturgeon (Russian or Danube) is a niche species with approximate global outputs of 100 tonnes per year, although the actual production may exceed this value [22]. Despite its small scale, the caviar of Russian sturgeon is a luxury product that is sold at prices of € 20004000 per kilogram [23] and has been exclusively produced in aquaculture since 1997 as a result of the wild supply prohibition [24]. This species is commonly reared in RAS at juvenile and oocyte maturation stages and its caviar, which is usually consumed as a raw-aged product, is particularly vulnerable to negative effects caused by off-odours, making it a valuable candidate to study the diversity of off-odours and varied absorption pathways. Identifying the origins of the exogenous compounds and their contributions to the organoleptic quality of the fillet may offer critical insights for the flavour management of its caviar. The present study aimed to investigate how water type (RAS and FT depuration) and feeding status (fed and unfed) influence off-odour development in RAS-reared juvenile Russian sturgeon (*Acipenser gueldenstaedtii*). Specifically, it aimed to characterise the composition of VOCs and their in-matrix dominance in one commercial feed, both water types, and sturgeon fillets under common controlled culture conditions, while also evaluating panellist-perceived odour attribute frequencies of fillets. By identifying potent odorants and linking them to sensory outcomes, this work seeks to explore how feeding status and water type may be associated with differences in aroma profiles, thereby supporting the optimisation of depuration practices and the improvement of sensory outcomes in RAS-reared sturgeon.

## 2. Materials & methods

### 2.1. Bioaccumulation experiment

The experimental work was conducted at a commercial RAS farm in France in October 2022. This study employed a two-factorial design to explore how commercial feeding regime and water type relate to the flavour of sturgeon fillets. Prior to the experiment, juvenile sturgeons were reared in 35 $m^3$ commercial tanks until they reached 20 months of age, without undergoing depuration. Four groups, each comprising three juvenile male sturgeons, with a mean total length of 66.0 ± 1.4 cm and mean mass of 2900 ± 480 g, were randomly selected for the study. The number of individual sturgeon used for the trial was agreed with the commercial entity to balance the economic burden with the trial's need for representative sampling. Two groups were transferred from the commercial tanks to FT 'purging' water conditioning, receiving fresh groundwater from a pristine natural stream. The remaining two groups were placed in 2000 L standalone rounded-corner square tanks connected to the main RAS water loop, receiving the same water as the commercial tanks. The experimental facilities maintained an ambient air temperature of 18.5 ± 3.5 °C, and fish were exposed to a natural photoperiod of 10:14 h (L:D). In the RAS loop, water temperature was controlled at 24.0 ± 0.5 °C, with a stable pH of 7.30 ± 0.05, salinity at 0.00 mg/L, and dissolved oxygen levels maintained at 11.0 ± 0.4 mg/L. Ammonia ($NH_3$), nitrite ($NO_2$), and nitrate ($NO_3$) concentrations were monitored using commercial kits and a spectrophotometer (Hanna Instruments, Woonsocket, RI, USA), yielding values of 0.035 ± 0.020 mg/L, <0.00002 mg/L, and <0.00002 mg/L, respectively. The groundwater stream had a water temperature of 11.0 ± 0.3 °C, a stable pH of 7.20 ± 0.02, and dissolved oxygen level of 8.0 ± 0.1 mg/L. The concentrations of $NH_3$, $NO_2$ and $NO_3$ were 0.005 ± 0.010 mg/L, <0.00001 mg/L, and <0.00001 mg/L, respectively. This study was conducted under commercial operating conditions and was not designed to reproduce the controlled thermal environment of a laboratory. Consequently, the large temperature difference between the RAS loop (~24 °C) and the depuration system (~11 °C) is acknowledged as an unavoidable inherent confounding factor potentially affecting metabolic activity and compound uptake. Within each water type, one group of sturgeon was subjected to a 25-day fasting period, a duration selected to reflect the upper range of commercial depuration practices typically applied to mitigate off-flavours in RAS operations [5,11,15,25]. The fed groups received the commercial farm diet at approximately 0.25 % body weight per day, administered in two daily feedings. The feed was a standard commercial sturgeon diet (E−2P Select Sturio Protec Gill, Skretting, Norway; crude protein 45 %, crude fat 22 %, crude cellulose 2.2 %, crude ash 8 %, digestible energy 20.1 MJ/kg). Feeding rates were consistent with routine farm management practices Hence, four conditioning group were established, comprising two fed conditions, i.e.,

sturgeon in depuration, fed (SDF) or sturgeon in RAS, fed (SRF), and two unfed conditions, i.e., sturgeon in depuration, unfed (SDU), and sturgeon in RAS unfed (SRU). At the end of the experimental period, the fish were euthanised by a percussive blow to the head, immediately filleted, and placed individually in sterile bags, subsequently frozen and stored at −20 °C for one month. On the same collection date, two samples of 250 mL water were collected from each of the four tanks and 150 g of commercial feed was collected, frozen and stored at −20 °C for one month. All samples were transported to the laboratory on ice packs within 24 h and upon arrival stored at −20 °C until analysis, which occurred within three months.

### 2.2. Odorant characterisation

The methods employed to extract and characterise the VOCs in samples, incorporating analyses by gas chromatography-mass spectrometry (GC-MS), were adapted from previous work [26]. The procedures are reported in brief below.

#### 2.2.1. Chemicals

To determine GC retention indices (RIs), a solution of a homologous series of *n*-alkanes dissolved in pentane (>99 % purity) was prepared (all reagents from Sigma-Aldrich, Steinheim, Germany). Sodium sulphate ($Na_2SO_4$) was used in its anhydrous form, while pentane and dichloromethane ($CH_2Cl_2$) were freshly distilled before use (all acquired from Th. Geyer GmbH & Co. KG, Renningen, Germany). Reference compounds used in this study were (*4S,4aS,8aR*)-4,8a-dimethyl-1,2,3,4,5,6,7,8-octahydronaphthalen-4a-ol (Geosmin) ≥ 97 % and (*1R,2R,4R*)-1,2,7,7-tet-ramethylbicyclo[2.2.1]heptan-2-ol (2-MIB) 98 % (both supplied from Merck, Darmstadt, Germany).

#### 2.2.2. Fish fillets, feed and water extraction

Aroma extractions were performed at Fraunhofer IVV. The fish replicates comprised a total of twelve fish, three per each group conditioning, namely sturgeon in depuration fed (SDF), sturgeon in RAS fed (SRF), sturgeon in depuration unfed (SDU), and sturgeon in RAS unfed (SRU), three commercial feed (CF) samples and four water samples, namely depuration water fed (WDF), depuration water unfed (WDU), RAS water fed (WRF) and RAS water unfed (WRU). Fish fillets were divided into portions of approximately 1 $cm^3$ and entire fish feed pellets of approximately 0.25 $cm^3$ were finely ground using a pestle and mortar, with consecutive additions of approximately 50 mL liquid nitrogen to obtain a fine freeze-dried powder. Samples of 50.4 ± 0.2 g of fish flesh powder and 5.01 ± 0.05 g of aquaculture feed powder were weighed and subjected to extraction with 200 mL and 100 mL of $CH_2Cl_2$ via dynamic maceration, respectively. The extraction involved stirring at 350 rpm on a magnetic stirrer (RO 10P, IKA, Staufen, Germany) for 30 min, followed by a resting period of 20 min at ambient temperature. Three water subsamples of 250 mL per conditioning group were first filtered to remove impurities via a rinsed filter paper (11 μm, Whatman Grade 1, Cellulose, Merck, Darmstadt, Germany) and subsequently extracted by hand mixing at a volume ratio of 3:1 with $CH_2Cl_2$, with three consecutive extractions conducted per sample. The extract was subsequently dried over anhydrous sodium sulphate and filtered through paper to collect flocculants. All sample extracts were subsequently subjected to distillation and enrichment. Fish fillets and aquaculture feed extracts were distilled via solvent-assisted flavour evaporation (SAFE) at 47 °C, while water samples skipped this step. Prior to chromatography analyses, all samples were further concentrated via Vigreux distillation and micro-distillation at 47 °C, which reduced the total volume of each sample extract to approximately 100 μL. Fish fillet extract replicates within each conditioning group were pooled into a single GC vial by transferring 30 μL from each original extract. This procedure resulted in four composite fillet extract samples, each representing a conditioning group. The same procedure was applied to replicate extracts of the commercial feed and water. In total, nine samples were analysed: four fish fillet extracts, four water extracts, and one commercial feed extract. Pooling fillet extracts within each experimental group was employed as a practical compromise to address the complexity and time-intensive nature of gas chromatography-olfactometry (GC-O) analysis. As the study aimed to characterise VOCs in fillets associated with water types and feeding regimes, extract pooling precluded within-group biological variability and statistical inference at the fish level. Hence, the multivariate analyses of VOCs were purely descriptive rather than a confirmatory comparative trial. Nonetheless, while optimising analytical efficiency for GC-MS/O and GC-O/AEDA, this approach preserved the within-group chemical diversity.

#### 2.2.3. GC-O-AEDA

GC-O (TRACE GC Ultra system, Thermo Fisher Scientific, Waltham, MA, USA) was employed in conjunction with aroma extract dilution assays (AEDA) to separate volatile constituents from distillates. Two capillary columns were employed: DB-FFAP (30 m × 0.32 mm × 0.25 μm; Agilent J&W, Santa Clara, CA, USA) and DB-5 (30 m × 0.32 mm × 0.25 μm; Agilent J&W). The initial temperature for both columns was set at 40 °C, maintained for 2 min. Subsequently, the temperature was increased at a rate of 8 °C/min to 240 °C, where it was held for 8 min for the DB-FFAP column and to 250 °C for the DB-5 column, held for 10 min. A volume of 2 μL was injected into the system using the cold-on-column technique, with helium at a flow rate of 2.2 mL/min as carrier gas. A Y-splitter divided the GC effluent equally (1:1) between the odour detection port (ODP) and the flame ionisation detector (FID) through two uncoated, deactivated fused silica capillaries (0.5 m × 0.2 mm). The FID was maintained at 250 °C, while the ODP was set to 270 °C. For odour detection, a minimum of three expert panellists was required to screen the undiluted distillate to minimise potential anosmia-related bias in the assessments. These panellists were recruited from the Fraunhofer IVV in-house trained sensory panel. The dominance of individual odour-active compounds on the overall aroma of the fish fillets was assessed via AEDA. This method, performed on the DB-FFAP column by a single panellist, determined flavour dilution (FD) factors through serial dilutions. A blank test using dichloromethane was performed prior to and between measurements to confirm that no compound carryover affected the results. The undiluted distillate (FD = 1) was diluted stepwise with $CH_2Cl_2$ at ratios of 1:3 v/v, yielding solutions per sample with FD factors ranging from 3 to 19683. The FD factor for each odorant represents the highest dilution at which the odour of the compound was still perceivable through GC-O analysis.

#### 2.2.4. GC-MS/O

Gas chromatography-mass spectrometry/olfactometry (GC-MS/O) analysis was conducted using an Agilent 7890 A GC system coupled to an Agilent 5975C Mass Selective Detector (MSD) (Agilent Technologies). The GC was fitted with a DB-FFAP column (30 m × 0.25 mm × 0.25 μm; Agilent J&W) and a CIS4 injection system (Gerstel GmbH & Co. KG, Mülheim an der Ruhr, Germany). The same oven temperature program as described above was applied. Analyses were performed in splitless mode using helium at a flow rate of 1.0 mL/min as carrier gas. Injections were made with an MPS 2 XL autosampler (Gerstel GmbH & Co. KG), with an injection volume of 1 μL. Mass spectra were acquired by electron ionisation (EI) at 70 eV operated in scan mode (*m/z* 35–400).

#### 2.2.5. Identification

The RIs, odour descriptions obtained by different panellists during GC-O analyses, as well as data from GC-MS/O analyses, were compiled using Microsoft Excel (v2308; Microsoft Corporation, 2023). Similar odour descriptions with RIs differing by ± 20 units were carefully evaluated and merged, with the mean RI value being adopted. The tentative identification of compounds was based on a combination of odour characteristics and comparison of RIs on two columns with different polarities (DB-FFAP and DB-5), calculated for each odour-

active compound using a homologous *n*-alkane series ($C_6$-$C_{30}$). Additionally, mass spectra were compared with those of authentic reference compounds from the Fraunhofer IVV in-house VOC library and the online NIST and LSB@TUM databases [27]. Final identification was achieved by comparing the criteria with reference standards of pure compounds, where applicable, and by consulting peer-reviewed publications on odour-active compounds isolated in aquaculture sources.

#### 2.2.6. Odour frequency

The relative frequency of odour attributes, i.e., the occurrence frequency of perceived specific odour attribute from trained panellists in each sample, was calculated following the methods described by Jones et al. (2022) and Mahmoud et al. (2024) [10,28]. In brief, for each sample, the total number of odour attributes assigned by three panellists to compounds characterised through GC-O and GC-MS/O was recorded and a list of unique descriptors was created by removing duplicates. The fractional frequency of each unique odour attribute for each panellist was then calculated by determining the proportion of occurrence relative to the total number of attributes assigned. This process generated three replicates, one per panellist, of quantitative fractional frequency data for each odour attribute.

### 2.3. Calculations and statistics

Data analyses were performed using R (v4.4.2; [29]) and Microsoft Excel (v2308; Microsoft Corporation, 2023) and figures produced in OriginPro (version 2025. OriginLab Corporation, Northampton, MA, USA). Compound FD values and odour attribute frequency data were processed (R-packages *tidyverse* [30] and *reshape2* [31]) for multivariate projections by $\log_{10}$ transformation with a small constant (0.001). Pareto scaling was applied to reduce the dominance of high-variance features, and missing FD values and attribute frequencies were imputed as zero. Assumptions of normality of distribution and homogeneity of variances were assessed both graphically and statistically. Multivariate normality was assessed using the Henze–Zirkler test (*MVN* package; [32]), and homogeneity of multivariate dispersion was tested via permutation-based beta dispersion test (*betadisper* function, R-package *vegan* [33]). As these criteria were not satisfied, subsequent descriptive analyses employed non-parametric methods. Variance structure of both datasets was explored via multivariate ordination for descriptive visualisation. Hierarchical clustering analysis (HCA) was conducted on the top ten compound FD values selected via Euclidian distance exploratory principal component analysis (PCA) and Ward's linkage method (*hclust* function [34], dendrogram was visualised using *heatmaply* [35]). PCA was performed on the processed odour attribute frequency data (R-package *FactoMineR* [36]) with component retention set at $\geq$ 95 % cumulative explained variance and graphical outputs generated (*ggplot2* [37]) and non-metric multidimensional scaling (NMDS, *metaMDS*, R-package *vegan* [33]) was performed to Bray–Curtis dissimilarity matrices [36] of raw odour-frequency data, supplemented with convex-hull overlays to illustrate treatment-level clustering and panellist spread. Finally, odorant and odour attribute frequency diversity and Shannon diversity indices were computed per treatment group, without replacement of missing values to avoid biasing zero counts.

## 3. Results

A total of 85 odour-active compounds were identified across the nine cumulative samples analysed in this study (Table S1 in Supplementary Material). Fifteen odour-active compounds identified across all samples in this study, selected according to sensory relevance, occurrence across matrices and treatment effect, are listed in Table 1.

### 3.1. Water

A total of 37 odour-active compounds were detected across all water samples, with RAS water samples (WRF & WRU; Fig. 1.) containing 36 odorants and the depuration water samples (WDF & WDU, Fig. 1) containing 32 odorants. Abundant chemical groups were equally distributed across water types, being each represented by aldehydes (six compounds), carboxylic acids (five compounds) and terpenoids (four compounds) in both RAS and FT depuration. Feeding coincided with marginally greater compound diversity in both RAS (31 compounds in WRF and 28 in WRU) and depuration water (25 in WDF and 23 in WDU), although these observations were not tested for significance. Dominant off-odour compounds (FD > 243) in RAS water included phenol (*ink-like, phenolic*), 1,3-benzothiazole (*rubber-like*), geosmin (*earthy, mouldy*), 2-MIB (*musty, wet soil*), 2,5-dimethylpyrazine (*popcorn, earthy*) and 2,3,5-trimethylpyrazine (*earthy, musty*). Five compounds were detected exclusively in RAS water, namely 2,5-dimethylpyrazine, 2-ethyltoluene (*butter-like, fishy, musty, cork-like*), 3-ethyltoluene (*fishy, green, cooked potato-like, terpene-like*), dimethyl trisulphide (*sulphuric, garlic-like, cabbage-like*) and ethyl hexadecanoate (*cardboard-like, wax-like*). Compound FD values in RAS showed no clear descriptive pattern associated with feeding, as evident by the several dominant FD values recorded irrespective of commercial feed addition, *e.g.*, butanoic acid (*sweaty*, FD = 729), pentanoic acid (*pungent, sweaty*, FD = 729) and $\beta$-ionone (*violet-like*, FD = 2187), as well as less dominant odorants, such as 1-octen-3-one (*mushroom-like*, FD = 3), phenol (*ink-like, phenolic*, FD = 3), dimethyl trisulphide (*sulphuric, cabbage-like*, FD = 81) and 2-methylbutanoic acid (*apple-like, fruity*, FD = 81), though as biological replication was absent, these trends should be interpreted cautiously. In RAS tanks with the commercial feed, a dominant $\delta$-undecalactone (*floral, soapy, peach-like, chocolate-like*, FD = 243), and odorants with lower FD values were found, such as caproic acid (*sweaty, goat cheese-like*, FD = 1), nonanoic acid (*soapy, musty*, FD = 1), $\gamma$-nonalactone (*coconut-like, sweet*, FD = 1), methyloctanoate (*soapy, coconut-like*, FD = 1), (*E,E*)-nona-2,4-dienal (*fatty, cooked potato-like*, FD = 1), 2,5-dimethylpyrazine and phenol in RAS, though these qualitative observations cannot be attributed to feeding. Depuration water contained off-odour compounds that generally exhibited low FD values and when compounds were common to RAS water, their intensities were lower, as was the case for geosmin (FD = 3 in WDF and WDU). In contrast to RAS, in depuration water only few off-odours with low FD values were present in WDU, such as 2-octanone (*sweaty, blue cheese-like*, FD = 3), geosmin and pentanoic acid (*fruity, sweaty, pungent*, FD = 3), while the addition of commercial feed increased the number and the intensities of dominant off-odours in WDF, as was the case for phenol (FD = 81) and a few compounds with FD = 9, i.e., 1,3-benzothiazole (*rubber-like, car tire-like, cardboard-like*), 2,3,5-trimethylpyrazine and 2,4-di-tert-butylphenol (*phenolic, leather-like, pungent*).

### 3.2. Fillets

A total of 64 compounds were characterised in sturgeon fillets. Samples from RAS (SRF & SRU, Fig. 1) contained 53 odorants, primarily aldehydes (15 compounds), terpenoids (11 compounds), and carboxylic acids (9 compounds). Sturgeon fillets in depuration water (SDF & SDU, Fig. 1) contained 48 odorants, with aldehydes (10 compounds), terpenoids (6 compounds), and carboxylic acids (8 compounds) being the most represented groups. Sixteen odorants were detected exclusively in RAS-held fish extracts. Among these, compounds with high FD values included methyl isoeugenol (*muddy, earthy, cork-like*, FD = 243) in SRF, and hexanoic acid (*coal-like, gas-like*, FD = 2187) and 2,4,6-trichloroanisole (*marine, cork-like, musty, ethereal*, FD = 243) in SRU. RAS fillets extracts contained several odorants with high FD values typically associated with *earthy, mouldy* off-odours, including geosmin (FD = 6561 in both SRF and SRU), 2-MIB (SRF = 729; SRU = 81), methyl isoeugenol (SRF = 243), but also *rubber-like* notes linked to 1,3-benzothiazole (FD = 729 in SRU and FD = 1 in SRF), *metallic, iodine-like, geranium leaf-like* notes associated to octanoic acid (FD = 2187 in SRU and FD = 27 in SRF) and 2-ethylhexylacrylate (FD = 243 in SRF) and *gasoline-like* notes

**Tables 1**

Fifteen odour-active compounds identified across all samples in this study. The nine cumulative samples analysed are reported as commercial feed (CF), sturgeon in depuration, fed (SDF), sturgeon in RAS, fed (SRF), sturgeon in depuration, unfed (SDU), sturgeon in RAS, unfed (SRU), depuration water, fed (WDF), depuration water, unfed (WDU), RAS water, fed (WRF) and RAS water, unfed (WRU). Selection criteria for the fifteen target odorants are based on sensory relevance, RAS enrichment, occurrence across matrices and treatment effect. Compounds represent dominant RAS off-flavours, feed-associated markers, and depuration aroma indicators.

| No. | Odorant | ID Code | | Odour Quality[a] | FD Factor[b] | | | | | | | | | Mean RI | | Identification Criteria[c] | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | CAS# | PubChem-CID | | CF | SDF | SRF | SDU | SRU | WDF | WDU | WRF | WRU | FFAP | DB5 | | |
| 1 | 2,5-dimethylpyrazine | 123-32-0 | 31252 | *Popcorn, earthy* | | | | | | | | 729 | | 1327 | 922 | RI, O, MS, LR | [12,38,39] |
| 2 | dimethyl trisulfide | 3658-80-8 | 19310 | *Sulphuric, garlic-like, cabbage-like* | 81 | | | | | | | 1 | 1 | 1360 | 969 | RI, O, MS, LR | [11,12] |
| 3 | nonanal | 124-19-6 | 31289 | *Citrus-like, soapy, metallic* | 1 | 1 | | 729 | 1 | | | | | 1378 | 1106 | RI, O, MS, LR | [12,38] |
| 4 | 2,3,5-trimethylpyrazine | 14667-55-1 | 26808 | *Earthy, musty* | 1 | | | | | 9 | | 729 | 1 | 1395 | 1004 | RI, O, MS, LR | [10] |
| 5 | 2-methylisoborneol | 2371–42-8 | 11062802 | *Musty, mouldy* | | 81 | 729 | 81 | 243 | 1 | 1 | 2187 | 3 | 1575 | 1185 | RI, O, MS, LR, RC | [10,38,40] |
| 6 | pentanoic acid | 109-52-4 | 7991 | *Fruity, sweaty, pungent* | 729 | 243 | | 1 | 243 | 1 | 3 | 81 | 3 | 1721 | 917 | RI, O, MS, LR | [12,41] |
| 7 | geosmin | 19700-21-1 | 29746 | *Earthy, beetroot-like, mouldy* | | 729 | 6561 | 6561 | 6561 | 3 | 3 | 6165 | 19683 | 1785 | 1431 | RI, O, MS, LR, RC | [10,11,38,39] |
| 8 | hexanoic acid | 142-62-1 | 8892 | *Coal-like, gas-like* | 81 | | | | 2187 | | | | | 1817 | 1016 | RI, O, MS, LR | [12,38–40] |
| 9 | β-ionone | 79-77-6 | 638014 | *Violet-like, floral, tobacco-like* | 2187 | | | | | | 1 | 1 | | 1930 | 1490 | RI, O, MS, LR | [11,12,16,40] |
| 10 | 1,3-benzothiazole | 95-16-9 | 7222 | *Rubber-like, car tire-like, cardboard-like* | | | 1 | 1 | 729 | 9 | | 729 | 729 | 1950 | 1240 | RI, O, MS, LR | [41] |
| 11 | phenol | 108-95-2 | 996 | *Ink-like, phenolic, green* | 3 | 27 | 81 | 1 | 729 | 81 | 3 | 2187 | | 1995 | 971 | RI, O, MS, LR | [38,39] |
| 12 | octanoic acid | 124–07-2 | 379 | *Musty, coriander-like, fatty, marine, iodine-like* | | 9 | 27 | 1 | 2187 | | | | | 2042 | 1198 | RI, O, MS, LR | [12,38–43] |
| 13 | p-cresol | 106-44-5 | 2879 | *Sweaty, Horse stable-like, faecal* | 1 | | | 1 | 1 | | | | | 2067 | 1092 | RI, O, MS, LR | [38,39] |
| 14 | thymol | 89-83-8 | 6989 | *Thyme-like* | | 81 | 81 | 81 | 81 | | | | | 2191 | 1285 | RI, O, MS, LR | [38] |
| 15 | methyl isoeugenol | 6379-72-2 | 637776 | *Muddy, mouldy, earthy, metallic, cork-like* | | | 243 | | | | | | | 2245 | 1400 | RI, O, MS, LR | [12,38,39] |

[a] Odour descriptors according to the Fraunhofer IVV in-house odorant database.

[b] FD factors relate to the following samples: CF = commercial feed; SDF = sturgeon depuration, fed; SRF = sturgeon in RAS, fed; SDU = sturgeon in depuration, unfed; SRU = sturgeon in RAS, unfed; WDF = depuration water, fed; WDU = depuration water, unfed; WRF = RAS water, fed; WRU = RAS water, unfed.

[c] Identification criteria are: RI = retention index; O = odorant description, MS = mass spectrum, LR = previously published in the peer-reviewed literature, RC = reference compound.

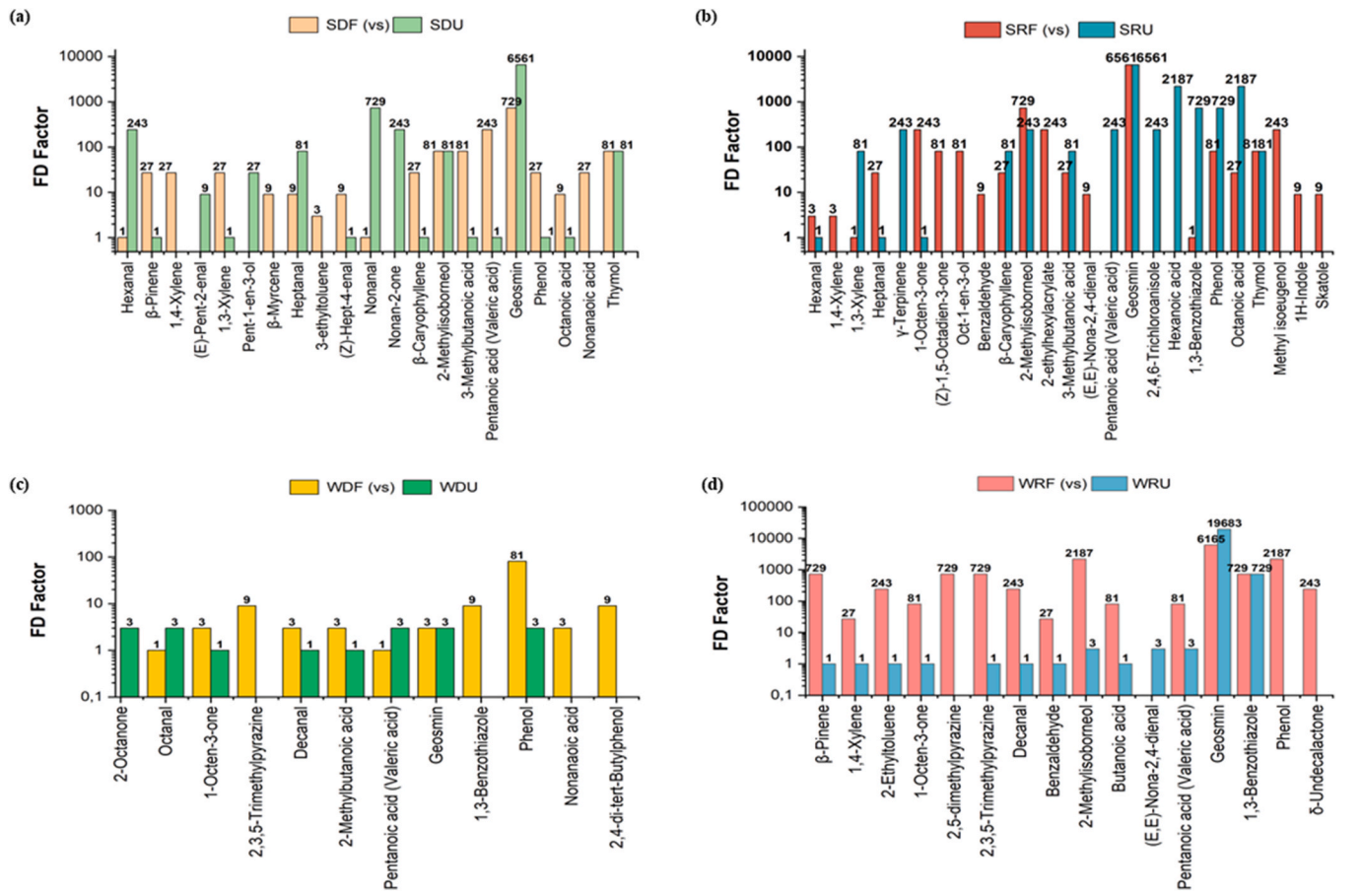



**Fig. 1.** Odorants characterised in sturgeon fillet reared in depuration water (sturgeon in depuration, fed = SDF vs sturgeon in depuration, unfed = SDU; a) sturgeon fillet reared in RAS water (sturgeon in RAS, fed = SRF vs sturgeon in RAS, unfed = SRU; b) depuration water (depuration water, fed = WDF vs depuration water, unfed = WDU; c) and RAS water (RAS water, fed = WRF vs and RAS water, unfed = WRU; d). Displayed compounds exhibited flavour dilution (FD) values > 1 in at least one feeding condition within each water type.

exhibited by hexanoic acid (FD = 2187 in SRF). In contrast, depuration water extracts were characterised by odorants with sensory attributes considered more desirable, including heptanal (*fishy, cooked potato-like*, SDF = 9 and SDU = 81), hexanal (*green, grassy*, SDF = 1, SDU = 243), nonanal (*citrus-like, soapy*, FD = 1, SDU = 729), and thymol (*thyme-like, herbal*, FD = 81 in SDF and SDU). Off-odours such as geosmin (SDF = 729; SDU = 6561) and pentanoic acid (SRF = 243; SDU = 243) were also present. Eleven odorants were detected only in depuration water extracts, generally with low FD values, except for nonan-2-one (*fruity, soapy water*, FD = 243). These observations and presence/absence patterns are descriptive only as they derived from pooled samples and do not imply statistically validated differences between treatments. Across experimental groups, 245 unique odour attributes were described in sturgeon fillets (Fig. 3). Fillets in SDF were mainly described as *faecal* (10 %), *fatty* (7.5 %), *cucumber-like*, *earthy* and *geranium leaf-like* (6 %). Conversely, SDU resulted exhibiting more desirable *green* notes (9 %) and prominent *fatty* (13 %) notes, while *faecal* (5.5 %) and *mouldy* (5 %) off-odours were less frequently described. Sturgeon fillets in RAS were generally richer in *earthy-mouldy* odours, with SRF mainly described as *fatty* (12 %), *earthy* (8 %) and *fishy*, *mouldy* and *musty* (5 %), while SRU were described with more favourable notes, such as *green* (10 %), *fatty* (6 %), *soapy* (5 %), but also *musty* (5 %) and *faecal* (4 %).

### 3.3. Feed

The commercial feed contained 29 odorants (Fig. 2), dominated by aldehydes (six compounds), terpenoids (six compounds), and carboxylic acids (six compounds). Among the aldehydes, dimethyl pentanedioate (*fishy*, FD = 81) was the most dominant, while *β*-ionone (*violet-like*, FD = 2187) exhibited the highest FD factor among the terpenoids. Two carboxylic acids with distinct *sweaty, cheesy and pungent* odours, *i.e.,* butanoic acid (FD = 729) and pentanoic acid (FD = 729), were also highly dominant. Of the 29 compounds identified in the commercial feed, 28 were also found in sturgeon groups, irrespective of their feeding status, indicating potential water exposure, though this cannot be quantitatively linked to feeding without replication and dedicated trial design. Dominant odorant compounds common in the commercial feed and sturgeon fillets were acetic acid (*vinegar-like*), 2-methylbutanoic acid (*fruity, apple, sweaty*), thymol (*thyme-like, herbal*), 1-octen-3-one (*mushroom-like*) and phenol (*ink-like, phenolic*), yet only few compounds were exclusively found in fed animals and feed, such as 2-methylbutanoic acid in SRF, limonene (*green, citrus-like*) and dimethyl pentanedioate (*fishy, popcorn-like*) in SDF. 2,3,5-Trimethylpyrazine and phenol were present in the commercial feed in RAS water where the feed was provided. Some palatable odorants that likely originated in the commercial feed were ubiquitous regardless of feeding, as in the case of thymol (with unvaried FD = 81), heptanal (*fishy, cooked potato-like*), hexanal (*green, grassy*), octanoic acid (*musty, coriander-like*), β-caryophyllene (*carrot-like, green, musty*) and phenol, among others. Phenol was present in sturgeon fillets regardless of the provision of feed. Six compounds characterised in the commercial feed (Table 2) presented favourable attributes, mild lipophilicity (log P < 3) and low odour threshold (OT), suggesting a potential favourable effect as flavour enhancement.

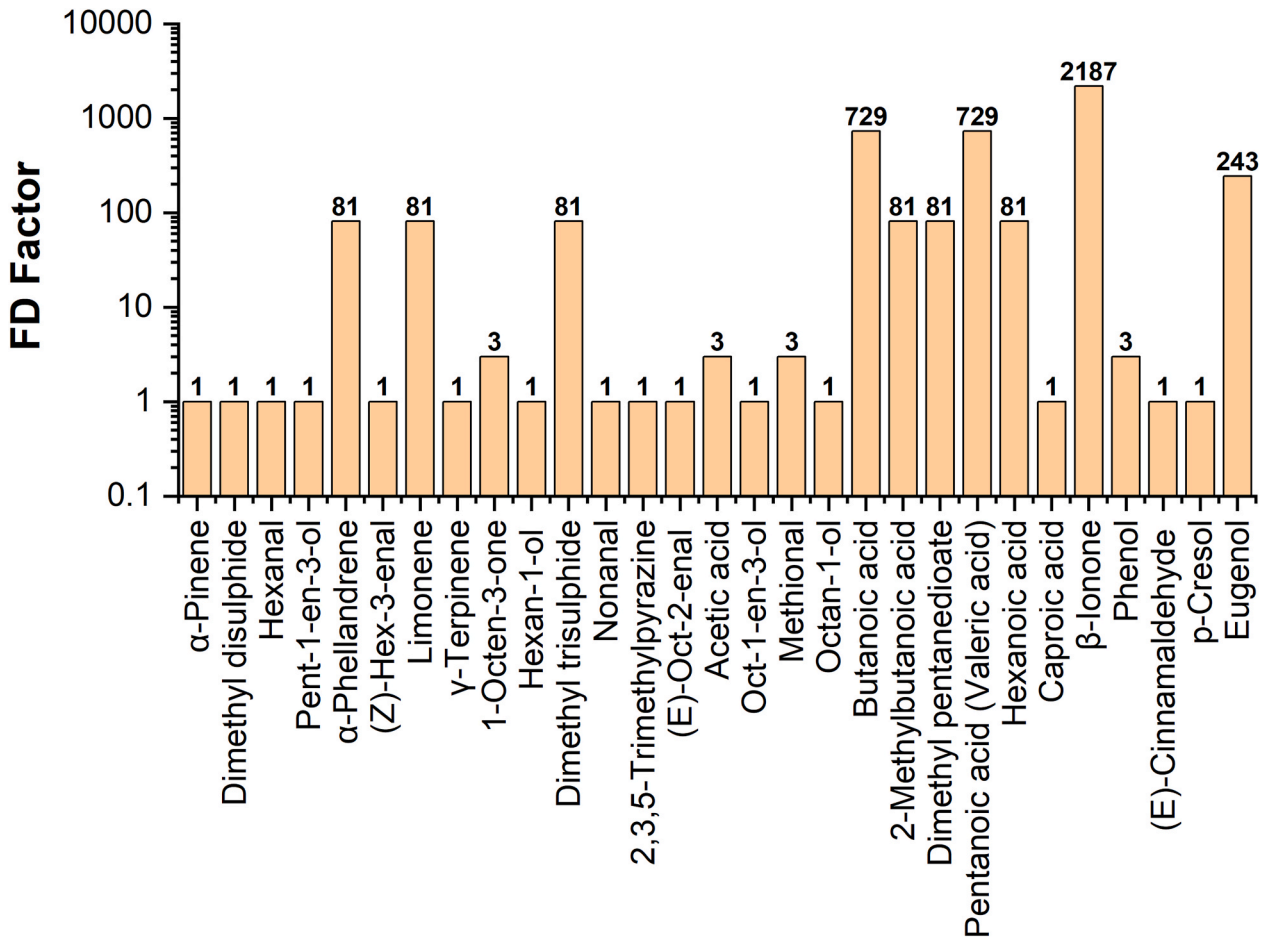



**Fig. 2.** Odorants characterised in commercial feed (CF). The y-axis represents the flavour dilution (FD) factors.

### *3.4. Calculations and statistics*

Assessment of both datasets indicated that variances were homogeneous across groups, but normality assumptions were not met, consequently all descriptive analyses were conducted using non-parametric methods. Hierarchical clustering of compound FD values showed only weak separation between samples (Fig. 4), indicating broadly similar chemical profiles across groups irrespective of water system or feeding status. The unfed RAS sample (SRU) formed the most distinct branch in the dendrogram; however, these patterns are descriptive only and were not subjected to statistical testing due to the pooled sample design. Ordination analyses of odour-attribute frequencies showed a similar overall structure. Both the NMDS (stress = 0.168) and PCA plots (Fig. 5) showed substantial overlap among groups, with convex hulls illustrating within-group variability, more pronounced in unfed groups. A marginal displacement of the depuration-fed sample (SDF) was visible in the 3D PCA space, while the remaining groups clustered more closely together. Compound-level diversity metrics assessments showed qualitative variation in the number of odour-active compounds and FD distribution, with higher compound counts and Shannon indices of FD values in SDF and SRU and lower values in SDU and SRF (Table 3). Odour attribute frequencies followed a broadly similar ordering, with SDF showing the greatest number of attributes and SRF the lowest, while Shannon diversity values were tightly clustered across all groups, indicating similar overall perceptual scale. While compound variation was more pronounced, variation across panellists remained rather moderate and appeared to reflect individual sensory responses rather than suggesting group-level divergence.

## 4. Discussion

The present study described the aroma composition of four groups of Russian sturgeon fillets under differing culture conditions (RAS or FT depuration) and feeding status (fed or unfed) within each system. Odorant characterisation techniques were applied to quantify the diversity of odour-active compounds and the relative dominance of high-intensity odorants, as indicated by FD factors, within each matrix. Perceptual similarity of aroma extracts across panellists was also evaluated using odour attribute frequency data for each sturgeon group. In addition, the Shannon diversity index was employed to characterise the distribution of FD values and sensory attribute frequencies. Odour-active compounds were additionally characterised in the commercial feed and in the water of both systems to associate compound origins and potential absorption pathways.

In water, RAS appeared to contain a greater diversity of odour-active compounds than depuration, regardless of whether the commercial feed was introduced, and ubiquitous compounds were detected at higher intensities in RAS. Off-odours exhibiting high FD values in RAS water included *ink-like* and *phenolic* notes from phenol, *rubber-like* notes from 1,3-benzothiazole, and strong *earthy, musty* qualities from geosmin, 2-MIB, and several pyrazines, e.g., 2,5-dimethylpyrazine, 2,3,5-trimethylpyrazine. Although this study did not address specific sources, these substances likely originated from microbial metabolism within the RAS mechanical and/or biological filtration compartments, as previously noted [6]. Additionally, non-enzymatic Maillard reactions between amino acids and reducing sugars derived from feed components and/or accumulated organic matter may also have contributed [44,45], which is consistent with previous findings in Russian sturgeon and commercial

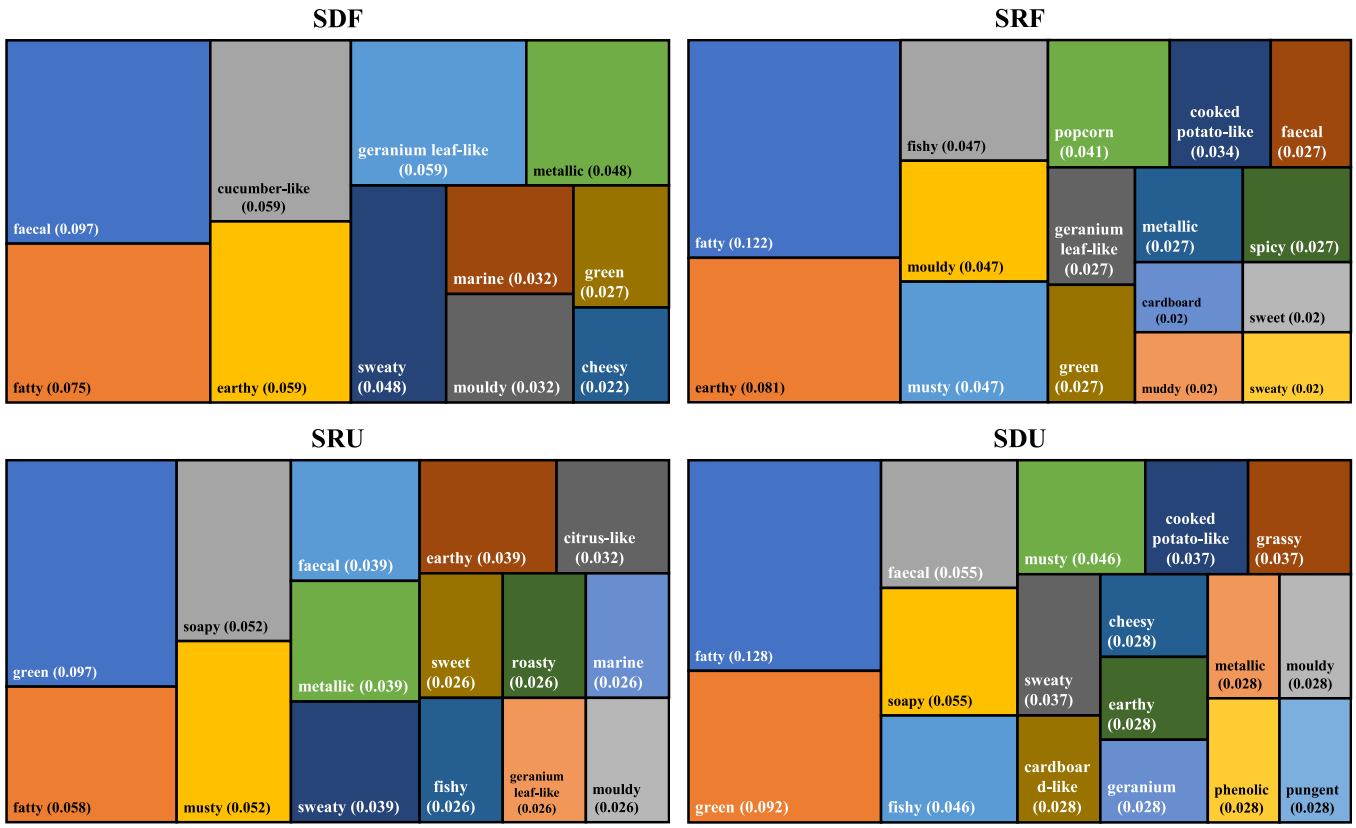



**Fig. 3.** Treemap of odour frequencies (number in brackets, >2 %) characterised in sturgeon fed in depuration water (SDF), sturgeon fed in RAS water (SRF), sturgeon unfed in RAS water (SRU) and sturgeon unfed in depuration water (SDU).

**Table 2**
Physicochemical properties and sensory attributes of six odour-active compounds identified in the commercial feed, characterised by favourable odour notes, mild lipophilicity (log P < 3), and low odour thresholds (OT), indicating potential for positive flavour modulation in sturgeon fillets.

| Odorant | Odour attribute | Log P | OT in water (μg/L [6]) |
|---|---|---|---|
| (*Z*)-Hex-3-enal | *Grassy, green* | 1.1 | 0.25 |
| 1-Octen-3-one | *Mushroom-like* | 2.4 | 0.005 |
| Dimethyl disulphide | *Cabbage-like, sulphuric* | 1.8 | 0.16 to 12 |
| Methional | *Cooked potato-like* | 0.3 | 0.2 |
| Oct-1-en-3-ol | *Mushroom-like* | 2.6 | 1 to 1.5 |
| α-Pinene | *Resin-like, conifer-like* | 2.8 | 6 |

caviar production systems [46]. Thus, the recirculating water environment and minimal discharge likely led to the accumulation of metabolites during intensive production, along with compounds from exogenous sources [47,48]. In contrast, the depuration water sourced from pristine local streams exhibited fewer VOCs and lower FD values, including a comparatively low concentration of geosmin (FD = 3) [3]. The introduction of commercial feed in both water types aligned with a marginal increase in compound diversity. In depuration, the addition of feed was associated to the presence of several high intensities (FD > 9) absent otherwise, some of which were also characterised in the commercial feed, e.g., phenol, 2,3,5-trimethylpyrazine. In RAS water, feeding also corresponded to additional feedborne compounds, e.g., caproic acid, nonanoic acid and (*E,E*)-nona-2,4-dienal, providing unfavourable *sweaty*, *fatty* and *musty* notes. Such odorants potentially eluted directly from feed pellets into recirculating water or originated from enzymatic and non-enzymatic degradation of feed material [6]. Nevertheless, in RAS high-FD value (FD > 729) waterborne compounds, such as geosmin, β-ionone and butanoic acid, remained dominant despite the introduction of feed.

Sturgeon fillets exhibited variations in VOC composition and in-matrix dominance across the culture conditions reflecting the water matrices. In RAS, sturgeon fillets exhibited a broader range of undesirable high-FD (FD > 729) odour-active compounds than in depuration water, irrespective of feeding status. These included *earthy, mouldy, metallic*, *rubber-like* and *coal-like* notes associated with geosmin, 2-MIB, hexanoic acid and 1,3-benzothiazole, among others. Contrarily, in depuration fillets predominantly contained high-FD odorants associated with desirable notes, e.g., *green, grassy, fishy, citrus-like*, attributed to aldehydes, such as hexanal, heptanal, and nonanal. While several high-FD off-odours were less abundant in depuration fillets, key dominant off-odours, such as geosmin, 2-MIB, pentanoic acid, persisted across all groups. As feed introduction coincided with higher VOC diversity in both water types, a similar tendency was anticipated in fillets, although this pattern was observed only in the depuration system. In this case, feeding was associated with a broader odour attribute profile, greater compound diversity, higher FD values and a more even distribution of FD values, suggesting a likely contribution of feedborne odorants to fillet aroma. In contrast, within the RAS, compound diversity appeared higher in the unfed group, with fed fillets exhibiting lower compound diversity (SRF = 31) than in unfed (SRU = 38), only marginal differences in odour attribute counts and slightly lower uniformity of FD values and odour frequencies. These observations may indicate a relatively greater influence of waterborne VOCs in closed-loop systems.

Multivariate projections suggested only minor differentiations between groups in both compounds and odour attribute frequencies. HCA showed weak differentiation in FD values, most notably separating the unfed group in RAS and indicating the lowest Euclidian distance between depuration groups (SDF and SDU). Analyses of odour attribute frequencies generally reflected these patterns: PCA and NMDS showed substantial overlap among groups, with greater within-group dispersion in unfed groups (SRU and SDU), suggesting higher perceptual variability

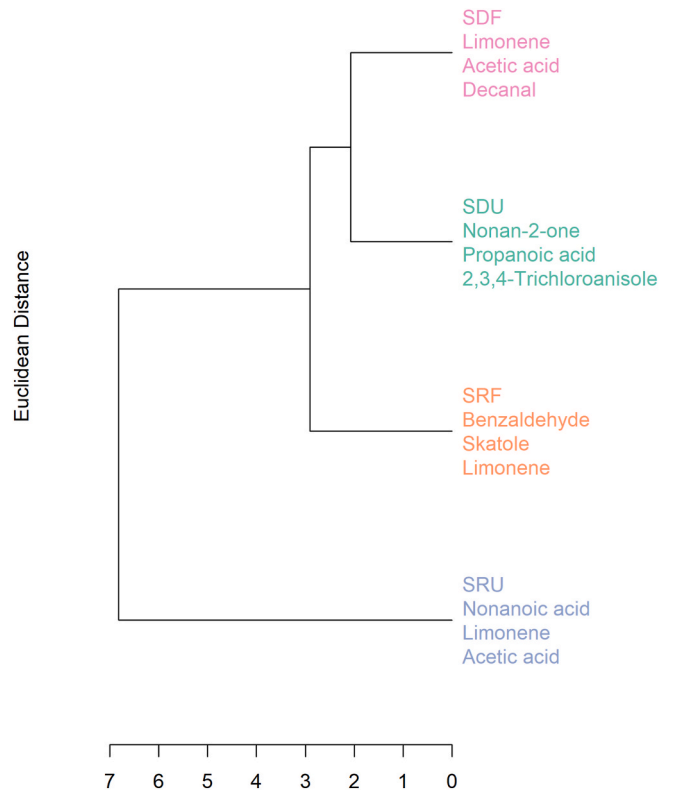



**Fig. 4.** Hierarchical clustering analysis dendrogram on Euclidian distance between sturgeon in depuration, fed (SDF), sturgeon in RAS, fed (SRF), sturgeon in RAS, unfed (SRU) and sturgeon in depuration, unfed (SDU) based on the top 10 odorants contributing to most variance in PCA. The **three compounds listed per sample** are the most distinctive in scaled and normalised FD values. Branch lengths indicate overall differences in multivariate odorant profiles.

among panellists compared to fed sturgeon. Notably, sturgeon unfed in RAS (SRU) formed a separate branch in HCA and exhibited high FD Shannon diversity alongside the widest dispersion in attribute frequencies, indicating an evenly distributed but compositionally complex aroma profile. In contrast, sturgeon fed under depuration (SDF) formed a more distinct cluster across multivariate analyses, with a broad and evenly distributed odour profile and high compound and attribute diversity. Overall, compound diversity and Shannon diversity were comparable across groups, and pairwise Bray–Curtis dissimilarities showed only moderate variation, with the largest dissimilarity between SDF and SRU (BC = 0.310 ± 0.082). Nevertheless, these observations are purely hypothesis-generating, hence do not indicate mechanistic interpretation. In fact, due to the analytical constraints of GC–MS/O, SAFE distillation, and AEDA, extracts from the three fish per group were pooled into a single composite sample. As a result, group-level compound comparisons infer on qualitative patterns only and do not support inferential conclusions regarding treatment effects. These findings indicate that panellist-perceived odour profiles were largely consistent across treatments, even when chemical differences were apparent, as shown in diversity indices. For instance, sturgeon unfed in RAS exhibited the highest compound diversity but the lowest odour attribute diversity. This reflects a common phenomenon in sensory analyses: as multiple compounds can elicit similar sensory impressions (e.g., *green*, *earthy*, *sweaty*), compound diversity does not always translate into perceptual differences, and even when chemical metrics show differentiation, sensory-level variation may not emerge. This observation highlights the limitations of analytical methodologies and reinforces the necessity of sensory evaluation and large-scale consumer testing in the study of food aromas.

Overall, the major odour-active compound groups identified in sturgeon fillets might be generated via endogenous oxidation of polyunsaturated fatty acids, as previously reported [38]. These included aldehydes, e.g., pentanal, hexanal, heptanal, octanal, nonanal, and decanal, alcohols, e.g., oct-1-en-3-ol, pent-1-en-3-ol, pentan-1-ol, hexan-1-ol, octan-1-ol, and 1-hexadecanol, and ketones, e.g., (*Z*)-1,5-octadien-3-one, 1-octen-3-one, nonan-2-one, and 2-octanone. These volatiles are commonly associated with freshwater fatty species, as previously observed in RAS-reared rainbow trout, Atlantic salmon, and brown trout [6,10]. Five compounds, *i.e.,* limonene (*green, citrus-like*), acetic acid (*vinegar-like*), 2-methylbutanoic acid (*fruity, sweaty*), dimethyl pentanedioate (*fishy, popcorn-like*), and oct-1-en-3-ol (*mushroom-like*), were solely identified in fed sturgeon and feed, some of which associated with desirable sensory traits. Yet, most compounds detected in the commercial feed were also found in sturgeon fillets regardless of feeding, including previously reported dominant feedborne off-odours with strong *vinegar-like*, *cheesy, sweaty* and *fruity* notes attributed to acetic acid, butanoic acid, and pentanoic acid [11,12]. At the same time, multiple desirable notes, such as *thyme-like*, *mushroom-like* and *marine, iodine-like* associated with compounds like thymol, 1-octen-3-one, and octanoic acid, were found across all groups regardless of feeding and water type, suggesting that many compounds characterised ubiquitously were either generated *in situ* due to endogenous oxidative processes in fish or absorbed via multiple pathways. Phenol serves as a compelling example of the complex interactions between waterborne and feedborne compounds. Though likely originated in the commercial feed, phenol was found at high FD in unfed fish reared in RAS (FD = 729), despite its absence in RAS water, suggesting adsorption from residual feed pellets and subsequent absorption in fish via water respiration. When feeding occurred, phenol was detected in RAS water at high FD value (FD = 2187), but at lower FD in fillets (FD = 81), possibly due to reduced uptake or compound metabolism. Conversely, in depuration water, phenol accumulated to a greater extent through dietary intake (FD = 27) compared to unfed conditions (FD = 1), matching its higher concentration in depuration water where animals were fed (FD = 81) than where they were unfed (FD = 3). These observations illustrate the complexity of possible absorption and storage pathways, which cannot be fully resolved without individual-level replication of exogenous odorant compounds in aquaculture systems. Overall, among all test groups, sturgeon fed in depuration displayed the lowest intensities of off-odours and the highest overall organoleptic quality based on the enhanced presence of desirable odour attributes, such as aldehyde-derived *green*, *fatty* notes. In contrast, RAS-reared fillets remained dominated by *earthy, musty*, and *mouldy* notes, irrespective of feeding, consistent with the persistent absorption of terpenoids and pyrazines from recirculating water.

Feeding during depuration coincided with lower descriptive FD values of certain dominant off-odours. While in RAS, odorants such as phenol, hexanoic and octanoic acids were lower or absent in fed fish, in depuration feeding was associated to two-to three-fold lower FD values of geosmin, hexenal, and nonanal, thus likely improving aroma quality. These observations align with previous findings suggesting that feeding during depuration may help reduce concentrations of geosmin and potentially other off-odours, possibly due to increased mobilisation of lipophilic compounds from tissue storage as a result of elevated blood lipid levels during feeding [21]. Unlike earlier research focused solely on geosmin depuration, however, the present study highlights that this benefit may be offset by the introduction of new feed-derived odorants, thereby complicating the sensory outcome of flavour modulation during purging. Thus, although feeding is here related to favourable lower geosmin content in the depuration system, this observation is context based and is not sufficient to suggest a revision of the current 'off-flavour purging' practices. Notably, the higher compound diversity here observed in fed sturgeon in depuration included undesirable odorants, like phenol (*ink-like*), 3-methylbutanoic acid (*cheese-like*) and pentanoic acid (*sweaty*), which may not be overall favourable, particularly in a luxury product like caviar, being mostly consumed dry-raw, where

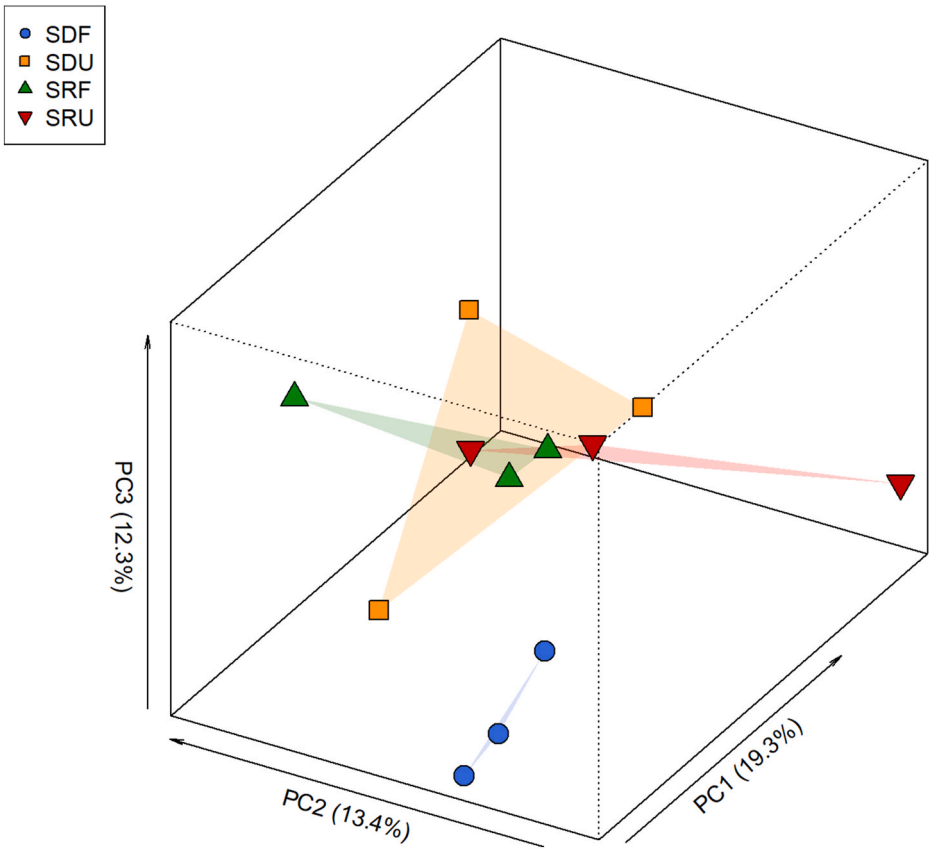



**Fig. 5.** Principal component analysis 3D boxplot summarising 45 % of variance of odour attribute frequencies in sturgeon in depuration, fed (SDF), sturgeon in RAS, fed (SRF), sturgeon in RAS, unfed (SRU) and sturgeon in depuration, unfed (SDU).

**Table 3**
Compound and Shannon diversity indices in the compound FD and odour attribute frequency datasets.

| Group | Compound | | Odour Attribute Frequencies | |
|---|---|---|---|---|
| | Diversity | Shannon_FD | Diversity (Mean ± SD) | Shannon_freq (Mean ± SD) |
| SDF | 38 | 1.67 | 36.00 ± 7.21 | 3.37 ± 0.22 |
| SDU | 29 | 0.78 | 30.67 ± 2.89 | 3.23 ± 0.15 |
| SRF | 31 | 1.01 | 28.67 ± 10.50 | 3.19 ± 0.41 |
| SRU | 38 | 1.83 | 29.34 ± 3.21 | 3.28 ± 0.15 |

compounds with probable feedborne origin have been recently described [40]. Therefore, aquaculture producers may consider experimentally evaluating feeding during depuration as a potential strategy to mitigate the economic costs associated with standard purging practices for *earthy* off-odours at farm level.

A confirmation of the present observation may mitigate important economic losses typically associated with depuration, such as the reductions in fish biomass and market weight due to feed withdrawal, delays in harvesting linked to extended depuration times, and increased water use associated with prolonged residence in flow-through systems [5,6,16,17,19,20]. Such an approach would be justifiable only if it resulted in improved aroma quality and remained compatible with other operational objectives of feed withdrawal, including intestinal tract emptying prior to harvesting and the reduction of organic loading on RAS filtration units [21]. At present, however, general recommendations cannot be made in the absence of a clear understanding of the underlying biochemical mechanisms, replicated sensory validation, and comprehensive consumer testing. Other possible explanations include altered ventilation or swimming activity, competitive absorption dynamics between VOCs, or changes in tissue matrix composition affecting aroma extraction. For instance, the temperature disparity between the system tested (RAS 24.0 ± 0.5 °C; depuration 11.0 ± 0.3 °C) was initially considered a possible contributor to prolonged appetite suppression affecting sensory outcomes. Here, it was observed that feeding associated with greater compound diversity in depuration than in RAS, hence violating this hypothesis. At the same time, temperature may have influenced waterborne VOC uptake via decreased activity, ventilation rate, and metabolic turnover [19,21] and potentially affected water microbiome release. However, both compound and odour-attribute distributions displayed parallel patterns across systems, with comparable chemical diversity across systems. These trends suggest that the observed odour patterns are attributable to volatile exposure pathways rather than temperature alone, although causal inferences cannot be drawn. Depuration employing the water of a natural stream without temperature modification was routine at the farm, and the experimental design was intended to reflect authentic operational conditions rather than physiological standardisation. Hence, the resulting temperature difference between systems was retained for operational convenience and commercial realism, while acknowledged as a confounding factor that restricts interpretation.

This study reinforces prior findings indicating the absorption of feedborne VOCs in fish, with feeding exerting both beneficial and adverse effects on flavour profiles [11,12]. Provided this factor, there exists a potential to explore flavour modulation through feed formulation and to develop specialised finishing feeds aimed at optimising fillet flavour profiles. For instance, 'purging' feeds designed to enhance the marketability of RAS-farmed fish could complement existing depuration practices. Such feeds should minimise the presence of undesirable odorants by including sensory assessments in the ingredients' selection, besides consider key physicochemical properties of odorant compounds,

e.g. concentration in the matrices, lipophilicity (log P) and odour thresholds (OT), which influence accumulation and sensory impact [10,38,49–51]. Compound concentration can be a decisive factor in defining hedonic tone. For example, dimethyl sulphide, characterised by a low odour threshold of 0.33 ng/ml in water, is reported to impart pleasant, *marine-like* aromas when present below certain limits. Yet, at higher concentrations, it has been described as having undesirable *petroleum--like*, *cabbage-like* and *garlic-like* notes [6,52–54]. This concentration-dependent odour profile suggests that the *a priori* classification of a compound as an 'off-odour' requires further attention [55,56]. Similar comprehensive discourses have arisen in other fields of sensory research, such as wine research, where efforts have been made for decades to distinguish between character, typicality, diversity, off-flavour, and taint [57,58]. While compounds like geosmin or butanoic acid are widely regarded as undesirable in fish fillets (though appreciated in foods such as beetroot), others, like dimethyl sulphide, may have opposite hedonic definitions depending on the concentration at which they are present. Furthermore, highly lipophilic, *i.e,* log P > 3, and low-OT compounds, *i.e.,* 0.01–100 μg/L, can cause significant absorption and accumulation of off-odours even when present at low concentrations [10,38,50,51]. Among the dominant compounds in this study, several odorants from RAS water exhibit moderate to high lipophilicity and low OT, such as geosmin (*earthy, mouldy*, log P = 3.57; OT = 0.01 μg/L), 2-MIB (*musty, mouldy*, log P = 3.31; OT = 0.029 μg/L) and dimethyl trisulphide (*sulphuric, garlic-like, cabbage-like,* log P = 3.3; OT = 0.34 μg/L). Odorants exhibiting similar physicochemical properties were also characterised in the feed, as in the case of dimethyl trisulphide, p-cresol (*sweaty, faecal*, Log P = 1.8; OT = 0.16–12 μg/L), *β*-ionone (*violet-like, tobacco-like,* log P = 3; OT = 0.007 μg/L), and nonanal (*soapy, metallic*, log P = 3.3; OT < 1 μg/L), potentially having worsened fillet palatability. Contrarily, odorants with palatable notes, such as *marine, crustacean-like, seawater-like, algae-like,* with higher OT and log P < 2, may enhance flavour when present at moderate concentrations [6,52–54]. These odour attributes commonly derive from sulphurous compounds, e.g., 1,3-benzothiazole, methional and dimethyl sulphide, and are typically lacking in aquaculture products compared to wild-caught seafood [6,52], besides having already been described in farmed Russian sturgeon [40]. The introduction of these compounds via finishing feed during off-odour depuration may constitute a significant benefit to RAS aquaculture practices. For instance, in this study, six feed-derived odorants (Table 2) with mild lipophilicity and OT and favourable odour profiles were described, having potentially enhanced fillet palatability.

Nevertheless, in-matrix odour dominance determined by AEDA and GC-MS/O may not always directly correlate with the overall sensory perception of food items. Other influencing factors, such as odorants synergistic effects, compound stability through metabolism and storage, and tissue distribution kinetics should be addressed comprehensively to clarify the impact on palatability [38,59–61]. For instance, current knowledge gaps persist regarding the absorption, metabolism, and retention of VOCs in fish. While some studies have modelled the depuration of geosmin [60,61], more comprehensive physiological models accounting for a broader range of compounds and metabolic pathways are lacking. A holistic approach is therefore needed to assess the impact of odorant compounds in fish products. The integration of VOCs characterisation, sensory panels, and controlled experiments with model compounds could establish accurate and comprehensive predictive frameworks for exogenous flavour management. Additionally, identifying 'ideal' flavour compounds could guide the development of optimised feed formulations and advance the understanding of biochemical mechanisms underlying odorant modulation during feeding and depuration. These prospects have the potential to improve sensory quality in aquaculture products while enhancing the economic sustainability of off-flavour purging strategies.

## 5. Conclusion

This study highlights the complex interplay between waterborne and feedborne odorants in the odour profiles of Russian sturgeon reared in RAS and FT depuration systems. Russian sturgeon extracts from RAS water were more diverse in dominant off-odour compounds than those reared in depuration water. Feeding was associated with differing VOC patterns across systems, with greater compound and odour attribute diversity in depuration and negligible influence in RAS, where waterborne VOCs likely remaining the primary exogenous contributors to fillet aroma. Feeding was associated with lower intensities of certain dominant off-odours (e.g., geosmin), suggesting the potential of combining depuration practices with carefully managed feeding. Among all groups, fed fish in depuration displayed the lowest off-odour intensities and most favourable aroma profiles according to odour attributes. However, feeding was associated to the presence of both desirable and undesirable odour attributes, potentially compromising sensory quality. Such results were, however, descriptive due to pooled samples, precluding inferential comparisons. Findings suggest avenues for future research on targeted feed innovations and depuration protocols to enhance the organoleptic quality of aquaculture products, but do not constitute confirmatory evidence granting a revision of purging practices. Future research should include replicated studies examining the biochemical fate of key VOCs and validated sensory panels to determine the perceptual relevance of observed trends during feeding and depuration. The development of specialised finishing feeds and optimised depuration protocols represents a promising avenue to enhance the marketability of RAS-grown fish.

## CRediT authorship contribution statement

**Matteo Egiddi:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mariana Rodrigues da Silva:** Writing – review & editing, Validation, Conceptualization. **Eva Ortner:** Writing – review & editing, Validation, Supervision, Conceptualization. **Bastien Debeuf:** Writing – review & editing, Resources, Conceptualization. **Helene M. Loos:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Andrea Buettner:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Jonathan Beauchamp:** Writing – review & editing, Supervision, Project administration, Conceptualization.

## Funding INFORMATION

This research was funded by the European Union's Framework Program for Research and Innovation Horizon 2020 under the Marie Sklodowska-Curie Training Network RASOPTA Grant Agreement No. 956481.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Bastien Debeuf reports a relationship with SCEA Sturgeon that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgement

The authors wish to thank all participants of the sensory panels the Fraunhofer IVV and the methodological support provided by Barbara Giocastro and Wellington Oliveira.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jafr.2025.102615.

## Data availability

Data will be made available on request.

## References


[1] M.B. Lukassen, R. Podduturi, B. Rohaan, N.O.G. Jørgensen, J.L. Nielsen, Dynamics of geosmin-producing bacteria in a full-scale saltwater recirculated aquaculture system, Aquaculture 2019 (500) (2018) 170–177, https://doi.org/10.1016/j.aquaculture.2018.10.008.

[2] P.C. Lindholm-Lehto, T. Kiuru, P. Hannelin, Control of off-flavor compounds in a full-scale recirculating aquaculture system rearing rainbow trout Oncorhynchus mykiss, J. Appl. Aquacult. 34 (2020) 469–488, https://doi.org/10.1080/10454438.2020.1866733.

[3] M.E. Abd El-Hack, M.T. El-Saadony, A.R. Elbestawy, et al., Undesirable odour substances (geosmin and 2-methylisoborneol) in water environment: sources, impacts and removal strategies, Mar. Pollut. Bull. 178 (March) (2022) 113579, https://doi.org/10.1016/j.marpolbul.2022.113579.

[4] S. Azaria, J. van Rijn, Off-flavor compounds in recirculating aquaculture systems (RAS): production and removal processes, Aquac. Eng. 83 (2018) 57–64, https://doi.org/10.1016/J.AQUAENG.2018.09.004.

[5] J.A. Moretto, P.N.N. Freitas, J.P. Souza, T.M. Oliveira, I. Brites, E. Pinto, Off-flavors in aquacultured fish: origins and implications for consumers, Fishes 7 (1) (2022) 1–12, https://doi.org/10.3390/fishes7010034.

[6] P.M. Noguera, M. Egiddi, J. Södergren, et al., More than just geosmin and 2-methylisoborneol? off-flavours associated with recirculating aquaculture systems, Rev. Aquacult. 16 (4) (2024) 2034–2063, https://doi.org/10.1111/raq.12949.

[7] M. Auffret, É. Yergeau, A. Pilote, et al., Impact of water quality on the bacterial populations and off-flavours in recirculating aquaculture systems, FEMS Microbiol. Ecol. 84 (2) (2013) 235–247, https://doi.org/10.1111/1574-6941.12053.

[8] E. Schoina, A.I. Doulgeraki, H. Miliou, G.J.E. Nychas, Dynamics of water and biofilm bacterial community composition in a mediterranean recirculation aquaculture system, Aquac J 2 (2) (2022) 164–179, https://doi.org/10.3390/aquacj2020008.

[9] D. Zheng, B.-M. Wilén, O. Öberg, T. Wik, O. Modin, Metagenomics reveal the potential for geosmin and 2-methylisoborneol production across multiple bacterial phyla in recirculating aquaculture systems, Environ. Microbiol. 26 (10) (2024) e16696, https://doi.org/10.1111/1462-2920.16696.

[10] B.C. Jones, M.M. Rocker, R.S.J. Keast, et al., Systematic review of the odorous volatile compounds that contribute to flavour profiles of aquatic animals, Rev. Aquacult. 14 (3) (2022) 1418–1477, https://doi.org/10.1111/raq.12657.

[11] R. Podduturi, M.A. Petersen, S. Mahmud, M.M. Rahman, N.O.G. Jørgensen, Potential contribution of fish feed and phytoplankton to the content of volatile terpenes in cultured pangasius (Pangasianodon hypophthalmus) and tilapia (Oreochromis niloticus), J. Agric. Food Chem. 65 (18) (2017) 3730–3736, https://doi.org/10.1021/acs.jafc.7b00497.

[12] M.A.A. Mahmoud, T. Tybussek, H.M. Loos, M. Wagenstaller, A. Buettner, Odorants in fish feeds: a potential source of malodors in aquaculture, Front. Chem. 6 (JUN) (2018), https://doi.org/10.3389/fchem.2018.00241.

[13] R.A. Dupre, R. Ardoin, J. Trushenski, et al., Dietary uptake of geosmin in rainbow trout (Oncorhynchus mykiss), Aquaculture (2023), https://doi.org/10.1016/j.aquaculture.2023.739458.

[14] N. Bar, Physiological and hormonal changes during prolonged starvation in fish, Can. J. Fish. Aquat. Sci. 71 (10) (2014) 1447–1458, https://doi.org/10.1139/cjfas-2013-0175.

[15] P.C. Lindholm-Lehto, J. Vielma, Controlling of geosmin and 2-methylisoborneol induced off-flavours in recirculating aquaculture system farmed fish—a review, Aquac. Res. 50 (1) (2019) 9–28, https://doi.org/10.1111/are.13881.

[16] C.S. Tucker, Off-flavor problems in aquaculture, Rev. Fish. Sci. 8 (1) (2000) 45–88, https://doi.org/10.1080/10641260091129170.

[17] SPACETASTE Consortium, Towards off-flavour Free Finfish Aquaculture, CORDIS, 2015. Retrieved December 4. 2024. from, https://cordis.europa.eu/project/id/604956/re.

[18] C. Tucker, C. Engle, G. Kumar, Economic impact of off-flavor in US farm-raised catfish production, World Aqua. Soc. Meet. (2023, February), 2023. Retrieved from, https://www.was.org/Meeting/Program/PaperDetail/162049.

[19] E. Schram, T. van Kooten, J.W. van de Heul, J.W. Schrama, J.A.J. Verreth, A. J. Murk, Geosmin depuration from European eel (Anguilla Anguilla) is not affected by the water renewal rate of depuration tanks, Aquac. Res. 48 (9) (2017) 4646–4655, https://doi.org/10.1111/are.13287.

[20] R. Wongprawmas, G. Sogari, F. Gai, G. Parisi, D. Menozzi, C. Mora, How information influences consumers' perception and purchasing intention for farmed and wild fish, Aquaculture 2022 (547) (2021) 737504, https://doi.org/10.1016/j.aquaculture.2021.737504.

[21] E. Schram, C. Kwadijk, A. Hofman, et al., Effect of feeding during off-flavour depuration on geosmin excretion by Nile tilapia (Oreochromis niloticus), Aquaculture 531 (July 2020) (2021) 735883, https://doi.org/10.1016/j.aquaculture.2020.735883.

[22] FAO, FishStat: acipenser gueldenstaedtii, in: Global Aquaculture Production 1950-2022, FishStatJ, 2025. Available at: www.fao.org/fishery/en/statistics/software/fishstatj.Licence:CC-BY-4.0. (Accessed 11 February 2025).

[23] B. Sicuro, The future of caviar production on the light of social changes: a new dawn for caviar? Rev. Aquacult. 11 (2019) 204–219, https://doi.org/10.1111/raq.12235.

[24] C. Raymakers, CITES, the convention on international trade in endangered species of wild fauna and flora: its role in the conservation of Acipenseriformes, J. Appl. Ichthyol. 22 (2006) 53–65, https://doi.org/10.1111/j.1439-0426.2007.00929.x.

[25] J. Davidson, K. Schrader, E. Ruan, B. Swift, J. Aalhus, M. Juarez, W. Wolters, C. Good, S.T. Summerfelt, Evaluation of depuration procedures to mitigate the off-flavor compounds geosmin and 2-methylisoborneol from Atlantic salmon Salmo salar raised to market-size in recirculating aquaculture systems, Aquac. Eng. 61 (2014) 27–34, https://doi.org/10.1016/j.aquaeng.2014.05.006.

[26] N. Buck, B. Lok, P. Denk, Detection of aroma compounds in food by gas chromatography-mass spectrometry/olfactometry, in: H. Koolen (Ed.), Mass Spectrometry for Food Analysis: Methods and Protocols in Food Science, Springer, 2022, https://doi.org/10.1007/978-1-0716-2107-3_13 [insert page range]).

[27] J. Kreissl, V. Mall, P. Steinhaus, M. Steinhaus, Leibniz-LSB@TUM Odorant Database, Leibniz Institute for Food Systems Biology at the Technical University of Munich, 2025. https://www.leibniz-lsb.de/datenbanken/leibniz-lsbtum-odorant-database/start. (Accessed 11 February 2025).

[28] M.A.A. Mahmoud, Ö. Kılıç-Büyükkurt, Fotouh MM. Aboul, S. Selli, Aroma active compounds of honey: analysis with GC-MS, GC-O, and molecular sensory techniques, J. Food Compos. Anal. 134 (2024) 106545, https://doi.org/10.1016/j.jfca.2024.106545.

[29] H. Wickham, Tidyverse: easily install and load the 'Tidyverse', R package version 1.3.0 (2019). https://CRAN.R-project.org/package=tidyverse.

[30] H. Wickham, Reshape: flexibly reshape data: a reboot of the reshape package (R package [Computer software], version 1.4.4, 2007. https://CRAN.R-project.org/package=reshape2.

[31] S.S. Shapiro, M.B. Wilk, An analysis of variance test for normality (complete samples), Biometrika 52 (3/4) (1965) 591–611, https://doi.org/10.2307/2333709.

[32] N. Henze, B. Zirkler, A class of invariant consistent tests for multivariate normality, Commun. Stat. Theor. Methods 19 (10) (1990) 3595–3617, https://doi.org/10.1080/03610929008830400.

[33] J. Oksanen, et al., Vegan: community ecology package, R package version 2 (2022), 6-2, https://CRAN.R-project.org/package=vegan.

[34] F. Murtagh, P. Legendre, Ward's hierarchical agglomerative clustering method: which algorithms implement ward's criterion? J. Classif. 31 (2014) 274–295, https://doi.org/10.1007/s00357-014-9161-z.

[35] T. Galili, A. O'Callaghan, J. Sidi, C. Sievert, Heatmaply: an R package for creating interactive cluster heatmaps for online publishing, Bioinformatics 34 (9) (2018) 1600–1602, https://doi.org/10.1093/bioinformatics/btx657.

[36] J.R. Bray, J.T. Curtis, An ordination of the upland forest communities of Southern Wisconsin, Ecol. Monogr. 27 (4) (1957) 325–349, https://doi.org/10.2307/1942268.

[37] J. Van Durme, K. Goiris, A. De Winne, L. De Cooman, K. Muylaert, Evaluation of the volatile composition and sensory properties of five species of microalgae, J. Agric. Food Chem. 61 (46) (2013) 10881–10890, https://doi.org/10.1021/jf403112k.

[38] P.C. Lindholm-Lehto, Developing a robust and sensitive analytical method to detect off—flavor compounds in fish, Environ. Sci. Pollut. Res. 1 (123456789) (2022) 55866–55876, https://doi.org/10.1007/s11356-022-19738-2.

[39] O. Kawaguchi, M. Tanaka, M. Yoshii, Y. Iwamoto, A. Midooka, F. Toutani, Off—Flavor of red sea bream Pagrus major reared in recirculating aquaculture systems with low salinity is caused by 2—methylisoborneol, Fish. Sci. 85 (3) (2019) 553–560, https://doi.org/10.1007/s12562-019-01307-1.

[40] M.R. Silva, M. da, M. Egiddi, B. Debeuf, A. Buettner, H.M. Loos, Aroma-active compounds in Russian sturgeon (Acipenser gueldenstaedtii) raised in recirculating aquaculture systems, J. Agric. Food Res. 18 (2024) 101443, https://doi.org/10.1016/j.jafr.2024.101443.

[41] G.M. Turchini, T. Mentasti, F. Caprino, S. Panseri, V.M. Moretti, F. Valfrè, Effects of dietary lipid sources on flavour volatile compounds of brown trout (Salmo trutta L.) fillet, J. Appl. Ichthyol. 20 (1) (2004) 71–75, https://doi.org/10.1046/j.0175-8659.2003.00522.x.

[42] V. Varlet, C. Knockaert, C. Prost, T. Serot, Comparison of odor-active volatile compounds of fresh and smoked salmon, J. Agric. Food Chem. 54 (9) (2006) 3391–3401, https://doi.org/10.1021/jf053001p.

[43] S. Selli, C.E. Rannou, C.A. Prost, J. Robin, T. Serot, Characterization of aroma-active compounds in rainbow trout (Oncorhynchus mykiss) eliciting an off-odor, J. Agric. Food Chem. 54 (25) (2006) 9496–9502, https://doi.org/10.1021/jf0619582.

[44] H. Fini E, S. Ayat, F. Pahlavan, Phenolic Compounds in the Built Environment, IntechOpen, 2022, https://doi.org/10.5772/intechopen.98757.

[45] M. R. da Silva, P.M. Noguera, B. Debeuf, M.A. Petersen, H.M. Loos, A. Buettner, Aroma profiling and volatile fingerprinting of commercial caviar (Acipenser baerii and Acipenser gueldenstaedtii), LWT - Food Sci. Technol. (Lebensmittel-Wissenschaft -Technol.) 230 (2025) 118261, https://doi.org/10.1016/j.lwt.2025.118261.

[46] S. Goddek, Aquaponics Food Production Systems, Springer, 2019, https://doi.org/10.1007/978-3-030-15943-6.

[47] P. Ruiz, J.M. Vidal, D. Sepúlveda, et al., Overview and future perspectives of nitrifying bacteria on biofilters for recirculating aquaculture systems, Rev. Aquacult. 12 (3) (2020) 1478–1494, https://doi.org/10.1111/raq.12392.

[48] A. Buettner (Ed.), Springer Handbook of Odor, Springer, 2017, https://doi.org/10.1007/978-3-319-17275-0.
[49] M. Czerny, M. Christlbauer, M. Christlbauer, et al., Re-investigation on odour thresholds of key food aroma compounds and development of an aroma language based on odour qualities of defined aqueous odorant solutions, Eur. Food Res. Technol. 228 (2) (2008) 265–273, https://doi.org/10.1007/s00217-008-0931-x.
[50] S.L. Bertelsen, A.D. Hoffman, C.A. Gallinat, C.M. Elonen, J.W. Nichols, Evaluation of log K(OW) and tissue lipid content as predictors of chemical partitioning to fish tissues, Environ. Toxicol. Chem. 17 (8) (1998) 1447–1455, https://doi.org/10.1002/etc.5620170803.
[51] B. Jones, R. Smullen, A.G. Carton, Flavour enhancement of freshwater farmed barramundi (Lates calcarifer), through dietary enrichment with cultivated sea lettuce, Ulva ohnoi, Aquaculture 454 (2016) 192–198, https://doi.org/10.1016/j.aquaculture.2015.12.017.
[52] R.G. Buttery, R.M. Seifert, D.G. Guadagni, L.C. Ling, Characterization of additional volatile components of tomato, J. Agric. Food Chem. 19 (3) (1971) 524–529, https://doi.org/10.1021/jf60175a011.
[53] F.B. Whitfield, Biological origins of off-flavours in fish and crustaceans, Water Sci. Technol. 40 (6) (1999) 265–272, https://doi.org/10.1016/S0273-1223(99)00567-3.
[54] M. Brattoli, E. Cisternino, P. Rosario Dambruoso, et al., Gas chromatography analysis with olfactometric detection (GC-O) as a useful methodology for chemical characterization of odorous compounds, Sensors (Switzerland) 13 (12) (2013) 16759–16800, https://doi.org/10.3390/s131216759.
[55] P. Giungato, A. Di Gilio, J. Palmisani, et al., Synergistic approaches for odor active compounds monitoring and identification: state of the art, integration, limits and potentialities of analytical and sensorial techniques, TrAC, Trends Anal. Chem. 107 (2018) 116–129, https://doi.org/10.1016/j.trac.2018.07.019.
[56] K.K. Schrader, Flavor wheel for sensory analysis of fish raised in recirculating aquaculture systems, N. Am. J. Aquac. 85 (1) (2023) 87–91, https://doi.org/10.1002/naaq.10275.
[57] C. van Leeuwen, J.-C. Barbe, P. Darriet, O. Geffroy, E. Gomès, S. Guillaumie, P. Helwi, J. Laboyrie, G. Lytra, N. Le Menn, S. Marchand, M. Picard, A. Pons, G. Revel, L. Riquier, B. Robillard, J. Rousseau, V. Renouf, C. Thibon, T. Tominaga, Recent advancements in understanding the terroir effect on aromas in grapes and wines, OENO One 54 (4) (2020) 985–1006, https://doi.org/10.20870/oeno-one.2020.54.4.3981.
[58] V. Picard, S. Tempère, G. de Revel, S. Marchand, L. Perrot, A sensory study of the ageing bouquet of red Bordeaux wines, Front. Chem. 5 (2017) 66, https://doi.org/10.3389/fchem.2017.00066.
[59] R.T. Marsili, C.R. Laskonis, Odorant synergy effects as the cause of fishy malodors in algal marine oils, J. Agric. Food Chem. 62 (40) (2014) 9676–9682, https://doi.org/10.1021/jf502252q.
[60] P. Howgate, Tainting of farmed fish by geosmin and 2-methyl-iso-borneol: a review of sensory aspects and of uptake/depuration, Aquaculture 234 (1–4) (2004) 155–181, https://doi.org/10.1016/j.aquaculture.2003.09.032.
[61] E. Schram, J.W. Schrama, T. van Kooten, et al., Experimental validation of geosmin uptake in rainbow trout, Oncorhynchus mykiss (Waldbaum) suggests biotransformation, Aquac. Res. 49 (2) (2018) 668–675, https://doi.org/10.1111/are.13496.