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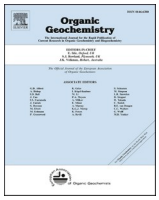

Note

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ABSTRACT

3-hydroxy fatty acids (3-OH FAs) produced by Gram-negative bacteria were recently proposed as promising temperature proxies. Nevertheless, the lipid adaptation mechanism of such microorganisms to temperature remains largely unexplored. Here, we investigated how growth temperature (5–25 °C) affects lipid profiles of non-hydroxylated (non-OH) and 3-OH FAs in two *Pseudomonas veronii* strains isolated from French alpine lakes. Membrane adaptation to rising temperatures was mainly driven by non-OH-FAs, characterised by a higher saturated/unsaturated ratio, while 3-OH FA total proportion slightly increased from 12 to 15% of total FAs. FA profiles showed a non-linear response, with minor changes between 5 and 18 °C cultivation temperature and a marked shift at 25 °C, as well as slight differences between the two isolates. Our findings illustrate varied lipid response to temperature with potential implications in using 3-OH FAs as temperature proxies in lakes.

1. Introduction

Bacteria can adjust the composition (e.g., degree of unsaturation and cyclization, chain length, branching) of their membrane fatty acids (FAs) in response to environmental changes (Denich et al., 2003) in order to maintain the membrane permeability and fluidity. This ability is particularly relevant for paleoclimate reconstruction, as lipids can be preserved in sediments over geological periods, their distribution reflecting the environmental conditions at the time of their biosynthesis. Among these molecules, 3-hydroxy FAs (3-OH FAs) with a chain length of 10 to 18 carbon atoms from the outer membrane lipids of Gram-negative bacteria have been proposed as proxies for temperature and pH in soils (Wang et al., 2016; Véquaud et al., 2021) as well as in oceans (Yang et al., 2020) and lakes (Yang et al., 2021; Ke et al., 2026). However, the development of global environmental proxies based on 3-OH FAs remains challenging due to diversity in Gram-negative bacteria communities across environments (Yang et al., 2021), differences in 3-OH FA profiles among taxa (Hellequin et al., 2023), and inherent differences in FA responses among different genetic strains (strain-level variability) (Lezcano et al., 2025).

To date, research on 3-OH FAs as environmental proxies has principally focused on soils (Wang et al., 2016; Véquaud et al., 2021), while lacustrine environments remain largely under-explored, despite the high sensitivity of lacustrine archives as recorders of past environmental conditions. Developing reliable 3-OH FA-based proxies requires a detailed understanding of bacterial lipid adaptation to environmental changes, which remains limited and mainly based on empirical studies. Only two studies investigated the strain-level responses of 3-OH FA composition to temperature and pH variations by using soil-derived bacterial strains (Hellequin et al., 2023; Zeng et al., 2025). While all strains showed 3-OH FA-based membrane adaptation, the patterns were strain-specific and were not necessarily consistent with the general patterns of lipid profiles observed in soil samples. This highlights the importance of bacterial community composition and underscores the need for further research on how 3-OH FAs respond to environmental changes across diverse strains and environments, to better constrain

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their use as environmental proxies.

To this aim, we investigated the temperature effect on membrane lipid composition of two strains of *Pseudomonas veronii, Pseudomonadota* being one of the more abundant phyla reported in lakes (Baumann et al., 2022) with diverse 3-OH FA production potential (Zeng et al., 2025). Lacustrine strains isolated at different altitudes in the French Alps allowed us to evaluate the role of the strain geographical origin on the lipid response, including both non-hydroxylated and hydroxylated FAs. A focus was made on 3-OH FAs in the light of the potential of these molecules as temperature proxies in lakes (Yang et al., 2021).

2. Materials and methods

Gram-negative bacteria were isolated from 1 g of suspended sediment matter (SSM) collected with sediment traps in two French alpine lakes: (i) Lake La Thuile (874 m a.s.l; Bajard et al., 2016), SSM collected at 6 m depth (Feb. to June 2024), and (ii) Lake Le Bourget (231 m a.s.l, Giguet-Covex et al., 2010), SSM collected at 40 m depth (Feb. to April 2024). Water temperature (T °C) was continuously recorded at each trap depth using TINYTAG Aquatic 2 probes, while pH and conductivity (cond) were periodically measured with YSI Exo 1 probes. Environmental conditions during sampling were: for lake La Thuile, T °C = 9.3 ± 2.5 °C, pH = 8.0 ± 0.2, cond = 406 ± 5.6 µS/cm; for lake Le Bourget, T °C = 7.6 ± 0.3 °C, pH = 7.9 ± 0.1, and cond = 334 ± 2.2 µS/cm.

Bacteria isolation and taxonomic identification were performed following Hellequin et al. (2023). *Pseudomonas* accounted for 56–85% of the recovered isolates depending on the lake, consistent with the high abundances reported for *Gammaproteobacteria* in lakes (Baumann et al., 2022; Garner et al., 2023). Two phenotypically similar *Pseudomonas* isolates — one from each lake — were selected based on taxonomic and morphological screening (i.e., form and colour of the colonies). Selected isolates were the only ones belonging to the same bacterial species, each originating from a different lake and both considered as different strains. Final identification was confirmed as *P. veronii* through whole-genome sequencing and *in silico* Average Nucleotide Identity (fastANI, https://doi.org/10.1038/s41467-018–07641-9), average Amino Acid Identity (fastAAI; https://doi.org/10.1093/nar/gkaf348), and genome-to-genome distance calculator (ggdc; https://ggdc.dsmz.de/ggdc.php; https://doi.org/10.1093/nar/gkab902). The ANIs were 99.06% identical based on the comparison of the circular genomes, reflecting different strains (Rodriguez-R et al., 2024). Sequences were deposited in the European Nucleotide Archive (ENA) accession numbers OZ350613 and OZ350614.

Growth curves were conducted at 5, 10, 18, 20, 25 and 30 °C to determine growth rates (µ) and identify the sampling point for lipid analysis, defined as mid-exponential phase at OD_{600} (optical density at 600 nm). Temperatures for experiments were selected to reflect the natural range of temperatures observed in the water column of the studied lakes (3–25 °C). Experiments were carried out at 5, 10, 18 and 25 °C in triplicate cultures of R2A liquid medium (pH 7.2, 180 rpm; Reasoner and Geldreich, 1985). We chose the temperature of 18 °C because this is an intermediate point, equally distributed between 10 and 25 °C and still very close to the optimal growth temperature (20 °C). Cultures were harvested at the defined OD, bacterial biomass was collected, frozen at −20 °C, and freeze-dried prior to lipid extraction. Total lipids were extracted from ca. 10 mg of biomass as described in Hellequin et al. (2023). Lipid extracts were silylated with BSTFA and analysed by GC–MS (TRACE 1310 – ISQ 7000 – Thermo Fisher). Analytical conditions were those reported by Hellequin et al. (2023). Common (non-hydroxylated) fatty acids — hereinafter referred as non-OH FAs — and 3-OH FAs — hydroxylated FAs, characteristic constituents of the lipopolysaccharide, which is the main component of the outer membrane of Gram-negative bacteria — were identified and integrated using total ion chromatogram (TIC). Each peak signal-to-noise ratio was > 3 (see an example of a lipid chromatogram in Fig. S1, supplementary material). A targeted *m/z* 175 mass trace (Huguet et al., 2019) was used to detect 3-OH FA homologues not visible in the TIC.

Data were analysed in R v4.3.3 (R-Core-Team, 2024). General lipid composition patterns were explored via Principal Component Analysis (PCA; stats::prcomp) and differences across growth temperatures and between strains were assessed using a two-way linear model (LM, stats::lm), followed by Tukey's HSD post-hoc (multcomp::glht) test (Crawley, 2007). Data were log-transformed when necessary to meet model assumptions.

3. Results and discussion

Growth curve analysis showed that both *P. veronii* strains grew between 5 and 30 °C, with an optimum at 20 °C, classifying them as psychrotrophs. However, the strain from Lake La Thuile (*Ps-Thu*; $\mu_{(5°C)} = 0.18 \pm 0.005\ h^{-1}$, $\mu_{(30°C)} = 0.59 \pm 0.004\ h^{-1}$) grew significantly faster ($P < 0.05$) than the one from Lake Le Bourget (*Ps-Bour*; $\mu_{(5°C)} = 0.14 \pm 0.004\ h^{-1}$, $\mu_{(30°C)} = 0.55 \pm 0.003$) at both temperature extremes (5 and 30 °C).

Lipid profiles in both strains were dominated by non-OH FAs, comprising 85–88% of total FAs. The most abundant homologues were *n*-$C_{16:1}$, *n*-$C_{16:0}$, and *n*-$C_{18:1}$ (Fig. 1A). Saturated and unsaturated homologues represented 25–32% and 53–62% of total non-OH-FAs, respectively (Table 1). 3-OH-FAs represented between 12–15% of the total FAs with *n*-$C_{10:0}$ and *n*-$C_{12:0}$ as the main components (Table 1, Fig. 1B). Notably, *n*-$C_{12:1}$ was the only unsaturated 3-OH-FA detected (Fig. 1B). FA profiles were consistent with previous reports on *Pseudomonas* (Oyaizu and Komagata, 1983; Mező et al., 2022).

Growth temperature had a significant effect on the relative abundance of all non-OH FAs (Table 1). Overall, temperature influenced the degree of FA saturation (Table 1): higher growth temperatures led to an increase in the abundance of saturated non-OH FAs and a decrease in the proportion of unsaturated homologues. While there was no significant temperature effect on the Sat/Uns ratio of the non-OH FAs for the cultivation experiments performed at the lower temperature (5 and 10 °C), higher growth temperatures (18 and 25 °C) resulted in an increase of this ratio for both strains; Table 1). This shift reflects a common homeoviscous adaptation, where unsaturated FAs dominate at lower temperatures to maintain membrane fluidity, while saturated FAs increase at higher temperatures to reduce permeability and maintain membrane properties compatible with cell physiology (Neidleman, 1987; Suutari and Laakso, 1994; Zhang and Rock, 2008). Similar trends have been observed in diverse cold-adapted Gram-negative bacteria (Hassan et al., 2020; Akulava et al., 2024).

In contrast to the non-OH FAs, temperature mainly affected the relative abundance of minor 3-OH FAs (i.e., < 5% of total 3-OH FAs), with some decreasing (*n*-$C_{12:1}$ and *n*-$C_{14:0}$) and others increasing (*n*-$C_{18:0}$) at higher growth temperatures (Table 1). Overall, the proportion of 3-OH FAs relative to total FAs exhibited no clear trend, even though it showed the highest values at 25 °C ($P = 0.06$). Previous work suggested that the increase in the relative abundance of 3-OH vs. non-OH FAs may help to maintain the membrane viscous state at low temperatures (Mező et al., 2022; Akulava et al., 2024), similar to how increased *anteiso* branching enhances membrane fluidity. However, this trend is not consistent across all Gram-negative bacterial strains, as previously shown (Mező et al., 2022; Hellequin et al., 2023; Akulava et al., 2024) and as also demonstrated in the present study.

The effect of temperature on the whole membrane lipid profiles (3-OH and non-OH FAs) was assessed via PCA (Fig. 1C). PC1 – explaining 57% of the total variance – was strongly associated with *n*-C_{16} non-OH-FA homologues and Sat/Uns ratio, both significantly influenced by temperature. Cultures grown at 25 °C were clearly separated from those at 5–18 °C along the temperature gradient defined by PC1. PC2 (14.1% of the explained variance) captured more subtle variation within the 5–18 °C range and was mainly linked to chain length and the 3-OH-FA *n*-$C_{12:0}$, variables not significantly affected by temperature. In contrast, the relative abundance of the 3-OH FA *n*-$C_{12:1}$ was significantly and

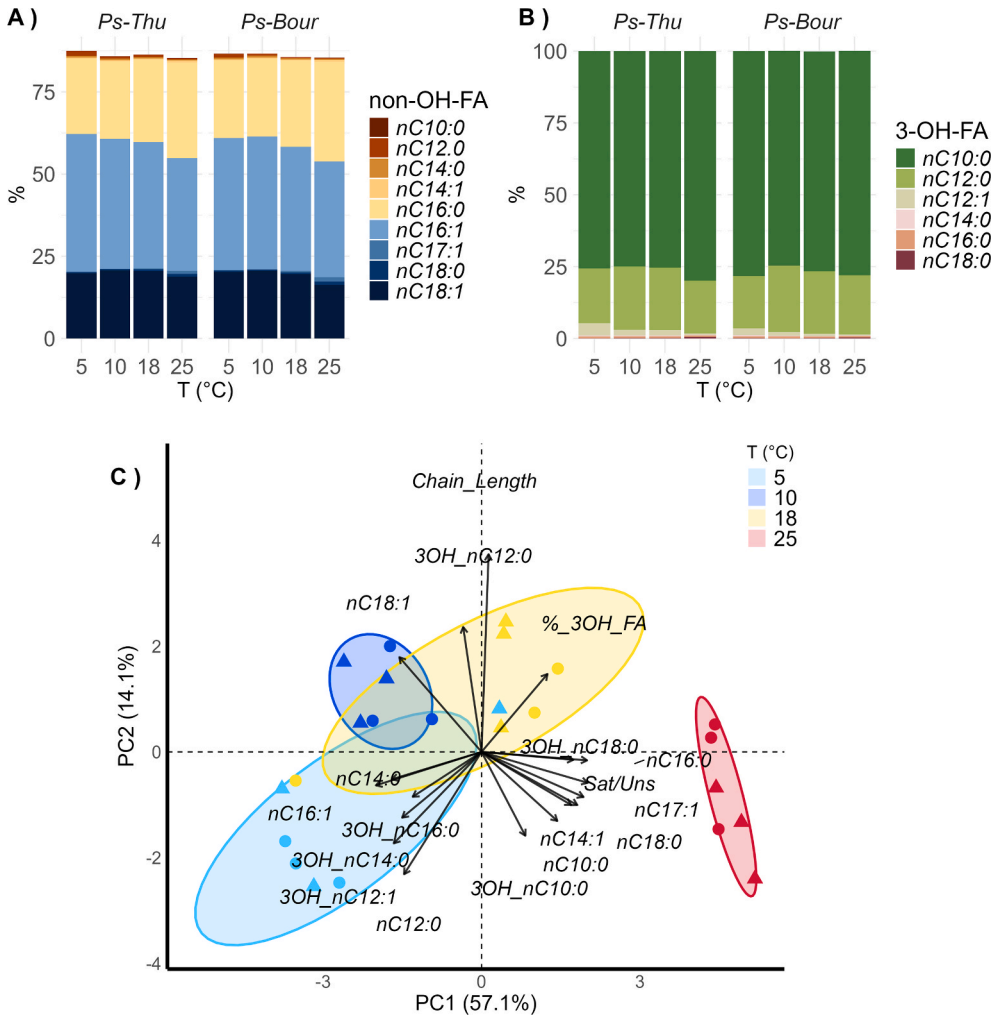

Fig. 1. Relative abundance of individual non-OH FAs vs. total FAs (A) and individual 3-OH FAs vs. total 3-OH FAs (B) as a function of the growth temperature. PCA (C) of lipid profiles including non-OH FAs and 3-OH-FAs for the two studied strains: *P. veronii* from lake La Thuile (*Ps-Thu*; circles) and *P. veronii* from lake Bourget (*Ps-Bour;* triangles). The percentage of the variance explained for each component is labelled on the x and y axes.

negatively correlated with temperature (Table 1), which can be related with the variations between the 5–18 °C treatments observed in the PCA (Fig. 1C). As previously observed for other species (Bajerski et al., 2017), *P. veronii* displayed a non-linear lipid response to temperature, with minor changes from 5 to 18 °C and a distinct shift at 25 °C, suggesting increased stress above the optimal growth temperature (~20 °C). This result supports the use of nonlinear models when developing lipid-based environmental proxies (Véquaud et al., 2021), as bacterial species may exhibit distinct responses to temperature.

The thermal adaptation of the two *P. veronii* strains involved a complex interplay of changes in the cell membrane lipid composition relying on all non-OH-FAs and to a lesser extent on 3-OH FAs, with subtle differences between the strains. *Ps-Thu* showed higher relative abundances of several FAs (Table 1) and better growth at 5 °C and 30 °C (see above). *Ps-Bour* changed its FA composition from 18 °C, while such a shift was visible only at 25 °C in *Ps-Thu* (Table 1: abundance of *n*-$C_{18:1}$ and Sat/Uns ratio). This aligns with the broader lake temperature range during SSM sample collection for *Ps-Thu* (5.4–13.9 °C) than for *Ps-Bour* (6.9–9.9 °C), suggesting greater thermal acclimatization. While it cannot be fully excluded that the slight differences in strain responses to temperature are due to lab-induced strain evolution, the short time between isolation and culturing, and limited sub-culturing, minimizes this risk. A few studies previously observed that the influence of temperature on the FA profile could differ for bacterial strains of the same species (e.g. Lezcano et al., 2025). Nevertheless, to the best of our knowledge, this is the first study showing such differences for lake strains. Although subtle, strain-level differences may influence lipid-based proxies, as for example those developed based on 3-OH-FAs (RIAN and RAN; Wang et al., 2016), depending on bacterial abundance and local variability.

In contrast to *P. veronii*, the whole suite of 3-OH FAs in soil *Bacteroidetes* was influenced by growth temperature, with an increase of the relative abundance of *anteiso* homologues at lower temperatures (Hellequin et al., 2023). This suggests a taxa-dependence of the 3-OH FA response to temperature. This makes the application of 3-OH FAs as temperature proxies highly dependent on the natural composition and diversity of Gram-negative bacteria in the environment (Garner et al., 2023), especially as the 3-OH FA lipid profile strongly differs between Gram-negative bacterial species (Zeng et al., 2025). This is reflected in the absence of *anteiso* and *normal* C_{13}, C_{15} and C_{17} 3-OH FAs in the lipid inventory of *P. veronii*, preventing the calculation of the RAN_{13}, RAN_{15} and RAN_{17}, previously proposed as temperature proxies in lakes and soils (Wang et al., 2016; Yang et al., 2020). Thus, the application of such temperature proxies will not only be highly dependent on the bacterial diversity, but also to the individual adaptation mechanisms to environmental variations and the relative abundance of individual species in the entire bacterial community. Further research on a larger number of Gram-negative bacterial strains is needed to better constrain the applicability of 3-OH FAs as temperature proxies in different environmental settings and to identify the main contributors to these parameters.

Table 1
Mean (±SE) relative abundance of non-OH FAs vs. total FAs and 3-OH FAs vs. total 3-OH FAs. Results of two-way linear models (LM), significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$), and Tukey post-hoc test ($P < 0.05$) for temperature (T °C, different letters) and strain (S, underlined higher value). N = 3.

	Ps-Thu				*Ps-Bour*				TWO WAY LM		
Non-OH FAs	**5 °C**	**10 °C**	**18 °C**	**25 °C**	**5 °C**	**10 °C**	**18 °C**	**25 °C**	**T°C**	**S**	**T°C: S**
Saturated											
n-C10:0	0.05 ± 0.01^{b}	0.06 ± 0.002^{b}	0.07 ± 0.005^{ab}	0.09 ± 0.007^{a}	0.05 ± 0.01^{b}	0.04 ± 0.01^{b}	0.04 ± 0.01^{b}	0.1 ± 0.01^{a}	***		
n-C12:0	1.4 ± 0.2^{a}	0.7 ± 0.1^{b}	0.6 ± 0.2^{b}	0.4 ± 0.05^{b}	1.1 ± 0.3^{a}	0.6 ± 0.01^{ab}	0.3 ± 0.01^{b}	0.3 ± 0.05^{b}	***	*	
n-C14:0	0.5 ± 0.02^{a}	0.5 ± 0.01^{a}	0.4 ± 0.08^{a}	0.3 ± 0.04^{b}	0.5 ± 0.09^{ab}	0.6 ± 0.03^{a}	0.4 ± 0.02^{ab}	0.3 ± 0.06^{b}	***		
n-C16:0	23.0 ± 0.4^{c}	23.6 ± 0.2^{bc}	25.0 ± 1.3^{b}	29.1 ± 0.1^{a}	23.7 ± 1.3^{c}	23.7 ± 0.2^{c}	26.3 ± 0.04^{b}	30.4 ± 0.2^{a}	***		
n-C18:0	0.4 ± 0.05^{c}	0.4 ± 0.03^{c}	0.6 ± 0.06^{bc}	0.9 ± 0.04^{a}	0.4 ± 0.07^{b}	0.4 ± 0.01^{b}	0.5 ± 0.01^{b}	1.0 ± 0.2^{a}	***		
Total	*25.4 ± 0.2^{b}*	*25.2 ± 0.09^{b}*	*26.7 ± 1.1^{b}*	*30.7 ± 0.2^{a}*	*25.7 ± 1.0^{c}*	*25.4 ± 0.2^{c}*	*27.6 ± 0.01^{b}*	*32.1 ± 0.31^{a}*	***		
Unsaturated											
n-C14:1	0.3 ± 0.03^{c}	0.3 ± 0.002^{c}	0.4 ± 0.05^{b}	0.6 ± 0.04^{a}	0.3 ± 0.04^{b}	0.2 ± 0.003^{b}	0.2 ± 0.03^{b}	0.5 ± 0.03^{a}	***	***	
n-C16:1	41.9 ± 0.7^{a}	39.6 ± 0.4^{ab}	38.5 ± 1.7^{b}	34.2 ± 0.2^{c}	40.2 ± 1.3^{a}	40.4 ± 0.3^{a}	37.7 ± 0.2^{b}	35.2 ± 0.2^{c}	***		
n-C17:1	0.02 ± 0.003^{b}	0.08 ± 0.004^{b}	0.2 ± 0.1^{b}	0.9 ± 0.08^{a}	0.1 ± 0.09^{c}	0.08 ± 0.001^{c}	0.5 ± 0.04^{b}	1.4 ± 0.1^{a}	***	**	
n-C18:1	19.8 ± 0.1^{a}	20.7 ± 0.1^{a}	20.5 ± 0.3^{a}	18.8 ± 0.4^{b}	20.3 ± 0.1^{a}	20.6 ± 0.1^{a}	20.0 ± 0.03^{b}	16.3 ± 0.2^{c}	***	***	***
Total	*62 ± 0.7^{a}*	*60.7 ± 0.4^{a}*	*59.6 ± 1.4^{a}*	*54.5 ± 0.5^{b}*	*60.9 ± 1.1^{a}*	*61.3 ± 0.3^{a}*	*58.0 ± 0.3^{b}*	*53.4 ± 0.2^{c}*	***		
Sat/Uns	0.41 ± 0.002^{b}	0.41 ± 0.002^{b}	0.45 ± 0.03^{b}	0.56 ± 0.004^{a}	0.42 ± 0.02^{c}	0.41 ± 0.001^{c}	0.48 ± 0.002^{b}	0.60 ± 0.007^{a}	***		
Chain Length	16.37 ± 0.01^{b}	16.44 ± 0.01^{a}	16.44 ± 0.02^{a}	16.42 ± 0.01^{a}	16.40 ± 0.02^{c}	16.43 ± 0.002^{ab}	16.44 ± 0.003^{a}	16.38 ± 0.003^{c}	***		*
3-OH FAs											
n-C10:0	75.6 ± 3.1	75.0 ± 2.8	75.3 ± 2.9	79.9 ± 1.5	78.3 ± 4.02	74.6 ± 1.3	76.6 ± 2.3	78.1 ± 3.4			
n-C12:1	4.3 ± 0.4^{a}	2.0 ± 0.3^{ab}	1.8 ± 0.8^{b}	0.4 ± 0.01^{c}	2.4 ± 0.8^{a}	1.3 ± 0.07^{a}	0.8 ± 0.07^{b}	0.4 ± 0.01^{c}	***	**	
n-C12:0	19.1 ± 2.6	22.0 ± 2.6	21.8 ± 2.1	18.4 ± 1.5	18.1 ± 3.7	23.1 ± 1.3	21.7 ± 2.4	20.5 ± 3.3			
n-C14:0	0.4 ± 0.04^{a}	0.3 ± 0.03^{b}	0.3 ± 0.06^{b}	0.2 ± 0.01^{b}	0.4 ± 0.04^{a}	0.3 ± 0.02^{b}	0.2 ± 0.02^{b}	0.2 ± 0.04^{b}	***	*	
n-C16:0	0.6 ± 0.07	0.6 ± 0.05	0.5 ± 0.1	0.5 ± 0.03	0.6 ± 0.06	0.7 ± 0.04	0.5 ± 0.02	0.5 ± 0.06			
nC18:0	0.02 ± 0.02^{c}	0.1 ± 0.01b^{b}	0.2 ± 0.07^{b}	0.6 ± 0.07^{a}	0.1 ± 0.06^{b}	0.05 ± 0.02^{b}	0.1 ± 0.06^{b}	0.3 ± 0.03^{a}	***		*
%3-OH/total FAs	*12.5 ± 0.9*	*14.2 ± 0.5*	*13.7 ± 0.7*	*14.7 ± 0.6*	*13.3 ± 0.4*	*13.3 ± 0.5*	*14.4 ± 0.3*	*14.5 ± 0.3*			

CRediT authorship contribution statement

Juanita Mora-Gomez: Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Sylvie Collin:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Adrienne Kish:** Writing – review & editing, Supervision, Conceptualization. **Christelle Anquetil:** Writing – review & editing, Formal analysis. **Marcelino T Suzuki:** Writing – review & editing, Methodology, Formal analysis. **Pierre Sabatier:** Writing – review & editing, Methodology. **Emmanuel Malet:** Writing – review & editing, Methodology. **William Rapuc:** Writing – review & editing, Methodology. **Céline Begorre:** Writing – review & editing, Methodology. **Mathieu Dellinger:** Writing – review & editing, Funding acquisition. **Arnaud Huguet:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.orggeochem.2026.105189.

Data availability

Data will be made available on request.

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