



HAL
open science

Post-mortem storage conditions and cooking methods affect long-chain omega-3 fatty acid content in Atlantic mackerel (*Scomber scombrus*)

Fany Sardenne, Eleonora Puccinelli, Marie Vagner, Laure Pecquerie, Antoine Bideau, Fabienne Le Grand, Philippe Soudant

► To cite this version:

Fany Sardenne, Eleonora Puccinelli, Marie Vagner, Laure Pecquerie, Antoine Bideau, et al.. Post-mortem storage conditions and cooking methods affect long-chain omega-3 fatty acid content in Atlantic mackerel (*Scomber scombrus*). *Food Chemistry*, 2021, 359, pp.129828. 10.1016/j.foodchem.2021.129828 . hal-03215360

HAL Id: hal-03215360

<https://hal.science/hal-03215360>

Submitted on 3 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 ***Post-mortem* storage conditions and cooking methods affect long-chain omega-3 fatty**
2 **acid content in Atlantic mackerel (*Scomber scombrus*)**

3

4 Fany Sardenne*, Eleonora Puccinelli, Marie Vagner, Laure Pecquerie, Antoine Bideau,
5 Fabienne Le Grand, Philippe Soudant

6

7 Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280 Plouzané, France

8 [*fany.sardenne@univ-brest.fr](mailto:fany.sardenne@univ-brest.fr)

9

10 **Abstract**

11 Long-chain omega-3 fatty acids such as eicosapentaenoic acid (EPA) and docosahexaenoic
12 acid (DHA) are health beneficial lipids found in high concentration in pelagic fishes,
13 including Atlantic mackerel. While EPA and DHA are sensitive to oxidative degradation
14 during fish storage and processing, *post-mortem* degradation in the first hours following fish
15 death is poorly documented. In this study, we stored fish at two temperatures (2–4°C and
16 18–20°C) and monitored EPA+DHA content in dorsal fillet 6, 12 and 24 hours after fish death
17 and after cooking (grill or steam). Storage duration was the most influencing factor, and
18 EPA+DHA loss was faster at 18–20°C. Six hours after fish death, and regardless of storage
19 temperature EPA+DHA content decreased by $1.3 \pm 1.3 \text{ mg.g}^{-1}$ ($9.6 \pm 9.5\%$ of the initial content).
20 EPA+DHA losses were highly variable among individuals, probably because of other sources
21 of variability (e.g., sampling position). Handling between fishing operation and deep-frozen
22 storage should be as short and as cool as possible to preserve EPA+DHA and for food safety.
23 Regarding cooking, both EPA+DHA and mono-unsaturated fatty acids increased in grilled
24 fillets.

25

26 *Key words: Oxidation, Fatty acids, Lipids, Small pelagic fish, Storage, Cooking method*

27 **1. Introduction**

28 Long-chain n-3 polyunsaturated fatty acids, and especially eicosapentaenoic acid (EPA;
29 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3) are essential lipids for several vital
30 functions in human (Siriwardhana et al., 2012; Swanson et al., 2012). Due to insufficient *de*
31 *novo* synthesis capacities, a daily dietary EPA+DHA intake of about 300 mg is recommended
32 for healthy adults (FAO/WHO, 2010; Plourde & Cunnane, 2007). Several human populations
33 however, face an EPA+DHA deficiency, caused by malnutrition or undernutrition (Stark et
34 al., 2016). EPA and DHA human supplies are mainly ensured by the consumption of marine
35 fish, which obtain these lipids through the food web, mainly from primary producers. Due to
36 climate changes that induces modifications in the physiology and community composition of
37 primary producers (Galloway & Winder, 2015), the global EPA+DHA production is predicted
38 to decrease (Hixson & Arts, 2016). Such a decrease, combined with human population
39 growth, might cause a shortage in EPA+DHA availability that may become a challenge for
40 human food security in the next decades (Hicks et al., 2019). Preservation of EPA+DHA in
41 food is thus of high importance.

42 Small and medium pelagic fish, also called blue-backed fish, play an important role in
43 food security, as they are cheaper than large fishes and rich in nutrients, including EPA+DHA
44 (Kawarazuka & Béné, 2011). Among them, the Atlantic mackerel *Scomber scombrus* is a
45 fatty fish occurring in cold and temperate regions of the northern Atlantic Ocean, where it
46 forms large schools near the surface to feed on zooplankton and small fishes. About one
47 million tons of Atlantic mackerel are fished yearly, mainly by purse seine or pelagic trawl
48 (FAO Fisheries & Aquaculture, 2020). Mackerels are generally frozen or chilled whole at
49 collection, for further processing ashore (Sone et al., 2019). Storage method and duration, fish
50 processing, and cooking procedures are critical steps for fish EPA+DHA preservation,
51 because EPA and DHA are highly sensitive to oxidation (Gladyshev & Sushchik, 2019; Secci

52 & Parisi, 2016). In the case of mackerel, whose lipid content can vary by a factor of three
53 among individuals, storage temperature is among the main factor determining a successful
54 storage (Romotowska et al., 2017). Studies have investigated lipid changes in long-term
55 storage of mackerel for a large panel of storage temperatures and duration, from -27°C to
56 +26°C and from a day to a year (Otero et al., 2019; Oucif et al., 2012; Romotowska et al.,
57 2016, 2017; Standal et al., 2018). However, as for many other fish species, initial reference
58 values were based on fish obtained from commercial fishing and the exact time of death was
59 not well documented. Consequently, having information on the EPA+DHA changes in the
60 first *post-mortem* hours could help detecting EPA+DHA losses during the first processing
61 steps of fish (e.g., between fishing and the processing plants).

62 The objectives of this study were to quantify in Atlantic mackerel (i) EPA+DHA changes
63 during the first *post-mortem* hours according to storage temperature; and (ii) the influence of
64 the cooking method (grill and steam) on the EPA+DHA content. Fatty acids, including
65 EPA+DHA, were quantified in the fillet of freshly euthanized mackerel, and at 6, 12 and 24
66 hours from death, on fish stored at two contrasted temperatures (2–4°C and 18–20°C).

67

68 **2. Material & Method**

69 2.1. Sample collection

70 Fifteen mackerels *Scomber scombrus* (25.2±3.3 cm, min-max=20-30 cm in fork length) were
71 collected by hand line in the Baie de Douarnenez, France on July 26th 2020. Seawater
72 parameters were 16.2°C and 34.8 PSU, and air temperature was 18-20°C throughout the
73 fishing operation. Fish were immediately euthanized by immersion in a 1 mL.L⁻¹ eugenol bath
74 (Fili@vet Reseau Cristal, France) for 5-10 min, then immediately labelled for later
75 identification, and dissected on board. Sampling was restricted to the dorsal fillet from the
76 right side of the fish (i.e., white muscle under the first dorsal fin). This area is homogenous in

77 both lipid content and lipid oxidation in *S. scombrus* (Icekson et al., 1998), and in lipid and
78 fatty acids contents in the related species *S. japonicus* and *S. australasicus* (Bae et al., 2010).
79 In a previous estimate conducted on three Atlantic mackerels kept frozen for 8 months at -
80 15°C, the EPA+DHA contents varied from ca. 7 % among the sampled positions (results not
81 shown). For each fish, about 0.5 g wet weight (ww) of dorsal white muscle was sampled
82 without skin, flash frozen in liquid nitrogen, and stored in a dry shipper frequently refuelled
83 with liquid nitrogen (T₀ sample). The total time between fish death and sample flash-freezing
84 was less than 10 min. Fishes were then kept whole (neither eviscerated, nor filleted), and
85 randomly stored either (i) at about 4°C in an insulated styrofoam box cooled with -20°C ice
86 packs (n=8 fish), or (ii) at ambient temperature in a styrofoam box (n=7 fish). To consider the
87 inter-individual variability, measurements were repeated over time on the same individuals.
88 Six hours after the first tissue sampling, another 0.5 mg ww sample of dorsal muscle was
89 taken on each fish next to the previous one (T₆) (Fig.1). Samples were flash frozen and stored
90 in a dry shipper, and fishes were stored back in their respective box (i.e., ice packs or
91 ambient). The same procedure was repeated 12 and 24 hours after the first tissue sampling
92 (T₁₂ and T₂₄, respectively) (Fig.1). Air temperature of the storage boxes (i.e., ice cold or
93 ambient temperature) was recorded before each tissue sampling and ranged 2–4°C and
94 18–20°C throughout the storage test, respectively.

95 After the last sampling, dorsal fillet from the left side was filleted and cooked on ethanol-
96 cleaned equipment, with neither oil nor condiment. Fillets with skin were either (i) grilled on
97 a griddle at 80–90°C for five minutes, or (ii) steamed with 130 mL of tap water brought to a
98 boil for 15 minutes (for each cooking method, half individuals were from each storage
99 temperatures; Fig.1). European populations commonly used these two methods, steaming
100 being particularly preferred for babies. After cooking, about 0.5 mg ww of fillet without skin

101 was collected, flash frozen, and stored in a dry shipper. All the samples were then stored at -
102 80°C for 40 days before subsequent analyses.

103

104 2.2. Moisture analysis

105 Moisture was determined by gravimetry. Samples were weighed before and after a 65-hours
106 freeze-drying (Christ Alpha 1-2 LD plus lyophilizer). The mean analytical variability was 1%.
107 Immediately after freeze-drying, samples were homogenized with ball mill (Restch MM400)
108 and stored back at -80°C for four days before lipid extraction. Moisture was expressed in
109 percentage of wet weight.

110

111 2.3. Fatty acid analysis

112 Lipids were extracted from ca. 60 mg of dry powder with 6 mL of solvent mixture
113 (CH₂Cl₂:MeOH, 2:1, v:v) directly added into glass vials (Sardenne et al., 2019). Extracts were
114 flushed with nitrogen gas, vortexed, sonicated for 15 min, and stored for 15 days at -20°C.
115 Tricosanoic acid (23:0) was added as internal standard to lipid extract. Lipids were then
116 transesterified with H₂SO₄ (3.8% in MeOH) at 100°C for 10 min. Fatty acid methyl esters
117 (FAME) were separated and quantified on a Varian CP8400 gas chromatograph (GC)
118 equipped in parallel with a Zebron ZB-WAX and a ZB-5HT column (both 30 m length, 0.25
119 mm internal diameter, 0.25 µm film thickness; Phenomenex) and flame ionisation detectors at
120 the Lipidocean core facility, University of Brest, France. GC parameters were set as in
121 Sardenne et al. (2019). FAME were identified by comparing sample retention times to those
122 of commercial standard mixtures (Supelco 37-component FAME mix, BAME, and PUFA no.
123 1 and 3 mixes; Sigma-Aldrich) using Galaxie 1.9.3.2 software (Varian). FAME content was
124 converted into fatty acids (FA) content based on 23:0 recovery. Total FA content was

125 calculated as the sum of 41 identified FA (16 poly-unsaturated FA (PUFA), 15 mono-
126 unsaturated FA (MUFA), and 10 saturated FA (SFA)). Data were expressed in mg.g^{-1} dry
127 weight to avoid confounding lipid changing content with water changing content. The mean
128 analytical variability was 4.2% for the GC and 11.9% for the whole FA analysis.

129

130 2.4.Data analysis

131 Contents in moisture, total FA, EPA+DHA, and FA families (SFA, MUFA, PUFA) were
132 compared among storage temperatures, durations and the interaction between both factors
133 tested using semi-parametric MANOVAs for repeated measures based on a central χ^2 -
134 distribution, which does not assume multivariate normality nor covariance homogeneity (RM
135 function from the ‘MANOVA.RM’ package; Friedrich et al., 2018). Non-parametric paired
136 Wilcoxon tests (V statistic) were used to refine differences between duration modalities.
137 Unpaired Wilcoxon test (W statistic) were used to test for differences between storage
138 temperatures at each duration, and between cooking modes. Spearman correlation tests (S
139 statistic) were used to test for correlation between EPA+DHA losses at T_6 , T_{12} , and T_{24} , and
140 FA content at T_0 , and linear regressions were used to test for fish length influence on FA
141 contents. Data were analysed using R software 3.5.0 (R Development Core Team et al.,
142 2018), and ‘stats’ and ‘MANOVA.RM’ packages.

143

144 3. Results

145 Initial EPA+DHA content was $16.2 \pm 4.0 \text{ mg.g}^{-1}$ dw), representing about 30% and 80% of total
146 FA and PUFA, respectively. The amount of FA varied as a function of fish length, with larger
147 individuals having a higher content of total FA and EPA+DHA (i.e. from 12.2 ± 0.2 to
148 $17.6 \pm 0.6 \text{ mg.g}^{-1}$ between 20 and 30 cm in fork length ; Fig 2). Biochemical contents of fish,
149 including EPA+DHA (Table 1), changed with storage duration, but was not affected neither

150 by storage temperature nor by the interaction between storage temperature and duration
151 (Table 2). Changes in EPA+DHA content between storage conditions were highly variable
152 among individuals (large SD; Table 1).

153 Regardless of the storage temperature, total FA content decreased between T_0 and T_{24} , from
154 60.9 ± 21.8 to 51.0 ± 24.1 $\text{mg} \cdot \text{g}^{-1}$ ($V=114$, $p<0.001$; Table 1, Fig. 3b). Variability in total FA
155 content (estimated through coefficients of variation) was lower at $2-4^\circ\text{C}$ than at $18-20^\circ\text{C}$ (T_6 :
156 32.2% and 42.8%, T_{12} : 44.0% and 49.9%, and T_{24} : 40.1% and 58.0% at $2-4^\circ\text{C}$ and $18-20^\circ\text{C}$,
157 respectively). Regarding cooking, total FA content did not change from T_{24} in either grilled or
158 steamed fillets ($W=42$, $p=0.12$; Fig. 3b).

159 EPA+DHA content decreased between T_0 and T_6 ($V=110$, $p<0.01$): paired differences
160 indicated a loss of 1.3 ± 1.3 $\text{mg} \cdot \text{g}^{-1}$ (0.9 ± 1.3 and 1.9 ± 1.1 $\text{mg} \cdot \text{g}^{-1}$ at $2-4^\circ\text{C}$ and $18-20^\circ\text{C}$,
161 respectively), equating to a loss of $9.6 \pm 9.5\%$ ($5.5 \pm 8.1\%$ and $14.2 \pm 9.3\%$, respectively) of the
162 initial EPA+DHA content. EPA+DHA content also decreased between T_6 and T_{12} ($V=103$,
163 $p<0.05$), but not after ($V=61$, $p=0.98$; Fig. 3c). No correlations between total FA content at T_0
164 and EPA+DHA losses at T_6 , T_{12} , and T_{24} were detected ($S=814$, $p=0.10$; $S=450$, $p=0.48$;
165 $S=438$, $p=0.43$, respectively). Regarding cooking, grilled fillet gained 3.4 ± 3.5 $\text{mg} \cdot \text{g}^{-1}$ and
166 steamed fillets lost 0.2 ± 3.4 $\text{mg} \cdot \text{g}^{-1}$ of EPA+DHA from T_{24} ($W=46$, $p<0.05$; Table 1). As for
167 EPA+DHA, PUFA, MUFA and SFA contents decreased between T_0 and T_6 (all $p<0.01$; Fig.
168 3d to f), but only PUFA continued to decrease between T_6 and T_{12} ($V=98$, $p<0.05$). Cooking
169 methods affected both EPA+DHA and MUFA contents, which were already lowered by
170 storage ($W=46$, $p<0.05$ and $W=47$, $p<0.05$): EPA+DHA and MUFA gained 3.4 ± 3.5 and
171 5.7 ± 5.4 $\text{mg} \cdot \text{g}^{-1}$ in grilled fillet and lost 0.2 ± 3.3 and 2.3 ± 6.3 $\text{mg} \cdot \text{g}^{-1}$ in steamed fillet,
172 respectively (Fig. 3c and e).

173

174 4. Discussion

175 EPA and DHA are sensitive to oxidation, but their loss during fish processing in the first *post-*
176 *mortem* hours of the Atlantic mackerel is not well documented. Here, we find that i) storage
177 duration was the only factor explaining FA losses in the first hours after fish death, and ii)
178 grilled fillet had higher EPA+DHA content than steamed fillet. However, changes in
179 EPA+DHA content were highly variable among individuals, probably in relation to other
180 sources of variability (e.g. sampling position, analytical variability).

181 High inter-individual variability was observed both in FA contents and in FA losses.
182 Fish length explained most of the variability in the initial FA content, and storage duration
183 was the only significant factor explaining FA losses, despite faster FA losses at the high
184 storage temperature (18–20°C). Other sources of variability in FA losses might be the
185 heterogeneity in FA compositions among tissue sampling positions, despite the fact that all
186 positions were close to each other, i.e., dorsal white muscle under the first dorsal spine. While
187 we tested the natural variability of EPA+DHA content in the dorsal fillet of frozen Atlantic
188 mackerel, and that this remains relatively low, this variability remains to be assessed for fresh
189 individuals. Regarding changes due to storage duration, FA contents decreased only six hours
190 after fish death with: $9.6 \pm 9.5\%$ of the initial EPA+DHA content been lost. Again, the large
191 inter-individual differences observed can be explained by the sources of variability previously
192 mentioned (i.e., sampling position and analytical variability). However, only PUFA continued
193 to decrease 12 hours after death. PUFA are generally considered as the FA the most sensitive
194 to degradation, especially to oxygen contact that causes peroxidation (Couturier et al., 2020).
195 While lipid hydrolysis tends to increase with fish fat content (Aubourg et al., 2005; Rudy et
196 al., 2016), this relationship has not been reported for mackerel, even over several storage
197 months (Aubourg et al., 2005). Similarly, we did not observe any relationship between the
198 initial fish FA content and EPA+DHA losses in the first *post-mortem* hours of mackerel.
199 These results highlight the importance of fast handling, and to a lesser extent of cool handling,

200 even before the *rigor mortis* that usually occurs at about 18-21 hours *post-mortem* in mackerel
201 (Anders et al., 2020). Although temperature did not play a crucial role for lipid oxidation on
202 the short time scale of this study (24 hours), it is relevant for other degradation mechanisms
203 such as hydrolysis or histamine production (Couturier et al., 2020; Zou & Hou, 2017).
204 Avoiding filleting, favoring fast frozen of fish, as well as the maintenance of low temperature
205 throughout long-term storage could save highly valuable FA in the Atlantic mackerel
206 (Aubourg et al., 2005; Romotowska et al., 2017), caveat that can probably be generalized to
207 other fatty and small pelagic fishes (e.g., Rudy et al., 2016). This procedure is also relevant
208 for scientific samplings of fish obtained from professional fisheries or from remote areas,
209 which could rapidly loose FA before analysis, including EPA+DHA, due to a lack of proper
210 storage.

211 Regarding cooking methods, grilled fish had higher FA contents, especially
212 EPA+DHA and MUFA, than steamed fish, as well as than T₀ fish (all in dry weight). A higher
213 FA content measured after grilling might be related (i) to changes in the fillet texture that
214 might improve FA extraction from tissue, as high heating is commonly used by the industry
215 for fish oil extraction (Adeoti & Hawboldt, 2014); or (ii) to FA exchanges with the
216 subcutaneous fat beneath the skin (fillets were cooked with the skin), favoured by the
217 increasing temperature. Studies have shown no exchanges of FA between fillet and skin of the
218 Atlantic mackerel during iced and frozen storage (Xing et al., 1993), but extensive exchanges
219 can occur during frying (Sebedio et al., 1993). In addition, the skin of small pelagic fish is
220 relatively rich in EPA+DHA: about 19%, 26%, 25% and 13% of total FA for the Atlantic
221 mackerel, *Rastrelliger kanagurta*, *Sardinella maderensis* and *Sardinella aurita*, respectively
222 (Njinkoué et al., 2002; Sahena et al., 2010; Zuta et al., 2003). This suggests that the skin
223 should be kept to cook Atlantic mackerel fillets. Extended tests including other cooking
224 methods should however be conducted to determine the best cooking method to preserved the

225 valuable EPA+DHA from the Atlantic mackerel. Indeed, the summer Atlantic mackerel is an
226 excellent food source of EPA+DHA: with about 4 to 5 mg.g⁻¹ in wet weight, a daily
227 consumption of 75 g (raw or steamed) or 60 g (grilled) of dorsal fillet would be enough to
228 cover the EPA+DHA daily requirements in adults.

229

230 **Acknowledgments**

231 We warmly thank J.-P. and P.-Y. Carval for welcoming us on-board for the fishing operation.
232 We also thanks O. Gauthier (University of Brest, LEMAR) for its advices with statistics, and
233 the two anonymous reviewers for their comments and suggestions on an earlier draft of this
234 work. F.S. was funded by the Regional council of Brittany (SAD program), and E.P was
235 funded by ISblue project, Interdisciplinary graduate school for the blue planet (ANR-17-
236 EURE-0015), co-funded by a grant from the French government under the program
237 "Investissements d'Avenir" and the SAD program. This study contributes to the OMEGA
238 project, funded by ISblue project.

239

240 **Author credits**

241 Fany Sardenne: conceptualization, methodology, software, investigation, writing – original
242 draft, review & editing. Eleonora Puccinelli: investigation, writing – review & editing. Marie
243 Vagner: writing – review & editing, funding acquisition. Laure Pecquerie: writing – review &
244 editing, funding acquisition. Fabienne Le Grand: validation, resources. Antoine Bideau:
245 methodology. Philippe Soudant: validation, writing – review & editing, funding acquisition.

246

247 **References**

248 Adeoti, I. A., & Hawboldt, K. (2014). A review of lipid extraction from fish processing by-
249 product for use as a biofuel. In *Biomass and Bioenergy* (Vol. 63, pp. 330–340). Elsevier
250 Ltd. <https://doi.org/10.1016/j.biombioe.2014.02.011>

251 Anders, N., Eide, I., Lerfall, J., Roth, B., & Breen, M. (2020). Physiological and flesh quality
252 consequences of pre-mortem crowding stress in Atlantic mackerel (*Scomber scombrus*).
253 *PLoS ONE*, *15*(2), e0228454. <https://doi.org/10.1371/journal.pone.0228454>

254 Aubourg, S. P., Rodríguez, A., & Gallardo, J. M. (2005). Rancidity development during
255 frozen storage of mackerel (*Scomber scombrus*): effect of catching season and
256 commercial presentation. *European Journal of Lipid Science and Technology*, *107*(5),
257 316–323. <https://doi.org/10.1002/ejlt.200401124>

258 Bae, J.-H., Yoon, S.-H., & Lim, S.-Y. (2010). A comparison of the biochemical
259 characteristics of different anatomical regions of Chub (*Scomber japonicus*) and Blue
260 mackerel (*Scomber australasicus*) muscles. *Korean Journal of Fisheries and Aquatic
261 Sciences*, *43*(1), 6–11. <https://doi.org/10.5657/kfas.2010.43.1.006>

262 Couturier, L. I. E., Michel, L. N., Amaro, T., Budge, S. M., da Costa, E., De Troch, M., Di
263 Dato, V., Fink, P., Giraldo, C., Le Grand, F., Loaiza, I., Mathieu-Resuge, M., Nichols, P.
264 D., Parrish, C. C., Sardenne, F., Vagner, M., Pernet, F., & Soudant, P. (2020). State of art
265 and best practices for fatty acid analysis in aquatic sciences. *ICES Journal of Marine
266 Science*. <https://doi.org/10.1093/icesjms/fsaa121>

267 FAO/WHO. (2010). *Report of the Joint FAO/WHO Expert Consultation on the Risks and
268 Benefits of Fish Consumption. Rome, 25-29 january 2010.*
269 <http://www.fao.org/3/ba0136e/ba0136e00.htm>

270 FAO Fisheries & Aquaculture. (2020). *Species Fact Sheets - Scomber scombrus (Linnaeus,
271 1758)*. <http://www.fao.org/fishery/species/2473/en>

272 Friedrich, S., Konietzschke, F., & Pauly, M. (2018). Analysis of Multivariate Data and
273 Repeated Measures Designs with the R Package MANOVA.RM. *Family Medicine*,
274 37(5)(01), 53–65. <http://arxiv.org/abs/1801.08002>

275 Galloway, A. W. E., & Winder, M. (2015). Partitioning the Relative Importance of Phylogeny
276 and Environmental Conditions on Phytoplankton Fatty Acids. *PLoS ONE*, 10(6),
277 e0130053. <https://doi.org/10.1371/journal.pone.0130053>

278 Gladyshev, M. I., & Sushchik, N. N. (2019). Long-chain omega-3 polyunsaturated fatty acids
279 in natural ecosystems and the human diet: Assumptions and challenges. In *Biomolecules*
280 (Vol. 9, Issue 9, p. 485). MDPI AG. <https://doi.org/10.3390/biom9090485>

281 Hixson, S. M., & Arts, M. T. (2016). Climate warming is predicted to reduce omega-3, long-
282 chain, polyunsaturated fatty acid production in phytoplankton. *Global Change Biology*,
283 22(8), 2744–2755. <https://doi.org/10.1111/gcb.13295>

284 Icekson, I., Drabkin, V., Aizendorf, S., & Gelman, A. (1998). Lipid oxidation levels in
285 different parts of the mackerel, *Scomber scombrus*. *Journal of Aquatic Food Product*
286 *Technology*, 7(2), 17–29. https://doi.org/10.1300/J030v07n02_03

287 Kawarazuka, N., & Béné, C. (2011). The potential role of small fish species in improving
288 micronutrient deficiencies in developing countries: Building evidence. *Public Health*
289 *Nutrition*, 14(11), 1927–1938. <https://doi.org/10.1017/S1368980011000814>

290 Njinkoué, J. M., Barnathan, G., Miralles, J., Gaydou, E. M., & Samb, A. (2002). Lipids and
291 fatty acids in muscle, liver and skin of three edible fish from the Senegalese coast:
292 *Sardinella maderensis*, *Sardinella aurita* and *Cephalopholis taeniops*. *Comparative*
293 *Biochemistry and Physiology - B Biochemistry and Molecular Biology*, 131(3), 395–402.
294 [https://doi.org/10.1016/S1096-4959\(01\)00506-1](https://doi.org/10.1016/S1096-4959(01)00506-1)

295 Otero, L., Pérez-Mateos, M., Holgado, F., Márquez-Ruiz, G., & López-Caballero, M. E.
296 (2019). Hyperbaric cold storage: Pressure as an effective tool for extending the shelf-life
297 of refrigerated mackerel (*Scomber scombrus*, L.). *Innovative Food Science and*
298 *Emerging Technologies*, 51, 41–50. <https://doi.org/10.1016/j.ifset.2018.05.003>

299 Oucif, H., Ali-Mehidi, S., & El-Amine Abi-Ayad, S.-M. (2012). Lipid oxidation and
300 histamine production in Atlantic Mackerel (*Scomber scombrus*) versus time and mode of
301 conservation. *Journal of Life Sciences*, 6, 713–720.

302 Plourde, M., & Cunnane, S. C. (2007). Extremely limited synthesis of long chain
303 polyunsaturates in adults: implications for their dietary essentiality and use as
304 supplements. *Applied Physiology, Nutrition, and Metabolism*, 32(4), 619–634.
305 <https://doi.org/10.1139/H07-034>

306 R Development Core Team, Team, R. C., R Development Core Team, Team, R. C., & R
307 Development Core Team. (2018). *R: A language and environment for statistical*
308 *computing* (3.5.0). R Foundation for Statistical Computing. [https://doi.org/3-900051-07-](https://doi.org/3-900051-07-0)
309 0

310 Romotowska, P. E., Gudjónsdóttir, M., Karlsdóttir, M. G., Kristinsson, H. G., & Arason, S.
311 (2017). Stability of frozen Atlantic mackerel (*Scomber scombrus*) as affected by
312 temperature abuse during transportation. *LWT - Food Science and Technology*, 83, 275–
313 282. <https://doi.org/10.1016/J.LWT.2017.05.024>

314 Romotowska, P. E., Karlsdóttir, M. G., Gudjónsdóttir, M., Kristinsson, H. G., & Arason, S.
315 (2016). Influence of feeding state and frozen storage temperature on the lipid stability of
316 Atlantic mackerel (*Scomber scombrus*). *International Journal of Food Science &*
317 *Technology*, 51(7), 1711–1720. <https://doi.org/10.1111/ijfs.13146>

318 Rudy, M. D., Kainz, M. J., Graeve, M., Colombo, S. M., & Arts, M. T. (2016). Handling and

319 storage procedures have variable effects on fatty acid content in fishes with different
320 lipid quantities. *PLoS ONE*, *11*(8), e0160497.
321 <https://doi.org/10.1371/journal.pone.0160497>

322 Sahena, F., Zaidul, I. S. M. M., Jinap, S., Yazid, A. M., Khatib, A., & Norulaini, N. A. N. N.
323 (2010). Fatty acid compositions of fish oil extracted from different parts of Indian
324 mackerel (*Rastrelliger kanagurta*) using various techniques of supercritical CO₂
325 extraction. *Food Chemistry*, *120*(3), 879–885.
326 <https://doi.org/10.1016/j.foodchem.2009.10.055>

327 Sardenne, F., Bodin, N., Metral, L., Crottier, A., Le Grand, F., Bideau, A., Brisset, B.,
328 Bourjea, J., Saraux, C., Bonhommeau, S., Kerzérho, V., Bernard, S., & Rouyer, T.
329 (2019). Effects of extraction method and storage of dry tissue on marine lipids and fatty
330 acids. *Analytica Chimica Acta*, *1051*, 82–93. <https://doi.org/10.1016/J.ACA.2018.11.012>

331 Sebedio, J. L., Ratnayake, W. M. N., Ackman, R. G., & Prevost, J. (1993). Stability of
332 polyunsaturated omega-3 fatty acids during deep fat frying of Atlantic mackerel
333 (*Scomber scombrus* L.). *Food Research International*, *26*(3), 163–172.
334 [https://doi.org/10.1016/0963-9969\(93\)90049-O](https://doi.org/10.1016/0963-9969(93)90049-O)

335 Secci, G., & Parisi, G. (2016). From farm to fork: lipid oxidation in fish products. A review.
336 *Italian Journal of Animal Science*, *15*(1), 124–136.
337 <https://doi.org/10.1080/1828051X.2015.1128687>

338 Siriwardhana, N., Kalupahana, N. S., & Moustaid-Moussa, N. (2012). Health Benefits of n-3
339 Polyunsaturated Fatty Acids. Eicosapentaenoic Acid and Docosahexaenoic Acid. In
340 *Advances in Food and Nutrition Research* (Vol. 65, pp. 211–222). Academic Press Inc.
341 <https://doi.org/10.1016/B978-0-12-416003-3.00013-5>

342 Sone, I., Skåra, T., & Olsen, S. H. (2019). Factors influencing post-mortem quality, safety and

343 storage stability of mackerel species: a review. In *European Food Research and*
344 *Technology* (Vol. 245, Issue 4, pp. 775–791). Springer Verlag.
345 <https://doi.org/10.1007/s00217-018-3222-1>

346 Standal, I. B., Mozuraityte, R., Rustad, T., Alinasabhematabadi, L., Carlsson, N. G., &
347 Undeland, I. (2018). Quality of Filleted Atlantic Mackerel (*Scomber Scombrus*) During
348 Chilled and Frozen Storage: Changes in Lipids, Vitamin D, Proteins, and Small
349 Metabolites, including Biogenic Amines. *Journal of Aquatic Food Product Technology*,
350 27(3), 338–357. <https://doi.org/10.1080/10498850.2018.1436107>

351 Stark, K. D., Van Elswyk, M. E., Higgins, M. R., Weatherford, C. A., & Salem, N. (2016).
352 Global survey of the omega-3 fatty acids, docosahexaenoic acid and eicosapentaenoic
353 acid in the blood stream of healthy adults. In *Progress in Lipid Research* (Vol. 63, pp.
354 132–152). Elsevier Ltd. <https://doi.org/10.1016/j.plipres.2016.05.001>

355 Swanson, D., Block, R., & Mousa, S. A. (2012). Omega-3 Fatty Acids EPA and DHA: Health
356 Benefits Throughout Life. *Advances in Nutrition*, 3(1), 1–7.
357 <https://doi.org/10.3945/an.111.000893>

358 Xing, Y., Yoo, Y., Kelleher, S. D., Nawar, W. W., & Hultin, H. O. (1993). Lack of changes in
359 fatty acid composition of mackerel and cod during iced and frozen storage. *Journal of*
360 *Food Lipids*, 1(1), 1–14. <https://doi.org/10.1111/j.1745-4522.1993.tb00230.x>

361 Zou, Y., & Hou, X. (2017). Histamine production by enterobacter aerogenes in chub mackerel
362 (*Scomber japonicus*) at various storage temperatures. *Food Science and Technology*,
363 37(1), 76–79. <https://doi.org/10.1590/1678-457X.07716>

364 Zuta, C. P., Simpson, B. K., Chan, H. M., & Phillips, L. (2003). Concentrating PUFA from
365 mackerel processing waste. *JAOCS, Journal of the American Oil Chemists' Society*,
366 80(9), 933–936. <https://doi.org/10.1007/s11746-003-0799-5>

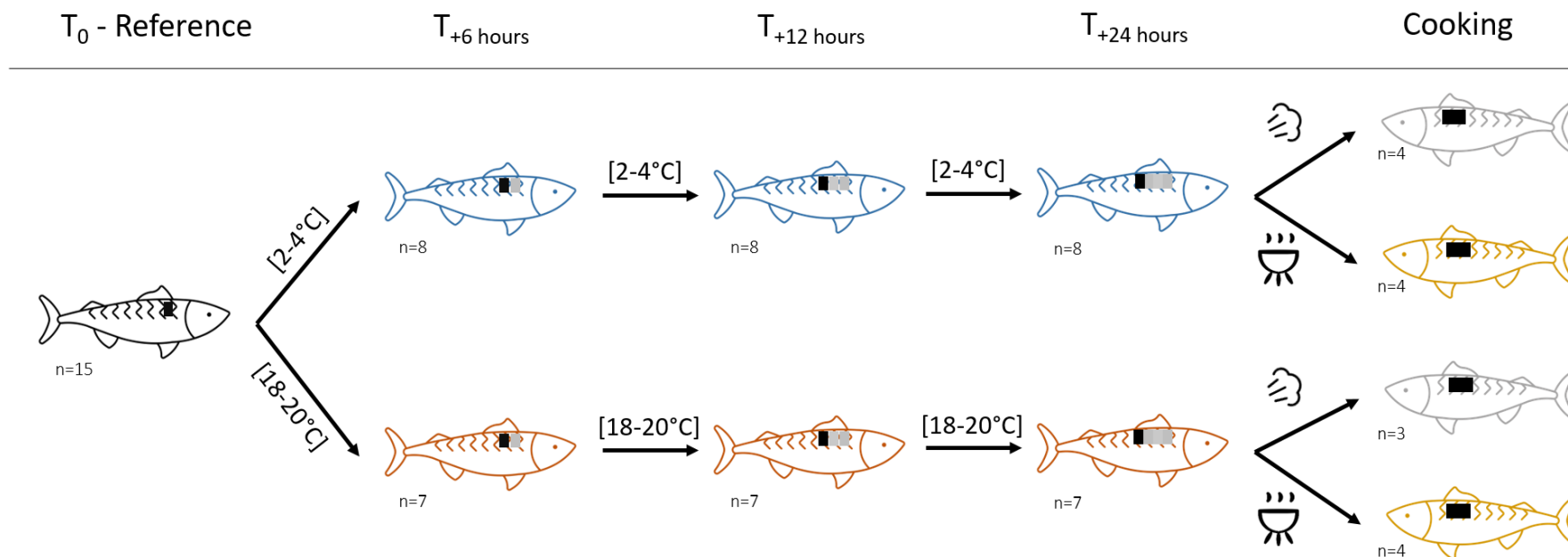


Fig. 1 | Outline of the sampling design testing for the influence of storage temperature (2-4°C and 18-20°C), storage duration (from T₆ to T₂₄ hours), and cooking method (grill and steam) on the fatty acid content of the Atlantic mackerel *Scomber scombrus*. Dark squares indicate the muscle sampling position at each step, and the grey ones the previously sampled positions. For cooking, we sampled the left side of the fish.

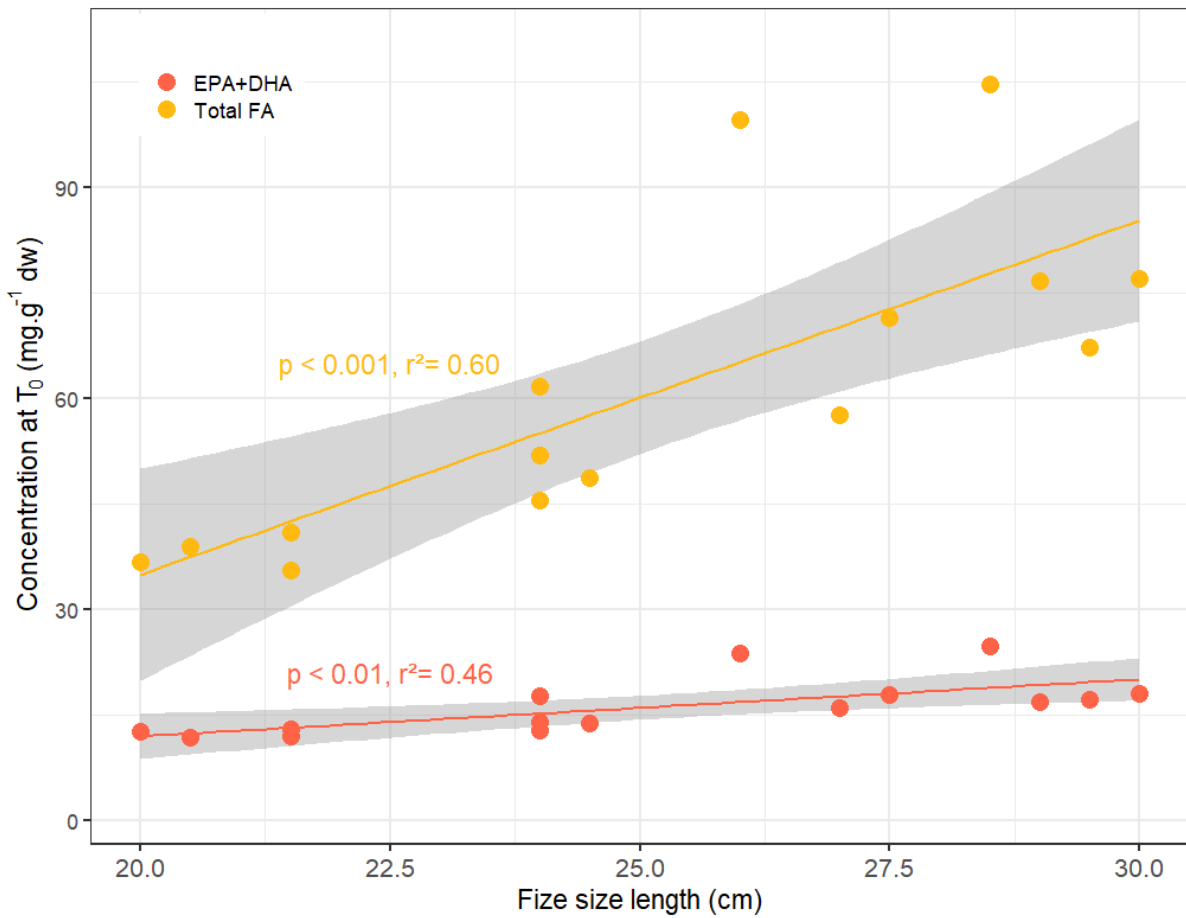


Fig. 2 | Total fatty acids (FA) and EPA+DHA contents (in mg.g⁻¹ of dry weight) in the dorsal fillet of Atlantic mackerel *Scomber scombrus* as a function of fish fork length. Fish (n=15) were collected from the Baie de Douarnenez, France, in July 2020. Grey areas are standard errors for the linear regressions.

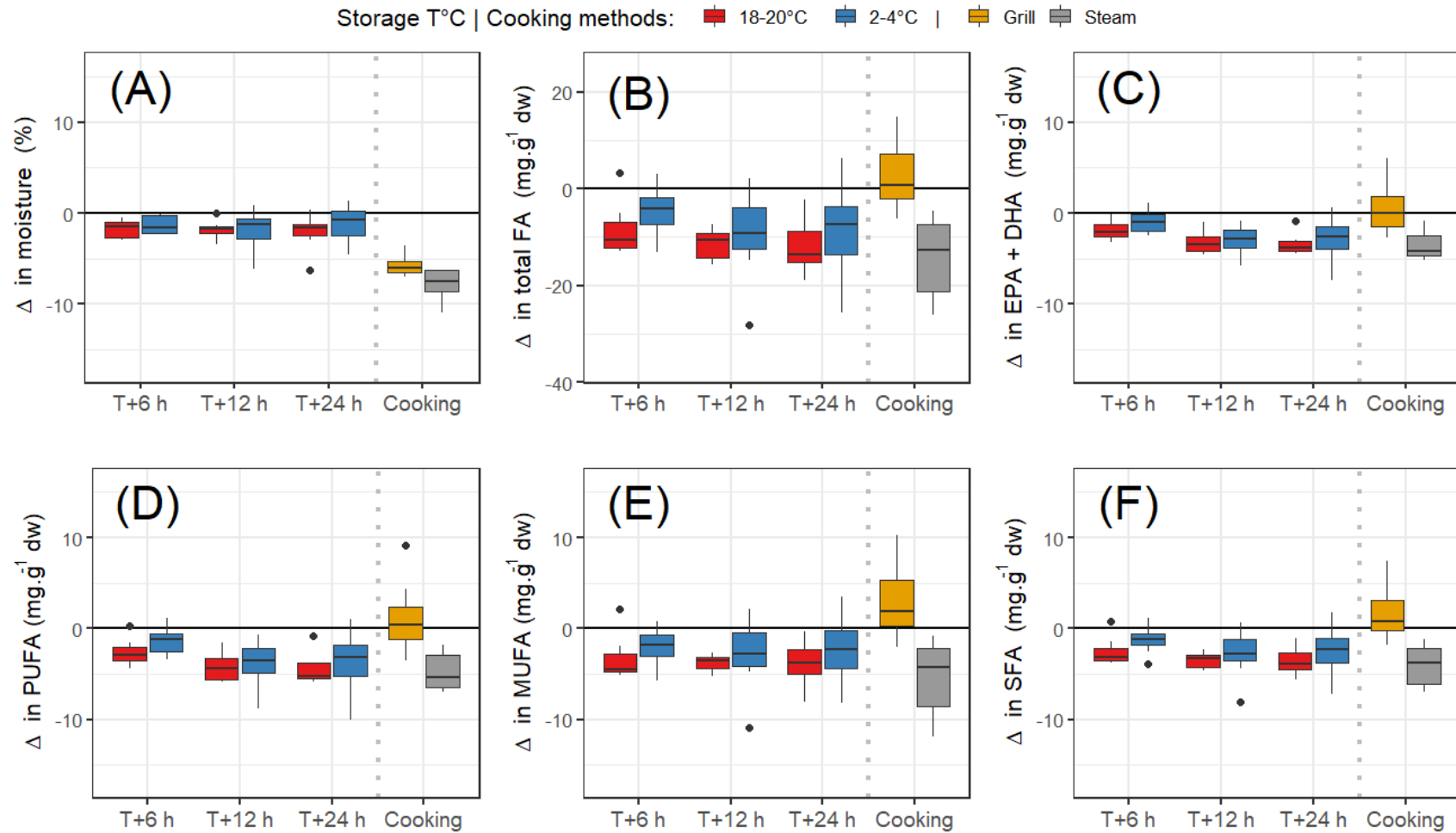


Fig. 3 | Boxplots of differences from initial values (T_0 = at fish death) for dorsal fillet contents in (A) moisture, (B) total fatty acids (FA), (C) EPA+DHA, (D) poly-unsaturated FA (PUFA), (E) mono-unsaturated FA (MUFA), and (F) saturated FA (SFA) during the first *post-mortem* hours (T_6 to T_{24}) and cooking of Atlantic mackerel, according to storage temperature and cooking methods (display by colour). In each boxplot, the thick black bar represents the median value, the box contains 50% of the data, and dots are outliers.

Table 1 | Mean \pm standard deviation for moisture in % per wet weight, total fatty acids (FA), EPA+DHA, poly-unsaturated FA (PUFA), mono-unsaturated FA (MUFA), and saturated FA (SFA) contents in $\text{mg}\cdot\text{g}^{-1}$ dry weight (dw), from the dorsal fillet of Atlantic mackerel after three storage durations (T_6 , T_{12} , and T_{24} hours) at two storage temperatures (2-4°C and 18-20°C), and after two cooking methods (grill and steam). N is the number of individuals.

	Reference	Storage test						Cooking method	
	T_0	T_6		T_{12}		T_{24}		Grill	Steam
		[2-4°C]	[18-20°C]	[2-4°C]	[18-20°C]	[2-4°C]	[18-20°C]		
N	15	8	7	8	7	8	7	8	7
Moisture (%)	75.4 \pm 3.0	73.5 \pm 2.9	74.3 \pm 3.4	72.9 \pm 4.3	74.3 \pm 3.3	73.7 \pm 3.2	74.0 \pm 4.7	69.2 \pm 2.7	68.3 \pm 3.1
Total FA ($\text{mg}\cdot\text{g}^{-1}$ dw)	60.9 \pm 21.8	60.6 \pm 19.5	48.0 \pm 20.5	55.6 \pm 24.4	44.8 \pm 22.3	56.7 \pm 22.7	44.5 \pm 25.8	66.5 \pm 21.0	46.9 \pm 19.7
EPA+DHA ($\text{mg}\cdot\text{g}^{-1}$ dw)	16.2 \pm 4.0	15.9 \pm 3.6	13.6 \pm 3.8	13.8 \pm 4.3	12.3 \pm 4.4	14.0 \pm 4.0	12.1 \pm 5.2	16.5 \pm 4.2	12.9 \pm 4.1
PUFA ($\text{mg}\cdot\text{g}^{-1}$ dw)	20.6 \pm 5.6	20.3 \pm 5.3	17.0 \pm 5.2	17.7 \pm 6.1	15.4 \pm 5.9	17.9 \pm 5.5	15.3 \pm 7.0	21.6 \pm 6.0	16.3 \pm 5.6
MUFA ($\text{mg}\cdot\text{g}^{-1}$ dw)	17.9 \pm 10.1	18.0 \pm 9.3	12.4 \pm 9.3	17.1 \pm 11.6	11.8 \pm 9.9	17.6 \pm 11.0	11.8 \pm 11.2	20.8 \pm 9.2	12.3 \pm 9.2
SFA ($\text{mg}\cdot\text{g}^{-1}$ dw)	16.2 \pm 6.3	16.0 \pm 5.5	12.3 \pm 6.0	14.6 \pm 7.0	11.4 \pm 6.5	14.9 \pm 6.4	11.3 \pm 7.5	17.8 \pm 6.0	12.1 \pm 5.5

Table 2 | Summary of the results obtained from the repeated MANOVA to test the influence of storage temperature, duration and their interaction on biochemical contents of Atlantic mackerel dorsal fillet (moisture, total fatty acids (FA), EPA+DHA, poly-unsaturated FA (PUFA), mono-unsaturated FA (MUFA), and saturated FA (SFA)).

	χ^2	df	p value
Moisture			
Storage temperature	0.3	1	0.580
Storage duration	35.5	3	<0.001
Storage temperature * duration	2.4	3	0.530
Total FA			
Storage temperature	0.9	1	0.332
Storage duration	68.6	3	<0.001
Storage temperature * duration	2.9	3	0.400
EPA+DHA			
Storage temperature	0.7	1	0.409
Storage duration	127.4	3	<0.001
Storage temperature * duration	3.6	3	0.305
PUFA			
Storage temperature	0.8	1	0.384
Storage duration	101.0	3	<0.001
Storage temperature * duration	3.3	3	0.342
MUFA			
Storage temperature	1.0	1	0.318
Storage duration	44.8	3	<0.001
Storage temperature * duration	2.2	3	0.533
SFA			
Storage temperature	1.0	1	0.328
Storage duration	73.1	3	<0.001
Storage temperature * duration	4.0	3	0.266