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Mickaël Péron, Romain Gonzalvez, Sarah Hue, Philippe Soudant, Fabienne Le Grand, et al.. Spatial and ontogenetic modulation of fatty acid composition in juvenile European sea bass (*Dicentrarchus labrax*) from two French estuaries. *Marine Environmental Research*, 2024, 197, pp.106456. 10.1016/j.marenvres.2024.106456 . hal-04586123

HAL Id: hal-04586123

<https://hal.univ-brest.fr/hal-04586123v1>

Submitted on 27 Aug 2024

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1 **Spatial and ontogenetic modulation of fatty acid composition in juvenile European**
2 **sea bass (*Dicentrarchus labrax*) from two French estuaries**

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9 **Abstract**

10 This study compared the fatty acid (FA) composition in the liver, muscle, and brain tissues of wild
11 European sea bass juvenile from two French estuaries (Loire and Seine), focusing on the variability
12 across ontogenetic stages (first, second and third year, i.e. G1, G2, G3, respectively). We highlighted
13 tissue-specific patterns, with the brain exhibiting a distinct FA composition from the two other
14 tissues. Ontogenetic stage and estuary influenced the general FA profile, and particularly essential FA
15 (EFA) like DHA, eicosapentaenoic acid (EPA), and arachidonic acid (ARA) in all tissues. The data also
16 revealed the ability of wild sea bass to modulate, at molecular level, FA biosynthetic pathways, and
17 suggests a potential dietary DHA deficiency in the natural environment, especially for Seine G1
18 juveniles. The differential distribution of FA within tissues might reflect shifts in diet, metabolic
19 demands, or adaptations to environmental conditions. The study provides insights about FA
20 dynamics in euryhaline fish during juvenile life stages, enhancing our understanding of their
21 metabolic and trophic interactions, and underscoring the need to further investigate potential effects
22 of FA depletion in a changing trophic environment.

23 Key words: Lipid composition, fish, euryhaline DHA, EPA, ARA

24 **1. Introduction**

25 Long-chain polyunsaturated fatty acids (≥ 20 carbon atoms, LC PUFA), particularly eicosapentaenoic
26 acid (EPA; 20:5-n-3), docosahexaenoic acid (DHA; 22:6n-3), and arachidonic acid (ARA; 20:4n-6), are
27 necessary for numerous biological functions in organisms, and are named essential fatty acids (EFA)
28 (Cottin et al., 2011). They are the major components of cell membrane phospholipids (polar lipids,
29 PL), influencing membrane fluidity, permeability, and functionality (van Meer et al., 2008). They are
30 also found in lesser proportions in triglycerides (neutral lipids, NL), which are a source and reserve of
31 energy. EPA and ARA serve as substrates for eicosanoid synthesis, a group of potent signaling
32 molecules that mediate numerous physiological processes, including inflammation, immune
33 response and reproduction (Calder, 2017; Gómez-Abellán and Sepulcre, 2016). These fatty acids (FA)

34 are distributed in a highly compartmentalized manner across different organs, reflecting their varied
35 roles in the organisms. High concentrations of DHA and ARA are usually found in neural tissue
36 phospholipids, indicative of their crucial roles in brain development and function (Mejri et al., 2021)
37 while the muscle, essential for locomotion, usually exhibits high levels of EPA (Tocher, 2003).
38 Studying NL and PL fatty acid composition can give insights about how storage and structural lipids
39 are regulated in tissues, and can be linked to physiological performances within an individual
40 (Twining et al., 2020).

41 LC PUFA, and especially LC n-3 PUFA are naturally synthesized by aquatic microalgae at the basis of
42 the food chain (Maltsev and Maltseva, 2021). Fish, as consumers, rely on the dietary supply of these
43 nutrients due to their limited LC n-3 PUFA biosynthetic capacity (REF). The enzymes involved in the
44 biosynthesis process are the fatty acyl desaturases (*fads*) and elongases of very long-chain fatty acids
45 (*elovl*) (Monroig et al., 2010) (Fig. S1). While the liver is the primary site for lipid biosynthesis both
46 liver and brain have shown LC-PUFA biosynthesis abilities (Galindo et al., 2021; Monroig et al., 2018).
47 This LC-PUFA biosynthesis has been shown to be modulated by environmental factors such as
48 temperature (Tocher et al., 2004), salinity (Zheng et al., 2005) and diet composition (Turchini et al.,
49 2011). Fish may also upregulate the expression of genes involved in the synthesis of LC PUFA to
50 partially compensate for dietary deficiencies (Glencross, 2009; Vagner et al., 2007b). Yet, this
51 upregulation at molecular level may not be sufficient to compensate for dietary deficiency in the
52 tissue FA composition (Vagner et al., 2009, 2007a)

53 Recent environmental changes of temperature, ocean pH, and oxygen concentration, pose a
54 significant threat to aquatic ecosystems (Gattuso et al., 2015; Pörtner et al., 2022). These
55 environmental alterations can lead to shifts in microalgae species assemblages and affect their
56 physiology, ultimately resulting in a decrease in LC PUFA production at the base of the marine food
57 web (Galloway and Winder, 2015; Hixson and Arts, 2016; Poloczanska et al., 2013). This would lead
58 to a lower LC PUFA availability for consumers, such as fish, and therefore limiting their ability to
59 adjust the LC-PUFA composition and thus functionality of their membrane (Brett et al., 2009). A
60 reduced LC PUFA content in fish cell membranes has been found to have profound cascading effects
61 on fish physiology, including reduced growth (Vagner et al., 2014), altered energy metabolism,
62 reduced immune function, and impaired reproductive success (Bell and Koppe, 2010; Schmitz and
63 Ecker, 2008; Vagner et al., 2019, 2015, 2014). The consequences of these physiological changes may
64 translate to population level, affecting ecosystem structure and functioning (Poloczanska et al.,
65 2013).

66 The European sea bass (*Dicentrarchus labrax*) is a key species in the coastal and estuarine
67 ecosystems of the Atlantic Ocean and Mediterranean Sea. This species has a complex life cycle, with
68 juveniles utilizing estuaries as nurseries to grow and mature, and adults migrating to offshore waters
69 for feeding and reproduction (Pawson et al., 2000). The distribution of sea bass within estuaries can
70 be highly variable and influenced by numerous factors such as temperature, salinity or food
71 availability (Blaber and Blaber, 1980; Pawson and Pickett, 1996). It is known to be an opportunistic
72 predator that feeds on the most abundant prey available (Pérez-Ruzafa and Marcos, 2014). As fish
73 grows, their dietary preferences shift, and they target larger prey potentially having different FA
74 compositions, influencing the FA profile of the fish.

75 Despite intensive research on effects of dietary FA in sea bass (Geay et al., 2010; Torrecillas et al.,
76 2017), little is known about the LC-PUFA metabolism of wild individuals, most of the research being
77 focused on the comparison of fatty acid composition between wild and farmed sea bass (Bhouri et
78 al., 2010; Fuentes et al., 2010; Orban et al., 2003; Tarricone et al., 2022).

79 The Seine and Loire estuaries, located along the French Atlantic coast, are essential estuaries for the
80 European sea bass, providing suitable environmental conditions for their growth, survival, and larvae
81 recruitment (Beck et al., 2001; Le Pape et al., 2003). These estuaries are characterized by highly
82 productive ecosystems, driven by nutrient inputs from their respective rivers and the coastal waters,
83 which support diverse assemblages of phytoplankton, zooplankton, and organisms of higher trophic
84 levels (Ménèsquen et al., 2018; Vasconcelos et al., 2015). They can exhibit broad differences in
85 temperature, salinity or nutrient availability that modulate the communities within the estuary
86 (Selleslagh et al., 2009). The Seine and Loire estuaries are also exposed to various anthropogenic
87 pressures, such as urbanization, agriculture, and industrial activities, leading to the degradation of
88 water quality, loss of essential habitat, disruption of food web dynamics and overall affecting the
89 survival of juvenile fish (Le Pape et al., 2007; Ménèsquen et al., 2018; Teichert et al., 2016) Climate
90 change is expected to exacerbate these pressures by altering temperature, precipitation, and sea
91 level, potentially affecting the functioning of estuarine ecosystems and the life cycle of the European
92 sea bass (Pörtner et al., 2022).

93 This study aimed to address critical knowledge gaps regarding the adaptive capacity of fish to
94 changing environmental conditions, with a focus on the role of FA in this process. Specifically, we
95 hypothesized that (1) different organs will exhibit distinct FA profiles related to their physiological
96 roles; (2) the ontogenetic stage and estuary of origin will influence these FA profiles, reflecting age-
97 related differences in metabolic needs and foraging patterns; and (3) a relationship exists between
98 LC PUFA profiles in fish tissue and the expression of genes involved in lipid metabolism. To test these

99 hypotheses, our investigation focused on the LC PUFA profiles of the liver, muscle, and brain of
100 juvenile wild sea bass from the Seine and Loire estuaries, together with the molecular modulation of
101 LC n-3 PUFA biosynthesis pathways.

102 **2. Material and Methods**

103 Ethical statement

104 Authorization and ethical approval for fish sampling were provided by national (DPMA) and regional
105 authorities (Normandie, Pays de la Loire); National & regional committees of professional fishermen
106 (CNPMEM, CRPM Normandie; COREPMEM Pays de la Loire) in 2019 (Ref. Osiris
107 PFEA400018DM0310001; ref. Ifremer: 18/2216441). All fish analyzed were dead by the time of tissue
108 sampling.

109 **2.1. Studied sites and sample collection**

110 Juvenile European sea bass were sampled in the Loire estuary for 3 days in July 2019 and in the Seine
111 estuary for 3 days in August 2019 during an annual NOURDEM survey funded by Ifremer (French
112 Institute for Sea research and Exploitation). Samplings were performed from upstream to
113 downstream of the estuary (for zones of capture, see Fig. S2). A bottom otter trawl (7m wide, 2.40m
114 high), specifically designed to capture demersal fish juveniles, was used to catch the fish (Le Goff et
115 al., 2022). Following each trawl, the catch was sorted to retain only sea bass individuals aged from 1
116 to 3 years (G1, one-year old, 12-20 cm; G2, 2-years old, 20-27 cm and G3, three-years old, 27-34 cm),
117 based on their length according to the length distribution referential implemented during the
118 NOURDEM survey. During the trawling, a probe measured the temperature and salinity (Table S1).
119 The collected sea bass were then euthanized using MS-222 (400 mg.L⁻¹). We measured fish total
120 length (nearest 0.1 cm), weight (nearest gram) and sampled a few scales to confirm the age of the
121 different fish. Brain and liver were entirely removed. About 200 mg of muscle were taken on the left
122 side of the fish, dorsally from the lateral line and just behind the head. Gallbladder was removed
123 from the liver. All samples were immediately flash frozen in liquid nitrogen until reaching the lab,
124 where they were stored at -80°C pending further analysis. A total of 76 individuals were collected: 12
125 for Seine G1 (SG1), 18 for Loire G1 (LG1), 10 for Seine G2 (SG2), 12 for Loire G2 (LG2), 12 for Seine G3
126 (SG3) and 12 for Loire G3 (LG3).

127 **2.2. Life history traits measurements**

128 We calculated Le Cren body condition factor (CF) (Le Cren, 1951) which is defined as the ratio
129 between the weight of the fish and a theoretical weight for its length obtained using observations of
130 the population :

$$K_n = W/aL^b$$

131 Where K_n is the Le Cren body condition factor, W is the observed mass, L the observed length and a
 132 and b are constants estimated from the length-weight relationships. This relationship was
 133 established a single time by pooling the fish from both estuaries and all of the age classes.

134 **2.3. FA profiles analysis**

135 **2.3.1. Sample preparation and lipid extraction**

136 Prior to any manipulation, all of the glassware was heated to 450°C for 6h and the metal or Teflon
 137 material were rinsed using acetone to prevent contamination of the samples. Frozen tissues (n=75
 138 liver, n=50 muscle and n=50 brain, for detail, see Table 1) were grounded in liquid nitrogen into a
 139 homogeneous powder and divided into a 6 mL mixture of chloroform/methanol (2:1, v/v) using from
 140 50 to 200 mg of wet weight of powder. To optimize the lipid extraction, all of the extracts were
 141 sonicated for 10 min and agitated for 20 min before being stored at -20°C under nitrogen
 142 atmosphere prior to further analysis.

143 Table 1: Number of samples for lipid analysis for each tissue. One sample in Seine G1 was excluded
 144 from analysis after being considered an outlier.

Group	Liver	Muscle	Brain
Loire G1	18	10	10
Loire G2	11	8	8
Loire G3	12	8	8
Seine G1	12	8	7
Seine G2	10	8	8
Seine G3	12	8	8

145

146 **2.3.2. Lipid separation**

147 For all the samples, lipids were separated into a neutral (NL) and polar (PL) fraction following the
 148 method described by Le Grand et al. (2014). An aliquot (from 750 to 3000 μ L, depending on the
 149 sample biomass) of the total lipid extract was evaporated to dryness, re-suspended three times using
 150 500 μ L of a mixture of chloroform/methanol (98:2, v/v) and deposited at the top of a silica gel (40
 151 mm x 4 mm, silica gel 60A 63-200 μ m rehydrated using 6% H₂O (70-230 mesh)). NL were eluted
 152 using 10 mL of a mixture of chloroform/methanol (98:2, v/v) and PL were then eluted using 20 mL of

153 methanol. After the elution, 2.3 µg of an internal standard (tricosanoic acid, C23:0) was added to
154 each fraction that was then evaporated to dryness using a Genevac centrifugal evaporator. 1600 µL
155 of H₂SO₄/MeOH (3.4%) were added and the samples were incubated for 10 mn at 100°C to form FA
156 methyl esters (FAME). FAMEs were extracted by adding 800 µL of hexane and 1500 µL of hexane-
157 saturated distilled water and by shaking and centrifuging both fractions 1 min at 738g at room
158 temperature. The aqueous phase was removed and the organic phase, containing the FAME was
159 washed two more times using hexane-saturated distilled water.

160 **2.3.3. FAME analysis**

161 FAMEs were analyzed in a Varian CP8400 gas chromatograph (GC) coupled with flame ionization
162 detector (FID) as described in Mathieu-Resuge et al., (2019). FAMEs were injected in splitless-mode
163 in parallel on two different columns (DBWAX 30m x 0.25 mm ID x 0.2 µm and DB5 30 m x 0.25 mm ID
164 x 0.2 µm, Agilent). Identification of FAME was realized by comparison of their retention times based
165 on those of commercial standards (Supelco, 37 Component FAME mix, PUFA N°1 and N°3, and
166 Bacterial Acid Methyl Ester Mix, Sigma). Internal standard allowed to calculate FA content (µg.mg⁻¹
167 WW). Fatty acid proportion was defined as the mass percentage of each fatty acid to the total fatty
168 acid content. For the brain, we focused on PL FA in the brain as NL fraction accounts for less than
169 20% of the total FA (data not shown) and are less scientifically relevant.

170 **2.4. Gene expression analysis**

171 Total RNA were extracted from the liver powder (n=75; see Table 1 for details) using Extract-all
172 reagent (Eurobio; Courtaboeuf, Essonne, France) coupled with purification steps on a Nucleospin
173 RNA column as described by Mazurais et al., (2020). The extraction protocol included one-step of
174 DNase treatment (Macherey-Nagel, Düren, Germany). Concentrations and purity of extracted RNA
175 were measured using a ND-1000 NanoDrop spectrophotometer (ThermoScientific Inc., Waltham,
176 MA, USA). An Agilent Bionalyzer 2100 (Agilent Technologies Inc, Santa Clara, CA, USA) was used to
177 evaluate the RNA integrity (RIN) and 72 samples had a RIN higher than nine.

178 Two positive and one negative reverse transcription (RT) reactions for cDNA synthesis were
179 performed using iScript cDNA Synthesis kit (Bio-Rad Laboratories Inc., Hercules, CA, USA) as
180 described in Mazurais et al. (2020). The relative expression levels of following transcripts were
181 investigated (Table S2): Fatty acid desaturase 2 (*fads2*), Lipoprotein lipase (*lpl*), Group XIIB secretory
182 phospholipase A2 (*plag12b*), Stearoyl-CoA desaturase 1b (*scd1b*) and Succinate dehydrogenase
183 cytochrome b560 subunit (*sdhc*). These genes were chosen because they are involved in the lipid or
184 LC-PUFA metabolism (Rimoldi et al., 2016). The primers used, as well as the GENBANK sequence

185 numbers are presented for each gene in Table S2. The relative quantity of these transcripts of
186 interest and those of three housekeeping genes (elongation factor 1-alpha, *ef1*; Beta Actin, *actin* and
187 Ribosomal protein L13a, *l13a*) was determined by qPCR using a CFX96 Touch Real-Time PCR
188 Detection system (Bio-Rad Laboratories Inc.). The relative quantities of transcripts were normalized
189 using the $\Delta\Delta C_t$ method (Livak and Schmittgen, 2001).

190 **2.5. Statistical analysis**

191 All analyses were conducted on RStudio (V4.2.1). The multivariate approach used for the general
192 fatty acid profile was realized using a PERMANOVA followed by pairwise tests (package *vegan*,
193 *pairwise adonis* function) to test for significant differences in the general FA profile between the
194 different groups within each tissue. The FA for the multivariate analysis were selected based on a
195 similarity percentage analysis (SIMPER, Clarke, 1993). to identify the major FA contributing to
196 differences between groups. Differences between estuaries and between ontogenetic stages for
197 weight, total length, condition factor, specific FA or gene expression were tested using a two-way
198 ANOVA. When the Estuary*Stage interaction was significant ($p < 0.05$), a new variable "Group",
199 combining Stage and Estuary, was created (*e.g* Seine G1). A one-way ANOVA was then performed
200 followed by a Tukey post hoc test to account for differences between groups. When the
201 Estuary*Stage interaction was not significant ($p > 0.05$), the differences between groups were tested
202 following the model: $X \sim \text{Estuary} + \text{Stage}$ where X is the tested variable (*e.g* DHA). A multiple-
203 comparison test (package *multcomp*, *glht* function) was used to account for differences between
204 groups. When the one-way ANOVA conditions were not met, a Kruskal-Wallis test was used instead.

205 **3. Results**

206 **3.1. Weight, length and condition factor**

207 For both estuaries, an increase in mean fish weight and length was observed from G1 to G3 (Table 2).
208 However, the Loire fish consistently had a greater weight and length than Seine fish at each stage.
209 These differences were statistically significant for both stage ($p < 0.001$) and estuary ($p < 0.001$). The
210 CF, however, remained constant across developmental stages for both estuaries and no significant
211 differences were observed in relation to either the stage or estuary.

212 Table 2: Weight (g), Total Length (TL, cm) and LeCren condition Factor (K_n) of the juvenile European
213 sea bass from the different ontogenetic (G1: one year old; G2: two years old; G3: three years old) and
214 location (Seine and Loire estuaries) groups. Values are expressed as mean \pm SEM. Potential
215 differences among groups were assessed by 2-way ANOVA and Tukey's post hoc test. Main effects
216 are given in the right columns – Stage: effect of the life stage; estuary: effect of the sampling site;
217 Stage x estuary: interaction of the two. Significance was accepted at $p < 0.05$. Values within each line
218 not sharing common letters are significantly different: *** $p < 0.001$, ** $p < 0.01$, - NS. Loire : G1
219 (n=17), G2 (n=12), G3 (n=12). Seine : G1 (n=11), G2 (n=10), G3 (n=12). One fish was not measured.

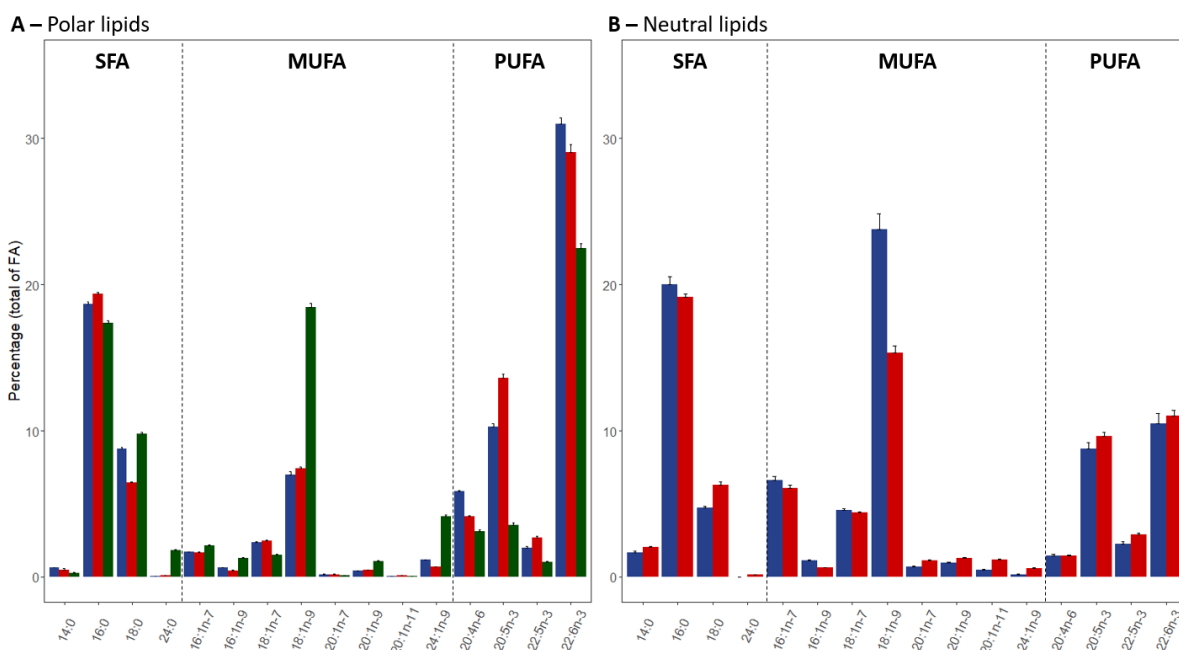
	LOIRE			SEINE			STATISTICS		
	G1	G2	G3	G1	G2	G3	Stage	Estuary	Interaction
Weight	44.8 ± 2.9 ^b	162.7 ± 6.2 ^d	307.4 ± 17.9 ^f	38.6 ± 2.8 ^a	137.5 ± 6.0 ^c	270.1 ± 15.2 ^e	***	***	-
TL	16.5 ± 0.3 ^b	25.3 ± 0.3 ^d	31.1 ± 0.6 ^f	15.3 ± 0.4 ^a	23.9 ± 0.4 ^c	29.8 ± 0.5 ^e	***	**	-
K _n	0.96 ± 0.04	1.01 ± 0.03	1.01 ± 0.01	1.08 ± 0.02	1.01 ± 0.02	1.01 ± 0.02	-	-	-

220

221 3.2. General FA profile

222 The main FA family found in PL of the three tissues was PUFA. Muscle and liver displayed higher
223 PUFA proportions compared to the brain (54, 53 and 33% respectively; detailed fatty acid
224 compositions of both NL and PL fractions of the three organs are presented in Table S2). DHA (22:6n-
225 3) was the major PUFA in PL in the three tissues followed by EPA (20:5n-3) (Fig. 1A). The brain
226 displayed the highest average monounsaturated fatty acid (MUFA) concentration (30 ± 0.4%) in PL
227 among tissues, which was more than twice that of the liver and muscle (14 ± 0.2 %). The oleic acid
228 (18:1n-9) was the major MUFA in the three tissues and its highest concentration was found in the
229 brain (18 ± 0.2%) (Fig. 1A). Interestingly, the 24:0 and 24:1n-9 were significantly higher in the brain
230 compared to muscle and liver (2% vs 0.1% (for both muscle and liver) for 24:0 and 4% vs 1.2% and
231 0.7% for 24:1n-9, respectively). The mean concentration of saturated fatty acid (SFA) in PL was
232 similar among the three tissues (about 29%) where 16:0 and 18:0 were the predominant FA (Fig. 1A).

233 In NL, only liver and muscle were analyzed and the proportions of the three FA families (SFA, PUFA,
234 PUFA) were relatively similar between both tissues. A balanced distribution among FA families was
235 observed in muscle, with relatively close concentrations: SFA (30%), MUFA (32%), and PUFA (33%)
236 with 16:0, 18:1n-9, EPA and DHA as major FAs in both tissues. Liver had the highest concentrations of
237 MUFA (40%; Fig. S2 B) with 18:1n-9 being the major FA (Fig. 1B).



238

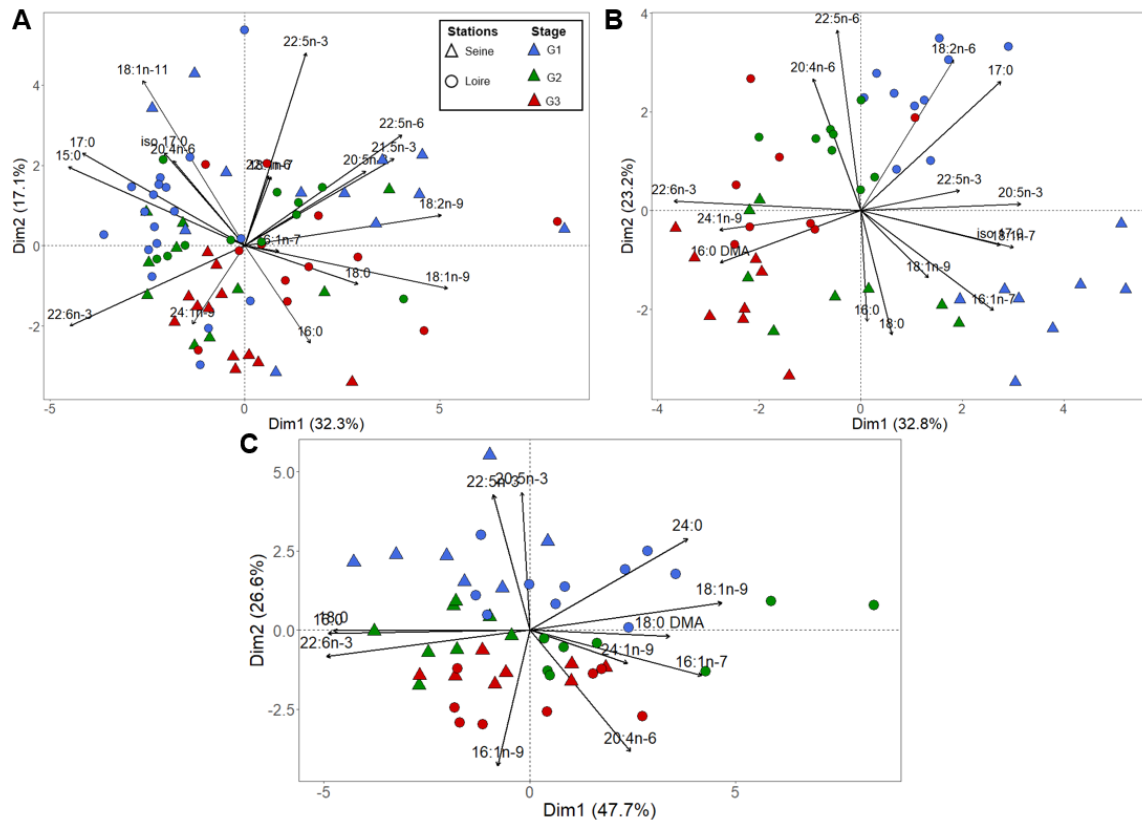
239 Figure 1: Proportions of fatty acids (mass percentage of total FA) in polar lipids (A) and neutral lipids
 240 (B) in the liver (blue, n=75), muscle (red, n=50) and brain (green, n=49) of juvenile European sea bass
 241 from all confounded Seine and Loire locations and ontogenetic stages. Only FA that are >1% for at
 242 least one tissue are presented. Data are presented as mean ± SEM. Neutral lipids have not been
 243 measured in the brain (cf material and method section for details). SFA = Saturated Fatty Acid, MUFA
 244 = Monounsaturated Fatty Acid, PUFA = Polyunsaturated Fatty Acid.

245 The inertia of FA composition in fish PL, according to their ontogenetic stage and sampling location is
 246 presented in the PCA in Fig. 2.

247 In the liver (Fig. 2A), significant differences in PL FA composition were found among the groups
 248 (PERMANOVA, Table S3, 4). In the Seine estuary, the G1 from Seine were different from the two
 249 other ontogenetic groups and appeared to be distinguished, among others by their EPA (20:5n-3)
 250 proportions, while G2 and G3 seemed to be distinguished by their DHA (22:6n-3) proportions (Fig.
 251 2A). However, that trend was not observed in the Loire estuary.

252 In muscle (Fig. 2B), significant differences were found among the groups (PERMANOVA, Table S3, 4).
 253 The Seine G1 group was different from all the other groups except from Seine G2. The first dimension
 254 distinguished the stages, with G1 being characterized by EPA and G2 and G3 being characterized by
 255 DHA. The second dimension distinguished the estuaries, with Seine that tended to be characterized
 256 by 16:0 and 18:0, and Loire by 22:5n-6 and ARA (20:4n-6). Brain FA composition in PL (Fig. 2C)
 257 was impacted by an interactive effect between site and ontogenetic stages, with the Seine G2 group
 258 being different from Loire G1 and Loire G2 (PERMANOVA, Table S3, 4). The G1 seemed to be
 259 distinguished by EPA and DPA (22:5n-3) and the G3 by ARA and 16:1n-9.

260



262

263 Figure 2: Principal Component Analysis (PCA) of polar lipid fatty acids in liver (A), muscle (B) and
 264 (C) of 1 (G1), 2 (G2) or 3 (G3) years old juvenile European sea bass from Seine and Loire. Only FAs
 265 that account for >80% of the contribution of dissimilarity between groups are shown (SIMPER test)
 266 Liver : Loire G1 (n=18), Loire G2 (n=11), Loire G3 (n=12), Seine G1 (n=12), Seine G2 (n=10), Seine G3
 267 (n=12). Muscle : Loire G1 (n=10), Loire G2 (n=8), Loire G3 (n=8), Seine G1 (n=8), Seine G2 (n=8), Seine
 268 G3 (n=8). Brain: Loire G1 (n=10), Loire G2 (n=8), Loire G3 (n=8), Seine G1 (n=7), Seine G2 (n=8), Seine
 269 G3 (n=8).

270 3.3. FA proportions and ratios between ontogenetic stage and estuaries

271 3.3.1. DHA proportions

272 In the liver (Fig. 3A), DHA proportions followed different dynamics in the two estuaries. It decreased
 273 with the ontogenetic stage in Loire, while it tended to increase in Seine. In muscle (Fig. 3 B), DHA
 274 significantly increased with the ontogenetic stage in Seine, while it remained similar in all
 275 ontogenetic groups in Loire. Seine G1 displayed a lower DHA proportion than all other groups. In the
 276 brain (Fig. 3C), the DHA content did not differ among the ontogenetic stage in Seine. The G2 in Loire
 277 had a lower DHA content than the G3 in Loire and was lower than all ontogenetic stages of Seine.

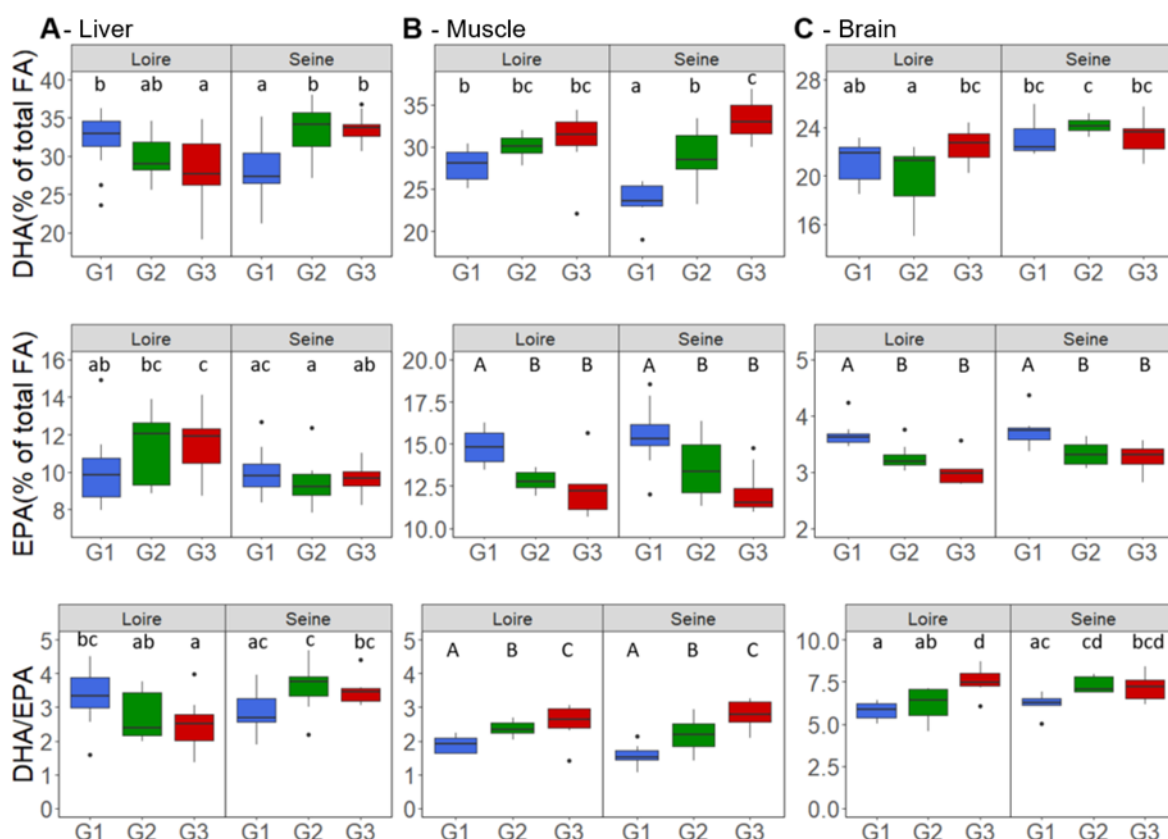
278 3.3.2. EPA proportions

279 For the liver (Fig. 3A) in Loire, the EPA proportions followed an opposite pattern to that of DHA, with
 280 Loire G3 having higher proportions compared to Loire G1. It was also significantly higher than in
 281 Seine G2 and Seine G3. However, EPA proportions remained stable in groups of Seine. In muscle and

282 brain (Fig. 3B, C), EPA proportions were significantly impacted by ontogenetic stages similarly in both
 283 estuaries, with significantly higher EPA proportions in G1 than in G2 and G3.

284 3.3.3. DHA/EPA ratios

285 In the liver (Fig. 3A), the DHA/EPA ratio followed the same trend as the DHA proportions (Fig. 4 A). In
 286 muscle (Fig. 3B), DHA/EPA ratio increased from G1 to G3 in both estuaries. In the brain (Fig. 3C), the
 287 DHA/EPA ratio was not different among the Seine groups, while in Loire it was lower for G1 and G2
 288 compared to G3.



289
 290 Figure 3: Proportions of DHA and EPA (percentage of total FA) and DHA/EPA ratio in the polar lipids
 291 of liver (A), muscle (B) and brain (C) of juvenile European sea bass from Seine and Loire. Different
 292 letters within a plot indicate significant differences. Letters in lowercase represent a significant
 293 interaction between the estuary and the stage (2-way ANOVA and Tukey's post hoc) and uppercase
 294 letters represent a significant difference between either stage or estuary without significant
 295 interaction. Significance was accepted at $p < 0.05$. Liver: Loire G1 (n=18), Loire G2 (n=11), Loire G3
 296 (n=12), Seine G1 (n=12), Seine G2 (n=10), Seine G3 (n=12). Muscle: Loire G1 (n=10), Loire G2 (n=8),
 297 Loire G3 (n=8), Seine G1 (n=8), Seine G2 (n=8), Seine G3 (n=8). Brain: Loire G1 (n=10), Loire G2 (n=8),
 298 Loire G3 (n=8), Seine G1 (n=7), Seine G2 (n=8), Seine G3 (n=8).

299 3.3.4. ARA proportions

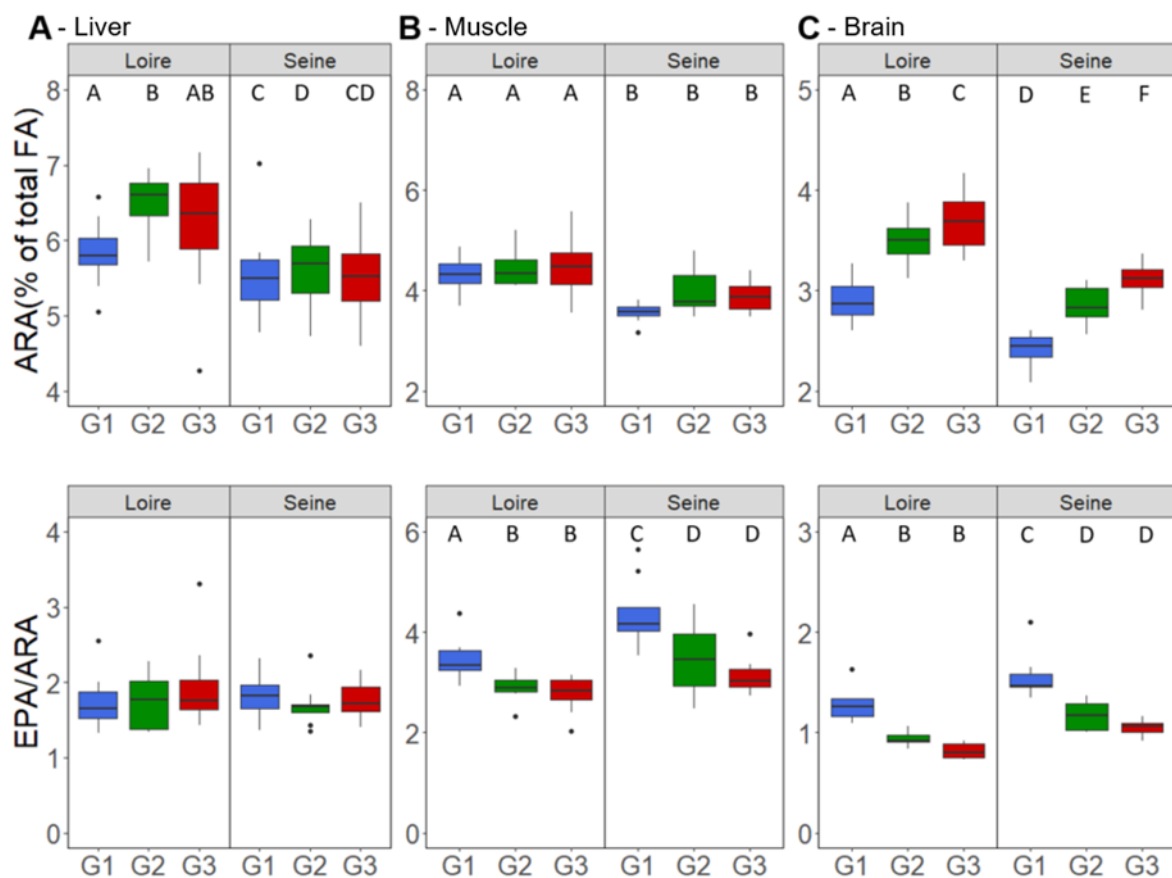
300 In all tissues, ARA proportions were higher in Loire than in Seine. In the liver (Fig. 4A), ARA
 301 proportions were higher in G2 than G1 in both estuaries. In muscle (Fig. 4B), it did not differ between

302 ontogenetic stages in any estuary, while in the brain (Fig. 4C), it increased consistently with stages in
 303 both estuaries.

304 3.3.5. EPA/ARA ratios

305 In the liver (Fig. 4A), no statistical difference was found for the EPA/ARA ratio. In the muscle and
 306 brain (Fig. 4B, C), the EPA/ARA ratio was higher in the Seine than in Loire and G1 had a higher ratio
 307 than G2 and G3.

308



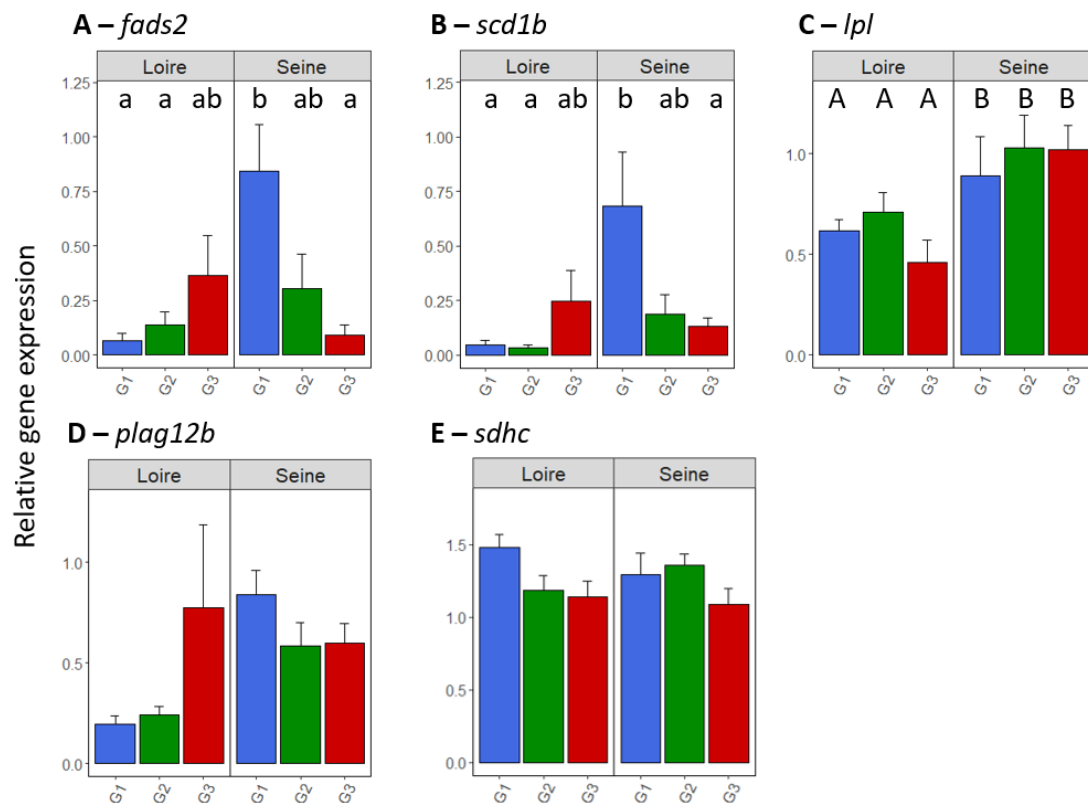
309

310 Figure 4: ARA proportions (percentage of total FA) and EPA/ARA ratios for liver (A), muscle (B) and
 311 brain (C) of juvenile European sea bass from Seine and Loire. Different letters indicate significant
 312 differences. Letters in lowercase represent a significant interaction between the estuary and the
 313 stage (2-way ANOVA and Tukey's post hoc) and uppercase letters represent a significant difference
 314 between either stage or estuary without significant interaction. Significance was accepted at $p <$
 315 0.05. Liver: Loire G1 (n=18), Loire G2 (n=11), Loire G3 (n=12), Seine G1 (n=12), Seine G2 (n=10), Seine
 316 G3 (n=12). Muscle: Loire G1 (n=10), Loire G2 (n=8), Loire G3 (n=8), Seine G1 (n=8), Seine G2 (n=8),
 317 Seine G3 (n=8). Brain: Loire G1 (n=10), Loire G2 (n=8), Loire G3 (n=8), Seine G1 (n=7), Seine G2 (n=8),
 318 Seine G3 (n=8).

319 3.4. Gene expression

320 The *fads2* and *scd1b* gene expressions followed the same pattern in all groups (Fig. 5A, B). Their
 321 highest expressions were measured in G1 from Seine, while their lowest expressions were measured

322 in the G1 and G2 from Loire, as well as in the G3 from Seine. Negative correlation between DHA and
 323 *fads2* expression was observed for the G1 Seine group as well as significant correlation between FA
 324 of the n-3 series (Fig. S3). The *lpl* gene expression did not differ significantly among ontogenetic
 325 stages, but significantly differed between the two sites, and were being globally lower in the Loire
 326 groups than in the Seine groups (Fig. 5C). The *sdhc* and *plag12b* gene expression were not
 327 significantly different between groups.



328

329 Figure 5: Relative expression of genes coding for enzymes involved in lipid metabolism in the liver of
 330 juvenile European sea bass from Loire and Seine, according to their ontogenetic stage (G1, G2, G3,
 331 corresponding to first, second and third years old, respectively). The *fads2*, fatty acid desaturase 2
 332 (A), *lpl*, lipoprotein lipase (B), *plag12b*, group XIIIB secretory phospholipase A2 (C), *scd1b*, stearyl-
 333 CoA desaturase 1b (D), *sdhc*, succinate dehydrogenase cytochrome b560 subunit (E). Different letters
 334 indicate significant differences among groups. Letters in lowercase represent a significant interaction
 335 between the estuary and the stage (2-way ANOVA and Tukey's post hoc), and uppercase letters
 336 represent a significant difference between either stage or estuary without significant interaction.
 337 Significance was accepted at $p < 0.05$. Loire G1 (n=15), Loire G2 (n=12), Loire G3 (n=11), Seine G1
 338 (n=12), Seine G2 (n=10), Seine G3 (n=12).

339 4. Discussion

340 The present study aimed to explore the distribution and molecular modulation of fatty acid in
 341 different tissues of juvenile European sea bass through the ontogenetic stages from two different
 342 estuarine environments. We highlighted that PL and NL FA were differently distributed across the
 343 liver, muscle and brain. Focusing on membrane lipids (PL), FA profiles were influenced by

344 ontogenetic stage and estuary of origin in muscle and in liver while only ontogenetic variations were
345 observed in the brain. Essential FA (DHA, EPA, and ARA) proportions were also influenced by
346 estuarine environment and ontogenetic stages. At molecular level, the activation of LC PUFA
347 biosynthetic pathways was the highest in the group that had the lowest DHA proportions in liver and
348 muscle (Seine G1).

349 **4.1. FA profile of juvenile European sea bass**

350 **4.1.1. SFA, MUFA and PUFA distribution in NL and PL**

351 Different trends were observed in FA proportions among tissues and between the two lipid fractions.
352 Our results showed that the main SFA, MUFA and PUFA were palmitic acid (16:0), oleic acid (18:1n-9)
353 and DHA (22:6n-3), respectively, whatever the fraction or the organ considered. Muscle and liver PL
354 had higher proportions of PUFA than brain PL, particularly in DHA (22:6n-3) and EPA (20:5n-3). This is
355 in accordance with previous studies reporting that white muscle specifically retains DHA from the
356 diet through selective incorporation mechanisms (Bell et al., 2001; Mourente and Bell, 2006).
357 However, the brain is also a tissue that is known to selectively retain DHA in order to preserve
358 cognitive functions (Lauritzen et al., 2001). Thus, the higher proportions of PUFA in the muscle and
359 liver than in the brain might suggest these FAs are not limitant for fish. They are sufficiently retained
360 in brain membranes, though they accumulate in muscle and liver to be likely further used as an
361 energy source (Betancor et al., 2021; Hong et al., 2014). Compared to the muscle and liver, the brain
362 exhibited a specific FA composition with high levels of MUFA (especially 18:1n-9 and nervonic acid,
363 24:1n-9) and low levels of EPA, which is consistent with previous results on the same species in
364 controlled conditions (Granafei et al., 2017; Skalli et al., 2006). In NL the higher 16:0 and 18:1n-9
365 proportions in NL compared to PL, especially in liver, could be related to energy storage. These FA
366 are produced by lipogenic activity and are known to be preferentially used as substrates for energy
367 through β -oxidation (Bell et al., 2004; Henderson and Sargent, 1985; Sargent et al., 2003; Tocher,
368 2003). The liver is also the major lipid storing site in lean marine fish such as sea bass, thus explaining
369 the storage of these FA in this organ (Mourente and Bell, 2006).

370 **4.1.2. FA profiles of PL according to estuaries and ontogenetic stage**

371 The muscle tissue also showed variation among both ontogenetic stages and estuaries. This might
372 indicate specific dietary preferences or prey availability, reflecting the distinct trophic systems of
373 each estuary (Darnaude et al., 2004). Indeed, some FAs are considered as trophic markers and can be
374 used to identify certain primary producers (Dalsgaard et al., 2003). Seine G1 FA profiles were
375 distinguished by high proportions of 16:1n-7, a diatom FA trophic marker (Cañavate et al., 2019) and
376 Loire G1 FA profile were distinguished itself by high proportions of 18:2n-6, a cryptophyte trophic

377 marker (Viso and Marty, 1993). This could indicate different primary production between each
378 estuary. Additionally, the differences in FA composition observed between ontogenetic stages may
379 be indicative of distinct life stages dependent metabolic requirements, as younger fish typically have
380 higher growth rates and metabolic demands (Jobling, 1995). It has been suggested that the
381 phospholipid requirements would decrease with development from larvae to juveniles (Tocher et al.,
382 2008) and could have a repercussion on the membranes of juveniles from different ages. Also, the G3
383 being closer to reproduction, this might have enhanced needs for essential FA (Izquierdo et al.,
384 2001). Interestingly, no discernible pattern of PL FA composition was found in the liver among the
385 groups (G1, G2, and G3) for both estuaries, even if some groups were statistically different from
386 others. As previously discussed, the liver is a primary site for lipid metabolism, and it tends to have a
387 dynamic fatty acid profile reflective of both diet and metabolic regulation (Tocher, 2003). This
388 absence of pattern may suggest a quick turn-over of the overall FA profile in the liver (Mohan et al.,
389 2016). Despite the not significant results, brain FA composition showed a trend with EPA
390 discriminating the G1 stage and ARA discriminating the G3 in both estuaries. This could result from
391 trophic difference between ontogenetic groups, as brain FA composition of fish has been proven to
392 be modulated by dietary FA in *D. labrax* (Pagliarani et al., 1986) and gilthead sea bream (*Sparus*
393 *aurata*, Carvalho et al., 2022) or from different needs for brain development.

394 **4.2. Spatial and ontogenetic variability of Essential Fatty Acids (EFA)**

395 The tissue-specific DHA proportion measured in wild fish in the present study are in accordance with
396 what is usually observed experimentally in fish from aquaculture when fed a controlled diet (Skalli et
397 al., 2006). The lower DHA proportions in fish liver from Loire G3 could also indicate a reallocation of
398 the DHA from the liver to the growing reproductive organs, as it has previously been shown in
399 zebrafish *Danio rerio* (Zhu et al., 2019). This hypothesis is supported by the greater length of the G3
400 fish from Loire than those from Seine, likely indicating a closer sexual maturity. It has been reported
401 to happen at a minimum of 32 cm for males in the Atlantic waters (Pawson and Pickett, 1996). The
402 increasing DHA content from Seine G1 to Seine G3 in muscle, concomitant with decreased EPA
403 content, could be explained by a shift of diet from zooplankton to diverse epibenthic fauna through
404 ontogenetic stages (Aprahamian and Barr, 1985; Pickett and Pawson, 1994). Fish as a prey are richer
405 in DHA than invertebrates (*e.g. Mysidacea*) that are richer in EPA (Daly et al., 2010), the older and
406 bigger fish would then incorporate more DHA in their muscle tissue where selective retention
407 happens. Interestingly, the lowest DHA proportion measured in the Seine G1 group was associated
408 with higher relative *fads2* and *scd1b* gene expressions in liver (Fig. S3). While the biosynthesis of LC-
409 PUFA (including DHA, EPA and ARA) has been shown to be very limited in most vertebrates (Tocher
410 et al., 2019), the upregulation of the *fads2* gene expression has been evidenced in controlled

411 conditions in which fish, including sea bass, were fed low quantities of LC-PUFA (Geay et al., 2010b;
412 González-Rovira et al., 2009; Vagner et al., 2009, 2007a). We could thus hypothesize that the lower
413 DHA content associated with the higher *fads2* expression measured in the Seine G1 group may be
414 related to (i) a lower LC-PUFA in their diet, combined to (ii) higher DHA demand due to a higher
415 cellular turn-over in this growing ontogenetic stage. Additionally, the mean DHA proportions
416 measured in the liver and muscle of Seine G1 were slightly lower than those reported by Skalli et al.,
417 (2006) (28% vs 30%, 23% vs 24%, respectively) in the same species, from aquaculture, and
418 experimentally fed with a low PUFA diet (0.4% EPA+DHA on dry matter basis). The needs have been
419 experimentally established at 0.7% EPA+DHA on dry matter basis for sea bass juveniles (Skalli and
420 Robin, 2004). Taken together, these results would support the hypothesis of a dietary limitation in
421 DHA for Seine G1 which would not match to their requirement at this age. Below the threshold of
422 0.7% EPA+DHA, growth of the juvenile was negatively affected (Skalli and Robin, 2004). However, it is
423 important to consider that this study was conducted in experimental conditions with a goal of
424 optimizing the aquafeed costs for European sea bass farming. Environmental conditions, such as
425 salinity or temperature, can also influence *fads2* expression in teleost fish (for review, see Vagner
426 and Santigosa, 2011), making it difficult to disentangle the reasons underlying the higher *fads2*
427 expression observed in the G1 from Seine. Remarkably, the brain DHA proportion in Seine G1 was
428 maintained as high as in all the other groups, showing likely the preservation of cognitive functions.
429 Despite that, the effects of a possible DHA dietary limitation for this group in the environmental
430 context should not be overlooked as it could impact growth, performances and ability to cope with
431 changing conditions (Bou et al., 2017). The DHA content in the brain was lower in Loire G2 compared
432 to Loire G3 and all ontogenetic stages in Seine. However, this difference was not seen in the muscle
433 or liver. Given that the brain is a stable tissue, as noted by (Carvalho et al., 2022) and (Hong et al.,
434 2014), it's difficult to attribute this difference to a lack of DHA in the diet. Instead, (Skalli et al., 2006)
435 found that *D. labrax* raised at 29°C had lower DHA content than those at 22°C, suggesting
436 temperature affects the FA composition more than diet does.

437 As observed for DHA, EPA and ARA proportions also displayed a tissue-specific response and differed
438 between estuaries and between ontogenetic stages. However as the pattern observed in the liver
439 was inversely related to that of DHA, this suggests some modulation by trophic interactions or
440 intense metabolic hepatic activity. Similarly, the distribution of EPA in the muscle was opposite to
441 that of DHA, with the youngest individuals displaying the highest levels of EPA. EPA was shown to be
442 an expendable PUFA for the brain in fish unlike DHA who make up for the majority of brain
443 membrane FA and have a proven role in neural functions (Emery et al., 2016; Trushenski et al., 2012).
444 Contrary to EPA, the ARA proportions in brain membranes increased with age and were higher in

445 Loire compared to Seine. Both EPA and ARA are precursors in the production of eicosanoids
446 (prostaglandins, leukotrienes and thromboxanes) (Gómez-Abellán and Sepulcre, 2016). Leukotrienes
447 play vital roles in the immune response of vertebrates, and can be produced by every tissue (Rowley
448 et al., 1995; Sargent et al., 1999). Prostaglandins are of physiological importance for respiratory
449 functions (McKenzie et al., 1998) and osmoregulation (Ruggeri and Thoroughgood, 1985). ARA has
450 also been proven to reduce stress in fish through the modulation of cortisol, a hormone linked to
451 stress regulation and modulated by prostaglandins (Koven et al., 2003; Van Anholt et al., 2004).
452 Lebigre et al., (2022) analyzed the cortisol content in the scales of juvenile European sea bass from
453 the same cohorts (including G1, G2 and G3) in both Seine and Loire estuaries. They found a peak of
454 cortisol in 2019, the year in which the fish were sampled in the present study, compared to other
455 years (2017 and 2018). They also reported that cortisol concentration increased with the ontogenetic
456 stage. The authors underlined the fact that chronic stress has a negative effect on the growth of the
457 fish. Then, the lower values of weight and size reported in fish from the Seine estuary could partly be
458 explained by a higher chronic stress may be due to higher pollution level or strong salinity changes
459 for example. All together, these results suggest that increasing ARA content in the brain with life
460 stages could be induced by the selective retention of this FA to produce eicosanoids and cope with
461 environmental and anthropogenic stressors.

462 **5. Conclusions**

463 In conclusion, our study addresses critical gaps in understanding the variability of FA composition in
464 wild European seabass. Our findings confirm the tissue-specific responses in FA distribution, with the
465 brain exhibiting a unique FA composition compared to muscle and liver. The influence of both
466 estuary and ontogenetic stage on membrane FA profiles, especially essential FA, highlights the
467 complex interaction of factors that modulate FA composition. Notably, our results indicate a
468 potential shift in prey selection as fish grow, impacting FA composition. The molecular activation of
469 the LC PUFA synthesis pathway, particularly associated with lower DHA levels in the liver, suggests
470 the ability of wild European sea bass to modulate their FA biosynthetic pathways at the molecular
471 level in response to a dietary deficiency in the natural environment. Future investigations should
472 delve into potential metabolic and behavioral implications of DHA depletion during the crucial
473 juvenile life stage, aligning with our hypotheses on distinct organ profiles, ontogenetic influences,
474 and the relationship between LC PUFA and lipid metabolism.

475 **6. Competing interests**

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

478 7. CRediT authorship contribution statement

479 **Mickaël Peron:** Conceptualization, Formal analysis, Investigation, Data curation, Writing- Original
480 draft, Visualization. **Romain Gonzalvez:** Validation, Formal analysis, Investigation, Data curation,
481 Writing – Review & Editing. **Sarah Hue:** Investigation. **Philippe Soudant:** Conceptualization,
482 Validation, Writing – Review & Editing, Supervision. **Fabienne Le Grand:** Conceptualization,
483 Validation, Writing – Review & Editing, Supervision. **David Mazurais:** Conceptualization, Validation,
484 Writing – Review & Editing, Supervision. **Marie Vagner:** Conceptualization, Methodology, Validation,
485 Resources, Writing – Review & Editing, Supervision, Project administration, Funding acquisition.

486 8. Acknowledgments

487 We thank Mickaël Drogou, Stéphane Martin, Loïc Le Ru and Christophe Lebigre for their help with the
488 collecting the fish during the NOURDEM campaign. We are grateful to Karine Salin and Eric Dabas for
489 their help with onboard fish dissections and sampling. We thank Antoine Bideau and Lauriane Madec
490 for their help with the lipid and molecular analyses. This work was supported by ISblue project,
491 Interdisciplinary graduate school for the blue planet (ANR-17-EURE-0015) and co-funded by a grant
492 from the French government under the program "Investissements d'Avenir", by the French National
493 program EC2CO (Ecosphère Continentale et Côtière), and the Scientific Council of the European
494 Institute of Marine Sciences.

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