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**Using gene expression to identify the most suitable environmental conditions for juvenile deepwater redfish (*Sebastes mentella*) growth and metabolism in the Estuary and the Gulf of St. Lawrence.**

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25 **Abstract**

26 Deepwater redfish *Sebastes mentella* will be among the most important resource-sustaining  
27 commercial bottom-fish fisheries in the years to come in the Estuary and Gulf of St. Lawrence  
28 (EGSL). In 2011, 2012, and 2013, three strong cohorts were recruited to the stock; their  
29 abundance in 2018 was 80 times higher than that of the 1993–2012 period. The main goal of this  
30 work was to deepen our knowledge of their growth regulation and metabolism in order to identify  
31 molecular indicators and determine how they are influenced by natural environmental conditions.  
32 Fish weight and water temperature explained 11% of the variation in relative mRNA levels of  
33 specific gene targets in liver and muscle among seven sites where deepwater redfish were  
34 captured in the EGSL. The relative expression of liver insulin-like growth factor-1 (*igf-1*) and  
35 white muscle A-chain lactate dehydrogenase (*ldh-a*) correlate positively with weight, whereas  
36 heavy chain muscle myosin (*myo*), heart citrate synthase (*cs*), and white muscle pyruvate kinase  
37 (*pk*) correlate negatively. The relative expression of heart cytochrome c oxidase subunit 1 (*cox-1*)  
38 and white muscle insulin-like growth factor-1 receptor isoform a (*igf-1ra*) correlate negatively  
39 with temperature. Deepwater redfish from the estuary were smaller than those caught at other  
40 sites. Since the growth potential of deepwater redfish was strongly correlated with temperature  
41 (being enhanced by higher temperatures), this study suggests an ecological advantage for this  
42 species in a climate-warming context.

43

44 Keywords: Redfish, Growth, Metabolism, Transcriptomics, Temperature.

45

46

47 **Introduction**

48

49 The redfish fishery in the Estuary and Gulf of St. Lawrence (EGSL) has historically targeted two  
50 species, the Acadian redfish (*Sebastes fasciatus*) and the deepwater redfish (*Sebastes mentella*).  
51 The two species look very similar but can be distinguished genetically and to a lesser extent  
52 morphologically (DFO, 2018a). In 2011, 2012, and 2013, three strong cohorts recruited to the  
53 stock. Genetic analyses have indicated that these cohorts were dominated by deepwater redfish,  
54 and all the deepwater redfish caught for this study belong to a unique ecotype or genetic group  
55 known as “*S. mentella* gulf,” which is the only one present in the EGSL (DFO, 2018b; Benestan  
56 *et al.*, 2021). Research survey data show that the abundance of deepwater redfish juveniles in  
57 2018 was 80 times higher than their average abundance for the 1993–2012 period (DFO, 2018a).  
58 Indeed, the Department of Fisheries and Ocean Canada (DFO) data suggests that redfish (both  
59 Acadian and deepwater redfish) should become the most important resource sustaining  
60 commercial bottom-fish fisheries in the years to come in the EGSL (DFO, 2018a). Most of the  
61 recent information for deepwater redfish in the EGSL comes from summer trawl surveys, and  
62 there is little information for other seasons on diet, distribution, and movements (Senay *et al.*,  
63 2021). Deepwater redfish is a benthic fish remaining on or near the sea bottom during the  
64 daytime and rising higher in the water column at night, presumably to feed (Scott and Scott,  
65 1988). The group of prey contributing the most to deepwater redfish diet is zooplankton (32%),  
66 followed by shrimp (29%) and other invertebrates (17%) (DFO, 2018a; Senay *et al.*, 2021).

67

68 Understanding deepwater redfish stock dynamics requires knowledge on the physiology of the  
69 species, including growth and metabolism. However, studying the physiology of deepwater

70 redfish presents specific challenges because of the low survival rate of fish caught in a deep  
71 environment (Saborido-Rey *et al.*, 2004). Maintaining deepwater redfish in a rearing environment  
72 that mimics their natural environmental conditions is almost impossible because of the depth and  
73 pressure encountered in nature. The transcriptomics study of genes involved in growth and  
74 metabolic regulation may offer new investigative tools that can overcome sampling and rearing  
75 challenges and allow us to evaluate the physiological response in their original environment.

76

77 In fishes, growth is controlled at the endocrine level, especially by the growth hormone (GH) /  
78 insulin-like growth factor-1 (IGF-1) axis (Björnsson, 1997; Wood *et al.*, 2005; Duan *et al.*, 2010;  
79 Vélez *et al.*, 2017). This axis is modulated by both biotic and abiotic conditions, such as the  
80 nutritional or thermal environment (Beckman, 2011; Reindl and Sheridan, 2012; Breves *et al.*,  
81 2016). GH is synthesized by the pituitary gland and regulates many functions, including somatic  
82 growth, energy metabolism, reproduction, digestion, osmoregulation, and immune response  
83 (Reinecke *et al.*, 2005; Kawaguchi *et al.*, 2013). It also stimulates the production of IGF-1 in the  
84 liver (Meier *et al.*, 2009; Volkoff *et al.*, 2010; Bergan-roller and Sheridan, 2018; Vélez *et al.*,  
85 2018). Its main effects on growth are thought to be via regulation of IGF-1 release (Beckman *et*  
86 *al.*, 2004; Reinecke *et al.*, 2005; Picha *et al.*, 2006; Beckman, 2011; Kawaguchi *et al.*, 2013). It  
87 has been shown that measures of IGF-1 (plasma concentration and liver mRNA levels) are also  
88 strongly correlated with specific growth rate in several teleost species and could be used as a  
89 proxy for growth (reviewed by Beckman, 2011). Indeed, plasma IGF-1 has a significant positive  
90 correlation with liver *igf-1* mRNA and specific growth rate in species closely related to  
91 deepwater redfish, such as olive rockfish *Sebastes serranoides* (Hack *et al.*, 2018) and copper  
92 rockfish *Sebastes caurinus* (Hack *et al.*, 2019) as well as in other fish species such as rainbow  
93 trout *Oncorhynchus mykiss* (Gabillard *et al.*, 2003) and chinook salmon *O. tshawytscha* (Pierce *et*

94 *al.*, 2005). Plasma IGF-1 also has a significant positive correlation with muscle *igf-1* mRNA in  
95 the hybrid striped bass *Morone chrysops* × *Morone saxatilis* (Picha *et al.*, 2008). In cabezon  
96 *Scorpaenichthys marmoratus*, another species closely related to deepwater redfish, Strobel *et al.*  
97 (2020) found not only a significant positive correlation between plasma IGF-1 and specific  
98 growth rate, but also evidence that fasting affected *igf-1* mRNA in liver but not in white muscle,  
99 indicating a negative correlation between muscle *igf1-r* mRNA and growth rate/food intake. In  
100 muscle tissue, IGF-1 has a role in the regulation of metabolism, facilitating the uptake of  
101 substrates that contribute to muscle growth and may promote the expression of other important  
102 genes involved in the myogenesis process (fiber regulation, activation of satellite cells,  
103 proliferation, differentiation, and maturation) (e.g., Duan *et al.*, 2010; Vélez *et al.*, 2016).  
104 **Specifically, the** myosin (*myo*) **gene** is involved in the two final stages of the myogenesis process,  
105 i.e., differentiation and maturation (Vélez *et al.*, 2017).

106  
107 Another important aspect to consider when studying growth is metabolism, since somatic growth  
108 is the result of the energetic balance between assimilated and consumed energy (Saborido-Rey  
109 and Kjesbu, 2005). In fishes, the activities of muscle pyruvate kinase (PK) and lactate  
110 dehydrogenase (LDH), indicators of anaerobic glycolysis, have been demonstrated to be  
111 correlated with growth (Pelletier *et al.*, 1993a). In heart and red muscle, the activities of citrate  
112 synthase (CS) and cytochrome c oxidase (COX) have been shown to be good indicators of the  
113 Krebs cycle and mitochondrial activity (aerobic metabolism) (*Salvelinus alpinus*: Le François *et*  
114 *al.*, 2005; *Anarhichas minor*: Desrosiers *et al.*, 2008; *Paralabrax nebulifer*: Yang and Somero,  
115 1996; different Antarctic fish species: Torres and Somero, 1988). LDH and PK activities have  
116 been shown to increase in spotted wolffish *Anarhichas minor* during development (Desrosiers *et*  
117 *al.*, 2008) and were positively correlated with growth rate in Atlantic cod *Gadus morhua*

118 (Pelletier *et al.*, 1993b) and body size in walking catfish *Clarias betranthus* (Tripathi and Verma,  
119 2004). Davies and Moyes (2007) showed that the mass-specific activity of CS scaled negatively  
120 with body size, the glycolytic enzyme PK showed positive scaling, and the ratio of mass-specific  
121 PK to CS enzyme activity increased with body size, whereas the ratio of *pk* to *cs* mRNA  
122 transcripts was unaffected in largemouth bass *Micropterus salmoides* and smallmouth bass  
123 *Micropterus dolomieu*, suggesting that the enzyme relationships were not due simply to  
124 transcriptional regulation of both genes.

125  
126 The main goal of this work was to deepen our knowledge of growth regulation (liver *igf-1*, white  
127 muscle *igf-1ra* and *myo*) and metabolism (heart *cox-1* and *cs*, white muscle *pk* and *ldh-a*) in  
128 **deepwater redfish**. We hypothesized that the expression of genes coding for hormones regulating  
129 growth (in liver and muscle) and for enzymes regulating metabolism (in liver, muscle, and heart)  
130 could be indicators of growth characteristics at different sampling sites and thus be indicative of  
131 habitat suitability for juveniles. We aimed to explore how characteristics of the capture sites  
132 could influence gene expression. Deepwater redfish were captured in various zones of the EGSL  
133 that differ in terms of dissolved oxygen, temperature, salinity, depth, and deepwater redfish  
134 biomass. This approach allowed us to obtain insight on which habitats would be the most suitable  
135 for deepwater redfish growth and condition factor. This information is valuable in a management  
136 context.

137

## 138 **Methods**

139

### 140 ***Redfish sampling***

141 Redfish were captured alive during the August 2018 scientific campaign carried out at seven sites  
142 in the EGSL (AG: Anticosti–Gaspé, ES: Estuary, GA: Gyre d'Anticosti, LC: Laurentian Channel,  
143 EC: Esquiman Channel, AC: Anticosti Channel, CSt: Cabot Strait; Figure 1) by DFO aboard the  
144 CCGS *Teleost* with a Campelen 1800 trawl. Data from 670 redfish individuals (random  
145 subsamples taken from the entire catch) were considered for this study. The tows were planned to  
146 last 15 minutes at a speed of ~3 knots. Bottom measurements of dissolved oxygen, temperature,  
147 and salinity along with depth data and standardized redfish biomass (weight of all individuals in a  
148 catch standardized for tow duration) were collected at sampling stations (AG, LC, EC, and AC:  
149 one sampling station; GA and CSt: two sampling stations; ES: three sampling stations). Once fish  
150 were caught, they were put into baskets to weigh the entire catch by station (hereafter called  
151 biomass). From these baskets, we randomly selected fish from among those that met the  
152 following three requirements: (1) the fish was alive; (2) fish length was between 20 and 23 cm;  
153 and (3) the fish had not regurgitated its stomach. We took tissue samples from the first 20 and the  
154 others were measured for the DFO survey. We did not have control over the number of stations  
155 per site: logistical decisions were based on the multiple research objectives of the survey.  
156 Salinity, temperature, and depth were measured using an SBE 19plus V2 SeaCAT CTD (Sea-  
157 Bird Scientific, Bellevue, WA, USA), and dissolved oxygen was measured using an Optode 4831  
158 (Aanderaa, Bergen Norway). Data are reported in Table 1.

159  
160 Fork lengths were measured on all fish (Table 2). At each site, 20 deepwater redfish with lengths  
161 between 20 and 23 cm were sacrificed by severing the spinal cord and were immediately  
162 dissected on ice for tissue samplings. This size standardization ensured that immature individuals  
163 belonging to the same cohort (2011–2013; Brassard *et al.*, 2017) were used for the gene response

164 evaluation (Table 3) and that the gene response was only related to growth and not gonad  
165 maturation. This decision was made based on information that was available when the project  
166 was planned. In the meantime, a study based on gonad histology that is currently in progress has  
167 indicated that most fish larger than 20 cm are undergoing maturation or are mature (C. Senay,  
168 unpublished results). However, we examined the gonads of all fish sampled for gene expression  
169 and found no visual evidence of developed gonads. Tissue samples from heart, liver, and a piece  
170 of epaxial muscle from just beneath the dorsal fin were immediately stored in *RNAlater*  
171 (Invitrogen, Waltham, MA USA) at  $-20^{\circ}\text{C}$  pending further analysis of relative gene expression  
172 (liver: *igf-1*; white muscle: *igf-1ra*, *myo*, *pk*, *ldh-a*; heart: *cox-1*, *cs*; Table 4). We were careful not  
173 to include the gallbladder to avoid RNAses. A piece of the pectoral fin was also removed from all  
174 individuals and stored in 100% ethanol for DNA-based species identification.

175

### 176 ***Fish condition***

177 The lengths and weights of all captured deepwater redfish were measured ( $n = 670$ ). The Fulton  
178 condition factor (K) was estimated for each sampled fish using the following formula:

$$179 \quad K = 100(W/L^3)$$

180 where W is the wet body weight in grams and L is the fork length in centimeters. For condition  
181 factor calculation, we assumed isometric growth since similarly sized individuals were used.  
182 Larger values ( $>1$ ) signified that a fish was heavy (and potentially had greater energy and fat  
183 reserves) for a given size (Fulton, 1904; Nash *et al.*, 2006).

184

### 185 ***Genetic identification of individuals***

186 *DNA extraction* – For each fish sampled for gene expression (n = 140), DNA was extracted from  
187 20 mg of fin tissue (wet mass) using the DNeasy blood and tissue kit (Qiagen, Inc., Mississauga,  
188 ON, Canada). The final concentration was adjusted to 50 ng ml<sup>-1</sup> for genetic analysis.

189  
190 *Genetic analysis* – Genetic analysis was conducted according to Valentin et al. (2014), with slight  
191 modifications, using the Qiagen multiplex PCR kit (Qiagen). Four of the original 13 markers  
192 allowing species identification (Seb9, Seb25, Seb31, and Seb33) were used to discriminate  
193 species. Electrophoresis was conducted on an ABI 3130 genetic analyzer (Applied Biosystems,  
194 Waltham, MA, USA) using 0.1 µl of the GeneScan™ 1200 LIZ™ dye size standard (Thermo  
195 Fisher Scientific, Waltham, MA, USA) for each sample. The GeneMapper® Software v5.2  
196 (Thermo Fisher Scientific) was used to perform data analysis/genotyping. The R pipeline  
197 EasyAssign (version 0.1.0; <https://github.com/GenomicsMLI-DFO/SebAssign>) was used to  
198 assign samples to species. Genetic analysis indicated that 6% of the sampled fish were *S.*  
199 *fasciatus* (captured at AG and GA), and species was undetermined in 23% of the fish. Of the 140  
200 fish sampled, 95 individuals were identified as « *S. mentella* gulf » (the threshold used for the  
201 assignment was 95%); from these, we randomly selected 10 fish per sampling site—a total of  
202 70—that were used for gene expression analyses (Table 3).

203

#### 204 ***Gene expression***

205 *Extraction of total RNA* – RNA was extracted from 30 mg of liver, heart, and epaxial muscle (wet  
206 mass) from 10 deepwater redfish per site (total of 70), using the RNeasy Plus Universal Mini Kit  
207 (liver; Qiagen, Inc.) or RNeasy Fibrous Tissue Kit (heart and muscle; Qiagen, Inc.) and diluted to  
208 a final concentration of 200 ng µL<sup>-1</sup> RNA. RNA purity, quality, concentration, and absorbance

209 ratio 260/280 were determined by SYBR Safe DNA Gel Stain 2% agarose gel electrophoresis  
210 (ChemiDoc XRS+ system, Biorad, CA, USA) and spectrophotometry (NanoVue Plus, GE  
211 Healthcare, Pittsburgh, PA, USA).

212  
213 *Reverse transcription* – Reverse transcription of messenger RNA (mRNA) into complementary  
214 DNA (cDNA) was performed in duplicate using the Quantitect reverse transcription kit (Qiagen,  
215 Inc., Mississauga, ON, Canada). cDNA was then diluted to a final concentration of 200 ng  $\mu\text{L}^{-1}$ ,  
216 separated into aliquots, and kept frozen at  $-20^{\circ}\text{C}$  until further analysis. Integrity was verified and  
217 cDNA concentrations were measured using a NanoVue Plus spectrophotometer. The efficiency  
218 of reverse transcription was verified by quantitative polymerase chain reaction (qPCR) using  
219 serial dilutions of a representative pool of cDNA samples collected from different sampling sites  
220 and compared to the ideal slope of  $-3.3$ .

221  
222 *PCR amplification, sequencing, and assembly of partial cDNAs* – Since there were no available  
223 sequences for target and reference genes in deepwater redbfish, primers were designed using  
224 sequences from closely related or other marine fish species (Suppl. Table 1). PCRs were  
225 performed in 25  $\mu\text{L}$  reaction volumes containing 12.5  $\mu\text{L}$  of AmpliTaq Gold 360 (Applied  
226 Biosystems), 0.5  $\mu\text{L}$  of 360 GC enhancer (Applied biosystems), 2.5  $\mu\text{L}$  of cDNA, 1.25  $\mu\text{L}$  each of  
227 forward and reverse primers (20 mM), and 7  $\mu\text{L}$  of nuclease-free  $\text{H}_2\text{O}$ . Reactions were amplified  
228 under a thermal profile at  $95^{\circ}\text{C}$  for 10 min, 40 cycles at  $95^{\circ}\text{C}$  for 30 s,  $60^{\circ}\text{C}$  for 30 s, and  $72^{\circ}\text{C}$   
229 for 1 min and 20 s, followed by 7 min at  $72^{\circ}\text{C}$ . PCR products were then tested by gel  
230 electrophoresis on 2% agarose gels. The amplified PCR products were purified using the QIA  
231 quick PCR purification kit (Qiagen) and forward and reverse sequenced using the BigDye

232 Terminator v3.1 Cycle Sequencing kit (Applied Biosystems) with the ABI PRISM 3130 Genetic  
233 Analyzer (Applied Biosystems). For each gene, the sequence obtained was compared with the  
234 sequence used for primer design using the BLAST® software (Altschul *et al.*, 1990). Sequence  
235 lengths and percentages of similarity to the reference sequences are presented in **Supp. Table 1**.

236  
237 *Design of primers and probes – S. mentella* TaqMan primers and probes were designed using the  
238 Primer Express software version 3.0 (Applied Biosystems) for each reference and **target** gene  
239 (Table 4).

240  
241 *Real-time PCR analysis and gene quantification* – Gene expression was quantified by qPCR  
242 performed in triplicate on deepwater redfish samples using a QuantStudio 3 Real Time PCR  
243 System (Applied Biosystems). Each reaction consisted of 2 µL of diluted cDNA, 5 µL of  
244 TaqMan Fast Advanced Mix (Applied Biosystems), 0.5 µL of Custom TaqMan Gene Expression  
245 Assays (Applied Biosystems), and 2.5 µL of sterile water, for a total volume of 10 µL. The  
246 thermal cycling of qPCR was done in two steps: (1) 2 min at 50°C for optimal AmpErase uracil-  
247 N-glycosylase activity followed by 20 s at 95°C to activate DNA polymerase, and (2) 45  
248 denaturation cycles for 1 s at 95°C and annealing / extension for 20 s at 60°C. Cycle thresholds  
249 ( $C_T$ ) were obtained with the QuantStudio Design Analysis software (ThermoFisher Connect).

250  
251 The relative quantification of gene expression was calculated according to the  $2^{-\Delta\Delta C_T}$  method of  
252 Livak and Schmittgen (2001), with  $C_T$  being a threshold cycle:

253  
254

$$2^{-\Delta\Delta C_T} = 2^{-(\Delta C_{Te} - \Delta C_{Tc})}$$

255  
256 where  $C_{Te} = C_T$  of the **target** gene -  $C_T$  of the reference genes for sample x, and  $C_{Tc} = C_T$  of the  
257 target gene -  $C_T$  of the reference genes for the calibrator (see below). In this study, the calibrator  
258 was deepwater redfish sampled from Cabot Strait (the deepest, saltiest, and most highly  
259 oxygenated site). The stability of reference gene expressions was verified with Expression Suite  
260 version 1.0, where the score was calculated according to **Vandesompele et al. (2002)**. The score  
261 is a measure of the stability of genes in the qPCR analysis, which can vary according to the  
262 tissue: the lower the score, the more stable the expression. The reference genes used were 18S,  $\beta$ -  
263 actin, and EF1 $\alpha$ , and the best combination of scores was kept for each tissue. For accurate  
264 averaging of the reference genes, we used the geometric mean instead of the arithmetic mean  
265 because the former better controls for possible outlier values and abundance differences between  
266 the different genes (Vandesompele et al., 2002). The efficiency of the qPCR was verified for each  
267 gene, and percent efficiency values are reported in Table 4.

268  
269 *Statistical analyses* – Length, weight, Fulton condition factor, and qPCR data were compared  
270 using one-way ANOVA ( $\alpha < 0.05$ ), with site as the explanatory variable. To assess ANOVA  
271 assumptions, data normality was verified using the Kolmogorov-Smirnov test and  
272 homoscedasticity was tested using the Levene test. If significant differences occurred, post-hoc  
273 HSD Tukey tests were used when homoscedasticity was verified and multiple-range Games-  
274 Howell tests were applied in cases of heteroscedasticity.

275  
276 An exploratory principal component analysis was run to verify whether fish from each site  
277 differed according to gene expression data, but no clear pattern discriminating the sites emerged  
278 (see Suppl. Fig. 1). Relationships were examined between the response variables (*igf-1*, *igf-1ra*,

279 *myo*, *cox-1*, *cs*, *pk*, *ldh-a*) and the explanatory variables describing site-scale characteristics  
280 (dissolved oxygen, temperature, depth, and deepwater redfish biomass at the entire capture site)  
281 and individual-scale characteristics (length, weight, and Fulton condition factor of analyzed  
282 individuals) using the 70 deepwater redfish on which qPCR analyses had been done. To do so, a  
283 global canonical redundancy analysis (RDA: *rda* function in the R *vegan* package) was run with  
284 all explanatory variables, and model probability and adjusted coefficients of determination  
285 (adjusted  $R^2$ ) were calculated. The adjusted  $R^2$  was quantified (*RsquareAdj* function in the R  
286 *vegan* package), and it accounts for the number of observations and number of degrees of  
287 freedom in the fitted model (Peres-Neto *et al.*, 2006; Legendre *et al.*, 2011).

288  
289 Variation partitioning was conducted to determine the relative contribution of site-scale  
290 characteristics (dissolved oxygen, temperature, salinity, depth, and total biomass of captured  
291 deepwater redfish at the sampling site) and individual-scale characteristics (length, weight, and  
292 Fulton condition factor of the analyzed individuals) to explain gene expressions (*varpart* function  
293 in the R *vegan* package). This method requires multiple partial RDAs to quantify the variance  
294 explained exclusively and jointly by groups of variables.

295  
296 A selection of variables contributing to the explained variation was achieved by using both  
297 forward and backward selection as well as a stopping criterion (*ordiR2step* function in the R  
298 *vegan* package; Blanchet *et al.*, 2008). This criterion limits overfitting by preventing selected  
299 variables included in the reduced model from explaining more variation than the full model  
300 developed with all explanatory variables. A triplot was produced with a type 1 scaling to  
301 illustrate distances among objects (i.e., individuals) and relationships with selected environmental  
302 variables based on the reduced model using only significant explanatory variables. In such a

303 representation, the distance between objects are Euclidean distances (objects closer to each other  
304 have similar variable values), while the angles between the vectors of response variables are  
305 meaningless. The angles between vectors of the response variables and explanatory variables  
306 reflect linear correlation.

307

## 308 **Results**

309

### 310 **Individual fish characteristics**

311 The lengths, weights, and Fulton condition factors of 670 deepwater redfish were significantly  
312 different among the sites (length:  $F= 65.62$ ,  $p < 0.0001$ ; weight:  $F= 42.80$ ,  $p < 0.0001$ ; Fulton  
313 condition factor:  $F= 46.67$ ;  $p < 0.0001$ ) (Table 2). Deepwater redfish captured in LC, EC, and  
314 CSt were the longest, while those captured in ES were the shortest (in average 42% shorter; Table  
315 2). Fish from LC, EC, and CSt were also significantly heavier than those from ES (Table 2).  
316 Deepwater redfish from CSt had the highest Fulton condition factor (Table 2) while those  
317 captured at ES had the lowest (24% lower than CSt). Condition factors were intermediate in  
318 deepwater redfish captured at other sites. Weight, length, and condition factor followed same  
319 tendencies in the 10 fish per site that were sampled for genomic analysis (Table 3).

320

321 **Genes involved in growth regulation.** The relative expression of *igf-1* in liver was the lowest at  
322 ES, where it was 68% lower than at CSt or AG ( $F = 3.97$ ,  $p = 0.0019$ ; Figure 2A) and  
323 intermediate to all other sites. The relative expression of its receptor, *igf-1ra*, in white muscle was  
324 476% higher in deepwater redfish captured at ES compared to those captured at AG, GA, and  
325 LC, with intermediate values at the other sites ( $F = 4.60$ ,  $p < 0.0001$ ; Figure 2B). The relative

326 expression of white muscle *myo* was the lowest in individuals captured at CSt ( $F = 2.73$ ,  $p =$   
327  $0.0210$ ; Figure 2C) while it was significantly higher—by 189%—at AC, but no significant  
328 correlation was detected at ES or LC because interindividual variations were too high. *Myo*  
329 expression was intermediate at other sites.

330  
331 **Genes involved in metabolism.** In white muscle, a 424% higher expression of *pk* was observed  
332 in individuals captured at ES ( $F = 9.10$ ,  $p < 0.0001$ ; Figure 3A) compared to those from CSt, GA,  
333 and LC, with intermediate values at other sites. Deepwater redfish captured at AG had a  
334 significantly higher expression of *ldh-a* (298%) compared to those in fish captured at all other  
335 sites except for CSt ( $F = 3.84$ ,  $p = 0.0025$ ; Figure 3B). The relative expression of *cox-1* in the  
336 heart was significantly higher in juveniles captured at ES (212%) compared to those captured at  
337 CSt, AG, LC, and AC, with intermediate values found in fish captured at the other sites ( $F = 2.97$ ,  
338  $p = 0.019$ ; Figure 3C). Fish captured in EC had higher expressions of *cs* (204%) compared to fish  
339 captured in GA and LC ( $F = 3.50$ ,  $p = 0.0046$ ; Figure 3D).

340  
341 **Relationships between genomic indicators and site-scale and individual-scale characteristics**  
342 Correlations among explanatory variables were investigated. Salinity was excluded from the  
343 analysis because it was highly correlated with depth (Pearson's  $r = 0.92$ ). The RDA model  
344 including all variables (individual-scale and site-scale) was significant ( $p = 0.001$ ) and explained  
345 18% of the variation in individual genomic indicators ( $\text{adj } R^2 = 18\%$ ). Variation partitioning  
346 revealed that site-scale characteristics alone explained 12% of the variation ( $p = 0.002$ ) and  
347 individual-scale characteristics alone explained 6% ( $p = 0.011$ ); no shared fraction was explained  
348 by both types of variables together (Figure 4A). Variable selection indicated that weight and

349 temperature had the strongest effect on genomic indicators: their importance was similar (weight,  
350  $F = 5.28$ ,  $p = 0.002$ ; temperature,  $F = 5.224$ ,  $p = 0.006$ ), and the reduced model explained 11% of  
351 the variation ( $p = 0.001$ ).

352  
353 An RDA triplot illustrating the reduced model showed that deepwater redfish captured in ES  
354 were found in cold water and had the lowest weight (Figure 4B). The relative expressions of *igf-1*  
355 in liver and *ldh-a* in white muscle were positively correlated to weight, whereas *cs* in heart as  
356 well as *myo* and *pk* in white muscle were negatively correlated to weight. The relative  
357 expressions of heart *cox-1* and liver *igf-1ra* were not strongly correlated with weight, but they  
358 were negatively correlated with temperature. Other genomic indicators were not strongly affected  
359 by temperature.

360  
361 **Discussion**

362 In this study, we hypothesized that the expression of genes involved in growth and metabolism  
363 could provide information about growth characteristics and habitat suitability for deepwater  
364 redfish juveniles. Since weight and temperature explained most variations in the genomic  
365 indicators, this analysis highlights the relationships of genes correlated with these variables. The  
366 importance of temperature could be the key to understanding growth differences of deepwater  
367 redfish in the EGSL.

368  
369 **Transcriptomic indicators and fish weight**

370 The lowest and the highest relative expression of liver *igf-1* were associated with the sites where  
371 the smallest and the heaviest deepwater redfish were captured, respectively. This positive  
372 correlation between weight and liver *igf-1* has been previously described in different fish (e.g.,

373 Beckman, 2011), including rockfish *Sebastes serranoides* reared under laboratory conditions, and  
374 indicates that differences in expression may be attributed to the quantity of ingested food (Hack  
375 *et al.*, 2018). We also expected that high liver *igf-1* expression would be correlated with a high  
376 expression of white muscle *igf1-ra*, since IGF-1 binds to receptors on the surface of muscle cells  
377 to exert its action on muscle growth. However, the reverse situation was observed at ES and CSt,  
378 with low expressions of *igf-1* occurring with high expressions of *igf-Ira*. Similar results were  
379 reported for *Sebastes* by Hack *et al.* (2019), suggesting a negative relationship between muscle  
380 *iglr* expression and fasting-associated decline in muscle *igf-1* expression that could indicate  
381 reduced muscle growth. Nevertheless, it is interesting to note that the opposite situation was  
382 observed in deepwater redfish captured at AG: the highest *igf-1* expression occurred with the  
383 lowest *igf-Ira* expression, even though the weights of individuals captured at this site were  
384 intermediate to those of fish captured at ES and CSt.

385  
386 Deepwater redfish captured at ES also exhibited the highest relative expression of white muscle  
387 *pk*. High expression of muscle *pk* has been associated with starvation in rainbow trout  
388 *Oncorhynchus mykiss* and may indicate the breakdown of muscle proteins to compensate for the  
389 lack of food intake (Johansen and Overturf, 2006). Results from a parallel study currently in  
390 progress (S. Brown-Villemin – Pers. Comm.) and made on the same fish as those used in our  
391 study showed that 70% of the stomachs from ES were empty while 90% of those from CSt were  
392 full. This possible starvation could explain why the fish caught in ES were smaller and had the  
393 highest *pk* expression. Furthermore, analysis of stomach content revealed that in both sites  
394 deepwater redfish were feeding on zooplankton but the occurrence of each zooplankton taxon  
395 identified differed.

396

397 The expression of *ldh-a* in white muscle was positively correlated with weight, but our data did  
398 not show any spatial pattern across the EGSL. A similar positive correlation was reported in  
399 *Sebastes goodei*, but negative correlations have also been found in *Sebastolobus alascanus*  
400 (Vetter and Lynn, 1997) and *Synaphobranchus kaupii* (Bailey *et al.*, 2005). It has been also  
401 reported that LDH activity might be sensitive to environmental oxygen levels (Vetter and Lynn,  
402 1997) and very sensitive to changes in nutritional condition during food limitation (Yang and  
403 Somero, 1996). According to this evidence, we could expect that deepwater redbfish from CSt  
404 (highest dissolved oxygen concentration) and ES (lowest dissolved oxygen concentration) would  
405 show significantly different *ldh* expressions, but this was not the case. Indeed, there was no  
406 correlation between dissolved oxygen content and relative gene expressions in the EGSL.  
407 Unfortunately, we have no data from stomach contents to examine potential nutritional  
408 differences, that could explain our results across the EGSL.

409  
410 The relative expression of white muscle *myo* was negatively correlated with weight in our study  
411 and differed only between fish captured at CSt and AC. These fish had significantly different  
412 weights, but no differences in terms of either length or condition factor. Contradictory results  
413 have been reported in gilthead sea bream *Sparus aurata* and rainbow trout, with negative  
414 correlations between weight and *myo* being reported by Azizi *et al.* (2016) and Overturf and  
415 Hardy (2001) and no correlation being reported by Alami-Durante *et al.* (2010) and Vélez *et al.*  
416 (2018). Therefore, the difference in *myo* gene expression observed between CSt and AC could be  
417 related to other factors, such as diet. However, an experiment with juvenile rainbow trout  
418 indicated that dietary differences were not responsible for the expression of different myogenic  
419 factors, including *myo* (Alami-Durante *et al.*, 2010).

420

421 In general, CS activity typically decreases in larger individuals, and a negative correlation with  
422 weight has been reported in black bass, sunfish (*Lepomis gibbosus*, *Lepomis macrochirus*; Davies  
423 and Moyes, 2007), barred sand bass (*Paralabrax nebulifer*; Yang and Somero, 1996), and  
424 *Sebastolobus altivelis* (Vetter and Lynn, 1997). Indeed, aerobic metabolic activity is thought to  
425 scale negatively with size due to economies in the cost of oxygen transport with increasing body  
426 size (Vetter and Lynn, 1997). However, it should be reminded that the gene expression does not  
427 necessarily represent direct changes in protein levels due to the action of post-transcriptional  
428 mechanisms, that may lead to a disparity between mRNA abundance and enzyme activity (Craig  
429 *et al.*, 2007; Vagner and Santigosa, 2011; Velki *et al.*, 2017).

430  
431 One may argue that the fish size standardization we did during sampling may have masked  
432 weight and length differences at different sites. However, we were able to find strong evidence  
433 that there are significant differences in gene expression between ES and the other sites. These  
434 results would suggest that even the slower-growing individuals at CSt would have a better growth  
435 potential than the faster-growing individuals at ES. Such differences in growth potential between  
436 sites could result from biotic and abiotic differences between sites that could lead to (1) a  
437 disparity in the regulatory pathway at molecular levels , as found in this study; (2) higher  
438 metabolic costs that left less energy available for growth; or (3) differences in the nutritional  
439 quality of prey.

440

#### 441 **Transcriptomic indicators and temperature conditions**

442 In ectotherms, growth strongly depends on environmental conditions, especially temperature  
443 (Fry, 1971). In deepwater redfish, the relative expression of heart *cox* was negatively correlated  
444 with temperature. This was clearly illustrated in our study when comparing the different capture

445 sites: fish caught in ES (the coldest zone) showed a higher expression of heart *cox* compared to  
446 the warmest sites (CSt, AG, LC, AC). Cold acclimation in wild fish typically leads to an increase  
447 in COX activity (Bremer and Moyes, 2011) due to an increase in mitochondrial gene expression.  
448 This may be a compensatory mechanism to overcome the negative thermodynamic effects of cold  
449 on processes relying on enzymatic reactions (e.g., Nathanailides, 1996). Indeed, changes in water  
450 temperature can have pronounced effects on physiological processes such as muscle and  
451 cardiovascular function as well as metabolism and growth (e.g., Little *et al.*, 2020). In Atlantic  
452 salmon *Salmo salar*, COX activity increased rapidly with lower temperature (Nathanailides,  
453 1996) In contrast, no relationship was observed between COX activity and temperature in  
454 Atlantic cod (Pelletier *et al.*, 1995). Contrary to our findings, *ldh* expression in black rockfish  
455 *Sebastes schlegelii* increased with warmer temperatures (Song *et al.*, 2019). Facing cold  
456 temperature, there are two metabolic strategies available for ectotherms: (1) to increase metabolic  
457 rate to compensate for temperature-mediated decreases in the metabolic rate, or (2) to decrease  
458 metabolic rate to reduce energy consumption (Song *et al.*, 2019). Deepwater redfish from ES,  
459 where water is the coldest, seem to use a combination of both: anaerobic metabolism (*ldh-a*) is  
460 down-regulated and aerobic metabolism (*cox-1*) is up-regulated.

461  
462 The relative expression of white muscle *igf-Ira* was negatively correlated with temperature. It is  
463 surprising that this gene did not show any strong correlation with weight and yet did with  
464 temperature. The mechanisms mediating the effects of temperature on growth—and more  
465 specifically, on the regulation of the GH–IGF1 axis—are not well understood.

466

467 The EGSL can be separated into three distinct depth layers characterized by temperature  
468 conditions: the surface layer, the cold intermediate layer, and the deepwater layer. The deepwater  
469 layer, where deepwater redfish were captured and where temperatures range around 5–6°C  
470 (> 250 m) throughout the year (Galbraith *et al.*, 2019), is mostly isolated from exchanges with the  
471 surface and is very stable across depth (150–500m). The temperature difference observed during  
472 the survey between the coldest (ES) and the warmest (CSt) sites was 0.7°C. However, according  
473 to Bourdages *et al.* (2019), the mean temperature in August 2018 (time of the sampling) at 300 m  
474 was 5.6°C in ES and 6.8°C in CSt (a difference of 1.2°C). Considering the stability of the  
475 deepwater layer, this difference could impact deepwater redfish physiology. This has been found  
476 to be the case in other fish species: Ghinter *et al.* (2021) found that a difference of 2°C can  
477 exceed the optimal temperature range for growth in Greenland halibut *Reinhardtius*  
478 *hippoglossoides* in the bottom waters of the EGSL. This suggests that even small increases in  
479 temperature associated with global change are likely to have strong effects on seabase physiology  
480 and thereby on populations and fisheries (e.g., Little *et al.*, 2020; Ghinter *et al.*, 2021).

481

#### 482 **Gene expression and other physicochemical variables**

483 Other variables (salinity, depth, and redfish biomass) do not appear to correlate with gene  
484 expression in deepwater redfish in the EGSL, but deepwater redfish captured in ES differed from  
485 those from the other sites. ES is also characterized by low oxygen content, but low oxygen  
486 conditions were also found at GA and AC. However, general fish condition (length, weight, and  
487 condition factor) seemed to be better at GA and AC compared to ES. Indeed, our analysis did not  
488 confirm any correlation with oxygen levels.

489

490 Considering the data from our study, energy costs seem to be higher in ES than in other sites, as  
491 suggested by the up-regulation of *cs* and *cox-1*, but we are not able to precisely identify the  
492 factors explaining this. Because energy may be diverted from growth when gonad maturation  
493 begins, it is important to compare individuals at the same developmental stage. Differences  
494 among sampling sites could be related to differences in maturation stage that were not visually  
495 observable during sampling. Even though we do not have data to support this statement, it seems  
496 unlikely that gonad maturation would have been more advanced in the coldest areas (with the  
497 smallest fish). Future studies targeting fish of different sizes from each site would be useful to  
498 address this question.

499

## 500 **Conclusion**

501 Deepwater redbfish from the same cohorts captured at different sites present different patterns of  
502 gene expression that are related to their weight and to the temperature conditions of the sites. We  
503 found that (1) the relative expressions of liver *igf-1* and white muscle *ldh-a* were positively  
504 correlated with weight; (2) white muscle *pk* and *myo* as well as heart *cs* were negatively  
505 correlated with weight; and (3) white muscle *igf-1ra* and heart *cox* were negatively correlated  
506 with temperature. We thus suggest that liver *igf-1*, white muscle *igf-1ra* and *pk*, and heart *cox-1*  
507 could be used as growth indicators for surveys in the field. **Since weight of deepwater redbfish is**  
508 **positively correlated with temperature (even enhanced at higher temperatures),** this study  
509 suggests an ecological advantage for this species in a climate-warming context. For this reason,  
510 monitoring the gene expression response related to increased water temperatures will certainly  
511 improve our understanding of this species' population dynamics **and help deepen further to better**  
512 **understand physiological mechanisms underlying the observed differences.** More broadly,  
513 transcriptomics could be an **important** tool for investigating growth in a deep-sea fish whose

514 physiology is difficult to study. However, the inclusion of more ecological variables such as prey  
515 abundance could help gain a better understanding of fish physiology in future studies.

516

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528

### 529 **Contributions**

530 M.A.M. contributed to data generation, data analysis, and manuscript preparation; M.V  
531 contributed to data analysis and manuscript preparation; C.S. contributed to data generation, data  
532 analysis, and manuscript preparation; and C.A. contributed with ideas, data generation, data  
533 analysis, and manuscript preparation.

534

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#### 740 **Figure Captions**

741 **Figure 1.** Deepwater redfish sampling sites in the Estuary and Gulf of St Lawrence. Circle sizes  
742 indicate oxygen saturation ( $\mu\text{mol/kg}$ ) and colours indicate depth. AG: Anticosti–Gaspé, ES:  
743 Estuary, GA: Gyre d'Anticosti, LC: Laurentian Channel, EC: Esquiman Channel, AC: Anticosti  
744 Channel, CSt: Cabot Strait.

745 **Figure 2.** Relative changes in gene expression (mean  $\pm$  SE) of three target genes related to  
746 growth in deepwater redfish captured at the sampling stations (AG: Anticosti–Gaspé, ES:  
747 Estuary, GA: Gyre d'Anticosti, LC: Laurentian Channel, EC: Esquiman Channel, AC: Anticosti  
748 Channel, CSt: Cabot Strait). (A) liver insulin-like growth factor 1 (*igf-1*), (B) white muscle  
749 insulin-like growth factor 1 receptor (*igf-1r*), (C) muscle myosin (*myo*). The dashed horizontal  
750 lines indicate the normalized values for the calibrator group (CSt: the deepest, saltiest, and most  
751 highly oxygenated site). Different letters indicate significant differences among sites (Tukey

752 HSD multiple comparison tests when data were homoscedastic [*igf-1*] and Games-Howell tests  
753 when data were heteroscedastic [*igf-1r*, *myo*];  $\alpha = 0.05$ ).

754 **Figure 3.** Relative changes in gene expression (mean  $\pm$  SE) of four target genes related to  
755 metabolism in deepwater redfish captured from the sampling stations (AG: Anticosti–Gaspé, ES:  
756 Estuary, GA: Gyre d'Anticosti, LC: Laurentian Channel, EC: Esquiman Channel, AC: Anticosti  
757 Channel, CSt: Cabot Strait). (A) white muscle pyruvate kinase (*pk*), (B) white muscle lactate  
758 dehydrogenase (*ldh*), (C) heart cytochrome c oxidase (*cox*), (D) heart citrate synthase (*cs*). The  
759 dashed horizontal line indicates the normalized values for the calibrator group (CSt: the deepest,  
760 saltiest, and most highly oxygenated site). Different letters indicate significant differences among  
761 sites (Tukey HSD multiple comparison tests when data were homoscedastic [*ldh*, *cs*] and Games-  
762 Howell tests when data were heteroscedastic [*pk*, *cox*];  $\alpha = 0.05$ ).

763 **Figure 4.** (A): Site-scale and individual-scale analyses. Variation partitioning, relationships  
764 between gene expression (Y) and site variables (X1: dissolved oxygen, temperature, depth, and  
765 redfish biomass) and individual variables (X2: length, weight, Fulton index). (B): Redundance  
766 analysis. *Scaling 1*- distance triplot (object focused). Selected explanatory variables are in black,  
767 indicators are in red, and fish from different sites are indicated by different symbols.

768 **Suppl. Figure 1.** Principal component analysis (PCA) of the variables of each site (left) and gene  
769 expression database (right; *igf-1*, *igf-1r*, *myo*, *cox*, *cs*, *pk*, *ldh*) associated with capture sites for  
770 deepwater redfish. Different colours represent different capture sites.