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1 **Isogenic lines of rainbow trout (*Oncorhynchus mykiss*) as a tool to assess how growth**
2 **and feeding behaviour are correlated to feed efficiency in fish**

3

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14

15 **Abstract**

16 Accurately measuring individual feed intake is required to include feed efficiency (FE) as an
17 objective in commercial breeding programs. Phenotyping individual feed intake through
18 direct measurements remains complex in fish reared in groups. One way to overcome this
19 challenge is to find proxies for estimating FE. This study aimed to investigate the correlations
20 between fish FE and potential predictive criteria in rainbow trout *Oncorhynchus mykiss*. As
21 predictive criteria, we considered the variations of body weight assessed as thermal growth
22 coefficients (TGC) and the feeding behaviour assessed as the number of feed demands over a
23 period and the proportion of the demands made before noon. Feed intake was assessed over
24 three different periods in ten isogenic lines allowing a recording for each of the ten genotypes
25 while keeping fish in groups. The protocol consisted of two successive feed deprivation and
26 refeeding phases after initial basal growth periods. Correlations were then calculated between
27 FE, measured either as feed conversion ratio (FCR) or residual feed intake (RFI), and the
28 different indirect criteria. We found positive phenotypic correlations between FCR and RFI
29 over the feed intake measurement periods ($r \geq 0.79$, $P < 0.001$). Assessment of the
30 relationship between FE traits (FCR and RFI) calculated over the three measurement periods
31 and TGC revealed no significant association. Regarding feeding behaviour, significant
32 differences in the daily profile of feed demands and their numbers were found among the ten
33 isogenic lines. RFI calculated from the first feed intake measurement period and feeding
34 behaviour, assessed as the number of feed demands were positively correlated ($r = 0.42-0.49$,
35 $P \leq 0.022$). Nevertheless, such correlations were not established for the two other
36 measurement periods following feed deprivation. While we demonstrated that the weight
37 variations during feed deprivation are not a good proxy for FE (FCR or RFI) in rainbow trout,
38 we also highlighted the interest in exploring more the relationships between FE and feeding
39 behaviour in fish.

40 **Keywords:** feeding behaviour, fish, residual feed intake, thermal growth coefficient, weight
41 variations

42 **1. Introduction**

43 Aquaculture is one of the fastest-growing animal protein supplies globally, while
44 approximately 70% of aquaculture production requires external feed inputs (FAO, 2020).
45 Nowadays, exogenous feeds for reared species are at the heart of concerns for the
46 sustainability of finfish aquaculture. While exogenous feeds can represent up to 70% of farm
47 costs (Doupé and Lymbery, 2004; de Verdal et al., 2018a), they are also responsible for
48 environmental impacts directly resulting from feeds manufacturing and then, indirectly, by the
49 release of nutrients by fish (Mente et al., 2006; Read and Fernandes, 2003). Furthermore, the
50 mobilization of resources and arable lands for aquafeed production raises concerns about
51 aquaculture's social impact (Troell et al., 2014). Therefore, selecting fish turning feeds
52 efficiently into meat is key to achieving the sustainable development of aquaculture.

53 In fish, feed efficiency (FE) has been traditionally measured by feed conversion ratio (FCR),
54 defined as the ratio of feed intake (FI) to weight gain. However, FCR values can result from
55 different biological conditions such as a reduced FI, an increase of biomass production or a
56 combination of both (Cantalapiedra-Hijar et al., 2020). Thereby, FCR is mainly used for the
57 zootechnical and economic performances assessment of a batch of animals at the farm level.
58 An alternative to FCR is the residual feed intake (RFI), defined as the difference between the
59 feed consumed by an animal and its expected consumption as predicted from a regression
60 model involving the requirements for maintenance and growth through the integration of
61 metabolic weight and weight gain over the recording period as the independent variables
62 (Koch et al., 1963). Therefore, contrary to FCR (Besson et al., 2020; Kause et al., 2006;
63 Thodesen et al., 1999), RFI is uncorrelated to body weight by construction and individuals
64 with a negative RFI are more efficient than the mean of the population, while individuals with
65 a positive RFI are less efficient.

66 Improvement of FE in fish can be achieved through various levers, including husbandry (El-
67 Sayed, 2002; Yilmaz and Arabaci, 2010), nutrition (e.g., Bowyer et al., 2020; Xu et al., 2001),
68 and genetic selection (e.g., de Verdal et al., 2018a, 2018b; Knap and Kause, 2018). Feed
69 efficiency is now among the main traits of interest for fish breeding programs (Chavanne et
70 al., 2016). However, except for family-based selection requiring heavy infrastructures and
71 human labour, as previously done for Atlantic salmon in Norway (Gjedrem, 2010), selection
72 for FE remains challenging, as the precise recording of individual FI is needed. Such
73 phenotyping is challenging in fish. Indeed, fish are usually reared in large groups making it
74 difficult to follow the FI of each individual. The usual way to measure FI in fish is to remove
75 and count uneaten pellets allowing to calculate FI as the difference between the weight of feed
76 given and the weight of feed uneaten by fish (wasted) (Jobling et al., 2001). Other approaches
77 have been developed to measure individual FI in fish including the use of dyed feed, X-
78 radiography and individual rearing (Besson et al., 2019; Jobling et al., 2001; Silverstein,
79 2006; Talbot and Higgins, 1983). An alternative method consisting of rearing small groups of
80 fish in aquaria (~5-15 fish together) with video recording has been proven to be efficient for
81 FI determination in fish (de Verdal et al., 2017, 2018b, 2019; Just et al., 2021) while
82 developments are currently performed to automate video analysis by artificial intelligence
83 (Zhou et al., 2018). Recently, Dvergedal et al. (2022) suggested that lipid deposition in
84 rainbow trout *Oncorhynchus mykiss*, which is related to FE, could be phenotyped through the
85 C stable isotope contents in feeds and fish. Nevertheless, all of these methods have
86 limitations, including measurement inaccuracies with a lack of repeatability and/or
87 measurement conditions too far from production conditions (reviewed by de Verdal et al.
88 (2018a)) while the most recent ones are still requiring methodological developments.

89 Because collecting individual FI data in fish through direct measurements remains complex,
90 many indirect criteria such as traits derived: 1) from bio-energetic models: lipid deposition,
91 nitrogen retention, oxygen consumption and 2) from growth models: growth and changes in

92 the body after starvation and refeeding periods, have been studied in recent years for
93 estimating FE. Focusing on body weight loss during starvation and gain during the subsequent
94 refeeding period, Grima et al. (2010a, 2010b) suggested that selection for European seabass
95 *Dicentrarchus labrax* losing less weight during the starvation period should improve FE and
96 increase muscle fatness. However, in rainbow trout, Grima et al. (2008) did not find any
97 significant correlation between RFI and weight variations during starvation or refeeding
98 periods. However, they highlighted that an index combining growth performances over all the
99 experimental periods explained up to 59% of RFI variations.

100 Feed efficiency can also be linked to feeding behaviour. Indeed, several authors have shown
101 that in terrestrial-farmed animals, feed-efficient individuals are less active while feeding (e.g.,
102 Kelly et al., 2010; Montanholi et al., 2010). In fish, Martins et al. (2006) have shown that
103 African catfish *Clarias gariepinus* with lower RFI spend less time eating. In Nile tilapia
104 *Oreochromis niloticus*, Martins et al. (2011a) found that RFI was negatively correlated with
105 feeding latency (i.e. the time each fish takes to consume the first pellet), while positive
106 correlations were found with the total feeding time and the number of feeding acts.
107 Nevertheless, such relationships have been poorly investigated in the literature and, based on
108 the limited information available, seem to be contrasted depending on the size of the fish used
109 (Martins et al., 2011b).

110 On an experimental scale, one tool to overcome the drawbacks of the usual FI assessment
111 methods in fish is using isogenic lines (Franěk et al., 2020; Komen and Thorgaard, 2007a;
112 Quillet et al., 2007b). In such lines, all individuals are genetically identical. Crossing
113 individuals from two homozygous isogenic lines allows to obtain genetically identical but
114 heterozygous individuals in the next generation (de Verdal et al., 2018a). Although isogenic
115 lines are produced for experimental purposes only, they are an excellent tool for studying the
116 variability of FE, which is highly sensitive to environmental variations. Because the genetic
117 variability within an isogenic line is null, fish belonging to the same line reared in the same

118 tank allow a precise assessment of FI of an individual genotype while maintaining social
119 interactions between individuals for each of the genotypes. In addition, combining
120 information from different isogenic lines gives access to the genetic variability of FE.

121 The aims of this study were: (1) to confirm the existence of genetic variability in FE, (2) to
122 estimate correlations between RFI, FCR and body weight variations during successive FD and
123 compensatory growth (CG) periods and (3) to investigate the link between feeding behaviour
124 and FE in rainbow trout.

125 **2. Materials and Methods**

126 2.1. Ethical statement

127 All the experiments were carried out at the INRAE experimental facilities (PEIMA, INRAE,
128 2021, Fish Farming systems Experimental Facility, DOI: 10.15454/1.5572329612068406E12,
129 Sizun, France) authorised for animal experimentation under the French regulation D29-277-
130 02. The experiments were carried out from January 2008 to July 2009 following the
131 Guidelines of the National Legislation on Animal Care of the French Ministry of Research
132 (Decree N°2001-464, May 29, 2001). At this date, project authorisation was not required.
133 Experiments were conducted under the official license of M. Dupont-Nivet (A29102).

134 2.2. Heterozygous isogenic lines

135 Experimental fish were produced and reared in the INRAE experimental fish farm (PEIMA,
136 Sizun, France) as described by Lallias et al. (2017) and Millot et al. (2014). Parents were
137 issued from the INRAE homozygous isogenic lines. These lines were previously established
138 after two generations of gynogenesis and further maintained within each line by single-pair
139 mating using sex-reversed XX males (Quillet et al., 2007b). Mating 24 homozygous females
140 from a single maternal isogenic line (spawning on the same day with similar egg weights)
141 with ten sex-reversed XX males from ten other homozygous isogenic lines produced ten
142 heterozygous isogenic lines. Eggs were mixed and then divided into ten batches, each batch

143 being fertilised by one of the ten homozygous males. To avoid confusion with the INRAE
144 homozygous isogenic lines, heterozygous lines will be named the line's original name where
145 the sire came from, plus "h" as heterozygous.

146 Since there is only one maternal line, progeny differs only through paternal genetic effects
147 across batches. Fertilised eggs were incubated at 11.4°C. At the eyed stage, 1500 eggs of each
148 of the ten produced heterozygous lines were distributed in 0.25 m³ indoor tanks (n = 3 per
149 line, 500 fish per replicate) supplied with natural spring water at the same temperature. Fish
150 were transferred in 1.8 m³ outdoor tanks (n=3 per line) supplied with dam water (11.3-16.0°C)
151 after 137 days post-fertilization (dpf) up to the end of the experiment (548 dpf). In order to
152 keep a density below 50 kg m⁻³, regular random eliminations were performed, and 100 fish
153 per replicate remained at 548 dpf. Commercial pellets (BioMar's Biostart range and Le
154 Gouessant's B-Mega range) were distributed by automatic feeders during the indoor phase and
155 self-feeders (Imetronic®, France) during the outdoor rearing phase (see Section 2.4.2 for
156 details). Feed ration was maintained *ad libitum* throughout the experiment. Mortality was
157 checked every day.

158 2.3. Successive experimental phases

159 The experiment reported here started at the beginning of the outdoor rearing phase (*i.e.* 137
160 dpf). The experimental protocol is summarised in Figure 1. After two basal growth periods
161 separated by chronic stress (see Lallias et al. (2017) for details), the protocol consisted of two
162 repeated phases of FD and refeeding periods. Following an FD period, fish tend to
163 compensate for the loss of growth experienced during the FD period by increasing their
164 growth more than usual, a phase known as the CG period (Ali et al., 2003). In literature, there
165 is a large variability in the protocols used to measure weight loss during FD, with
166 measurements performed on groups or on isolated fish, with different durations of feeding
167 periods, with repetitive FD periods or not, and with different sizes and ages of fish at the

168 beginning of the experiment (reviewed in Ali et al., 2003). Here, we followed a FD protocol
169 adapted from Grima et al. (2008) and targeting an average weight loss equivalent to
170 approximately 10% in order to be able to highlight contrasting performances between lines
171 while avoiding deleterious effects. It is for this reason in particular that the duration of the
172 second fasting phase was extended following an intermediate weighing (see below).

173 The experiment was divided into six different phases: two basal growth periods (bg_1 ; from
174 day 1 to day 129, *i.e.* 128 d and bg_2 ; from day 186 to day 277, *i.e.* 91 d), FD period 1 (fd_1 ;
175 from day 278 to day 300, *i.e.* 22 d), CG period 1 (cg_1 ; from day 301 to day 335, *i.e.* 34 d), FD
176 period 2 (fd_2 ; from day 336 to day 387, *i.e.* 48 d), and CG period 2 (cg_2 ; from day 388 to day
177 415, *i.e.* 29 d). Feed intake (FI) was measured three times during the experiment, as shown in
178 Figure 1. The first period of FI assessment was carried out from day 129 to day 161 (*i.e.* 32 d)
179 to provide FE of the tested isogenic lines under normal growth conditions. The period from
180 day 162 to day 185 was not considered here because fish were exposed to stress challenges
181 which strongly influenced their growth (Figure 2B). Then, the other FI measurement periods
182 (fi) were performed during cg_1 and cg_2 .

183 2.4. Traits measured

184 2.4.1. Body weight variations

185 Body weight was measured at the beginning and then 11 times throughout the experiment ($n \approx$
186 100 fish per replicate). Fish were starved for 24h before any sampling. Weight gain or loss in
187 each period of interest (*i.e.* bg_1 , bg_2 , fd_1 , cg_1 , fd_2 , cg_2) was expressed as thermal growth
188 coefficient (TGC), offering a standardised measure of growth that is unaffected by body
189 weight, time interval, and water temperature (Iwama and Tautz, 1981; Grima et al., 2010b)
190 that varied from 5 to 17°C over the experiment (Figure 2A). TGC was calculated according to
191 the following equation:

$$TGC = \frac{(BW_f^{\frac{1}{3}} - BW_i^{\frac{1}{3}})}{\Sigma T} \times 1000$$

192 where BW_f and BW_i are the final and initial average body weights of the considered period,
 193 and ΣT is the sum of daily temperatures. Growth rates are referred to as TGC_{bg1} , TGC_{bg2} ,
 194 TGC_{fd1} , TGC_{cg1} , TGC_{fd2} and TGC_{cg2} for the different separated periods.

195 2.4.2. Feed efficiency and feed demands

196 Self-feeders were used throughout the experiment to characterise the feeding behaviour of
 197 each isogenic line. This feeding technique is based on the learning ability of fish, and feed is
 198 delivered depending on their demand (Azzaydi et al., 2007). In a self-feeding system, fish are
 199 assumed to precisely control the feed distribution by activating a "trigger" sensor (Mambrini
 200 et al., 2004; da Silva et al., 2016). In order to limit involuntary demands and subsequent
 201 waste, sensors were placed just above the water. In addition, the self-feeders, one per tank,
 202 were configured to make access to the pellets more difficult according to the quantity of feed
 203 distributed over the day by increasing the inhibition time of the probe and by requiring two
 204 triggerings for pellet distribution. The protocol was adjusted over time according to the
 205 number of demands and the fish appetite. All the self-feeders were connected to a computer
 206 system (Imetronic®, France), allowing a continuous recording of all the fish's feed
 207 distribution (sorted as rewarded demands when they led to feeding or unrewarded demands if
 208 not) during the FI measurement periods.

209 Two indicators of FE were used. The first one was the feed conversion ratio calculated as
 210 follows:

$$FCR = \frac{FI}{BWG}$$

211 where FI is the feed intake and BWG is the body weight gain. Despite the simplicity of
 212 calculation and interpretation, one of the problems with FCR lies in the fact that the ratio

213 obtained can result from different biological conditions: (1) a decrease in ingestion, (2) an
214 increase in growth or (3) a combination of the two (Cantalapiedra-Hijar et al., 2020). Other
215 criteria have been proposed in animal genetic selection to overcome the problems associated
216 with ratios. The most frequently used criterion by geneticists is the residual feed intake (RFI;
217 Koch et al., 1963), which was used as the second indicator for FE. RFI is calculated according
218 to the following equation:

$$219 \quad RFI = FI - \beta_0 - \beta_1 \times BW^{0.8} - \beta_2 \times BWG$$

220 with β_0 the regression intercept and β_1 the partial regression coefficient of the animal's FI on
221 metabolic body weight. Average weights over the measurement period ($\frac{BW_{initial} + BW_{final}}{2}$) are
222 scaled to metabolic weights ($BW^{0.8}$; Clarke and Johnston, 1999; Jobling, 2002), while β_2 is
223 the partial regression coefficient of the animal's FI on BWG. This model allocates the FI
224 according to expected maintenance and growth requirements, the remaining part being
225 defined as the RFI (Koch et al., 1963; de Verdal et al., 2018a).

226 2.5. Statistical analyses

227 The significance level for statistical analyses was set to $\alpha = 0.05$. All statistics were performed
228 using R freeware version 4.3.1 (R Development Core Team, 2020). The final body weight
229 was compared between lines using a linear mixed model with "line" as a fixed effect and
230 "replicate" as a random effect. The model was fitted using the *nlme* package, and contrasts
231 were analysed using the *emmeans* package. Assumptions of normality and homoscedasticity
232 were checked by visual inspections of residuals against fitted values.

233 Differences in weight variations, TGC, FI and RFI estimated for each experimental period
234 between lines were tested using the aligned rank transformation for nonparametric factorial
235 analysis (*art()*, *ARTool* package) using the tanks as the experimental units. Contrasts were
236 computed using the function *art.con()* from the same R package.

237 Regarding the feeding behaviour data, for each of the three FI measurement periods, the
238 number of daily feed demands was compared between lines as described above for final
239 weight. The daily feeding profile (% demand activity h^{-1} per day) for each FI measurement
240 period was compared between lines with a generalised linear mixed model with "line" and
241 "hour" as fixed effects while "replicate" was included as a random effect. The model was
242 fitted using the *glmmTMB* package allowing to fit generalised linear mixed models with
243 various extensions.

244 The correlations between the variables (averaged by tank for rewarded and unrewarded feed
245 demands) were examined with the *rcorr()* function of the *Hmisc* package.

246 **3. Results and Discussion**

247 3.1. Effects of feed deprivation on survival and growth

248 Feeding management regimes based on short cycles of FD/CG periods have been suggested to
249 improve water quality as well as reducing feed and labour costs in fish farming (Eroldoğan et
250 al., 2006; Hayward et al., 1997). Here, as expected, fish overcame starvation, and the two FD
251 periods did not affect survival in mortality rate (mortality rate $< 1\%$ over fd_1 and fd_2).
252 Weatherley and Gill (1981) already highlighted the ability of rainbow trout to deal with
253 prolonged starvation (*i.e.* up to 13 weeks) without deleterious effects on subsequent
254 zootechnical performances. The final individual weights by line after the 415-d experiment
255 (*i.e.* 552 dpf) ranged from 704 ± 119 g to 958 ± 123 g for N38h and A02h, respectively
256 (Figure 2B), while TGC significantly differed between the lines over the experiment ($P <$
257 0.001). The ten lines differed slightly for response to FD, with an average weight loss ranging
258 from 5 to 10% during the first FD period (fd_1) vs from 8 to 13% during the second FD period
259 (fd_2), with significant differences recorded among the lines for both periods ($P < 0.002$).
260 These results confirm the existence of genetic variability in response to feed deprivation
261 (Grima et al., 2008) and highlight differences in the requirements for maintenance between

262 lines. Thermal growth coefficients estimated from the two FD periods were always highly
263 correlated with weight loss ($r \geq 0.96$, $P < 0.001$; Table 1) and were significantly different
264 between lines (TGC_{fd1} : $P < 0.001$, and TGC_{fd2} : $P = 0.001$; Table 2). The correlation between
265 TGC recorded during the two FD periods was low (TGC_{fd1} and TGC_{fd2} ; $r = 0.19$, $P = 0.326$;
266 Table 1 and Figure 3). For the first CG period, the TGC average values ranged from 3.18 to
267 3.94 and were similar between lines (TGC_{cg1} , $P = 0.121$; Table 2), while TGC values
268 estimated for the second CG period were ranging from 3.30 to 3.75 with a significant line
269 effect (TGC_{cg2} , $P = 0.007$; Table 2). In contrast, TGC recorded during the two CG periods
270 was moderately but significantly correlated (TGC_{cg1} and TGC_{cg2} ; $r = 0.39$, $P = 0.035$; Table
271 1). Overall, the lines that lost the least weight during the FD periods are those that gained the
272 most during the CG periods, with a significant negative correlation observed between TGC_{fd1}
273 and TGC_{cg1} ($r = -0.53$, $P = 0.003$; Table 1). These findings are in accordance with Dupont-
274 Prinnet et al. (2010) showing that there was a negative correlation between body weight losses
275 during FD and body weight gain during CG in European sea bass.

276 The differing level of response between the periods may also be the consequence of rapid fish
277 adaptation to a repeated cycle of feed deprivation and refeeding (Blake et al., 2006), with
278 modulation of their physiological responses as suggested by Grima et al. (2008).

279 3.2. Feed intake and feed efficiency measurements

280 The duration of the feed efficiency measurement period can affect the quality of the trait
281 measurement and the correlations with other measured performances. There are many
282 examples in terrestrial animals (e.g., Archer and Bergh, 2000; Wang et al., 2006). In fish,
283 mainly because of the difficulties inherent in measuring individual FI, most of the studies
284 focusing on correlations between traits limited the duration of individual FI measurement
285 periods between 7 to 21 days (e.g., Besson et al., 2019; de Verdal et al., 2018b; Grima et al.,
286 2008: 2010). Interestingly, Rodde et al. (2020) demonstrated that selecting Nile tilapia based

287 on a 2-weeks FCR measurement instead of a 6-month FCR was efficient to rank of the fish
288 suggesting that short FI measurement periods can be an efficient tool for FE selection in fish.

289 In our study, for each isogenic line, keeping fish in a group allowed us to record FI (see Table
290 2) from at least 29 consecutive days. This period exceeds the number of meals needed to
291 obtain a reliable mean value of FI in Nile tilapia (i.e. at least 11 out of 19 meals over a 10-day
292 period; de Verdal et al., 2018b) while maintaining social interactions between individuals for
293 each genotype. In this study, measurements of FI were performed either during the basal
294 growth period (fi_1) or in CG periods (fi_2 and fi_3). We observed that the increase in FI between
295 fi_1 and fi_2 was, overall, low and line dependent, while FI_{fi_3} was considerably higher in the ten
296 lines (Table 2). Most studies agree that compensatory growth in fishes is enabled by an
297 increase in FI, even if the pattern of FI differs between species (Wu et al., 2002). The
298 effective improvement of FE during compensatory growth is debatable. It was demonstrated
299 in rainbow trout (Nikki et al., 2004) and pikeperch *Sander lucioperca* (Mattila et al., 2009)
300 that compensatory growth was permitted by increasing FI but with no improvement of FE. In
301 contrast, Mambrini et al. (2004) in rainbow trout and Oh et al. (2007) in red sea bream *Pagrus*
302 *major* observed both an improvement of FE measured as the inverse of FCR and a rise of FI
303 during refeeding in fasted fish compared to control unfasted fish.

304 We found significant differences in FCR and RFI between lines only in fi_2 , while variability in
305 FCR and RFI remains high among the replicates of a given line (Table 2). Over the second FI
306 measurement period (i.e. fi_2), the line A22h was the most feed-efficient with values of FCR
307 and RFI of 0.79 ± 0.02 and -15.38 ± 4.15 , respectively, while A36h was the less feed-efficient
308 line with FCR of 0.96 ± 0.10 and RFI of 18.58 ± 19.00 (Table 2). Few studies investigated the
309 correlations between FCR and RFI in fish. Overall, we found high phenotypic correlations
310 between FCR and RFI measured over the same period, with a slightly lower correlation
311 during the first period (fi_1 ; $r = 0.79$, $P < 0.001$; Figure 3) and very high during the last two
312 measurement periods (fi_2 and fi_3 ; $r = 0.99$ and 0.97 , $P < 0.001$; Figure 3). These results are in

313 line with the literature on rainbow trout. Indeed, Kause et al. (2016) found strong positive
314 phenotypic correlations between FCR and RFI in fish older than two years. Based on the data
315 from Grima (2010) and Grima et al. (2008), we were able to recalculate a positive phenotypic
316 correlation between FCR and RFI in isogenic lines of rainbow trout with fish of comparable
317 size to the individuals used in our experiment. Using ten different isogenic lines, we
318 confirmed genetic-based variation of FE in rainbow trout, a requirement to implement
319 breeding programs. However, such variations are not consistent over time, presumably due to
320 the feeding practice. Indeed, while previous works argued that self-feeding minimises
321 competition for feed because feed is more accessible (Boujard et al., 2002; Mambrini et al.,
322 2004), the observed high variability in FCR and especially RFI between replicates of a given
323 isogenic line suggested that social interactions can strongly affect FE even when fish are fed
324 using self-feeders. Indeed, within the same rearing unit, FI is not necessarily homogeneous
325 among fish, and this can be exacerbated using self-feeders where a few high-triggering fish
326 can drive group feeding behaviour, as shown in European sea bass and such social
327 interactions can change over time (Millot and Bégout, 2009).

328 Overall, the correlations between the three FCR and the three RFI values derived from the
329 three FI periods were, as shown in Figure 3, low between FCR_{fi1} , RFI_{fi1} and the two other
330 measurements (FCR_{fi2} and FCR_{fi3} : $r = 0.11$ and 0.12 , $P \geq 0.450$; RFI_{fi2} and RFI_{fi3} : $r = 0.14$, P
331 ≥ 0.468). Interestingly, the correlations were significant only between the last two FCR and
332 the last two RFI measured during CG periods ($r = 0.53$ and 0.55 , $P \leq 0.003$). Such
333 inconsistency over time can be explained by: (1) the difference in age of the fish and/or (2)
334 the fact that the two last FI measurement periods occurred after feed deprivation in large fish
335 (≥ 350 g) while the first FI period was done during a basal growth period in smaller fish (\leq
336 200 g). Here, the phenotypic correlations established between the FCR and RFI measured at
337 three different periods indicate that these traits are reliable for phenotyping FE but may
338 require repeated measurements. These results suggest that our measurement methodology,

339 allowing FI recording over several consecutive weeks, exhibits relatively high repeatability.
340 Nevertheless, although of high experimental interest, the acquisition of individual FI value for
341 each genotype from fish kept in groups is conditioned by the use of isogenic lines and,
342 therefore, this method is not directly applicable in a breeding program.

343 3.3. Correlations between feed efficiency and weight variations

344 We did not find significant phenotypic correlations between TGC recorded in basal growth
345 periods (TGC_{bg1} and TGC_{bg2}) and FE traits (FCR and RFI) (Figure 3). In livestock species, FE
346 is generally correlated with growth, but this is still debatable in fish. In rainbow trout, while
347 Silverstein (2006) estimated negative phenotypic correlations between TGC and RFI ($r = -$
348 0.57 to -0.31), Kause et al. (2016) found no phenotypic correlations between daily weight
349 gain (DWG) and RFI ($r = 0.08$). Interestingly, strong genetic correlations have been
350 highlighted between DWG and FCR ($r = -0.63 \pm 0.30$; Kause et al., 2016) and between BW
351 and inverse of FCR ($r = 0.63-0.99$; Henryon et al., 2002). Nevertheless, no significant genetic
352 correlations have been found between DWG and RFI (Kause et al., 2016).

353 In practice, fish breeders expect to improve FE by selecting the fastest growing fish,
354 hypothesising that faster-growing fish will be more efficient (Besson et al., 2020; Kause et al.,
355 2016; Knap and Kause, 2018). Still, few selection response studies have investigated the
356 correlated response in FE to selection for growth and provided contrasting results. Recently,
357 Vandeputte et al. (2022) estimated realised genetic gains on FCR and other traits in a
358 commercial population of rainbow trout selected for improved growth, carcass yield and fillet
359 fat over ten generations. The authors demonstrated significant improvement in FCR even if
360 the trait was not directly included in the breeding goal.

361 We based our study on previous works showing that performance traits (i.e. weight variations)
362 during successive FD periods can be correlated to FE in fish (e.g. Grima et al., 2010; Li et al.,
363 2005). In our experiment, an assessment of the relationship between FE traits (FCR and RFI)

364 calculated over the three FI measurement periods and growth-related traits (TGC) revealed no
365 significant correlation. In particular, the correlations between RFI during the basal growth
366 period (i.e. RFI_{fi1}) and TGC_{fd1} or TGC_{fd2} were very low ($r = 0.08$ and $r = -0.14$, respectively;
367 Figure 3). The only exception was the significant negative correlations between TGC_{fd2} and
368 FCR_{fi2} or RFI_{fi2} with respective $r = -0.49$ and -0.47 ($P \leq 0.006$) (Figure 3). These results
369 suggest that the fish that had lost the least weight during the second phase of FD were the
370 most feed efficient during the previous CG period (fi_2). Using weight loss during FD periods
371 as an indirect criterion to select FE required that it is genetically correlated to RFI, the most
372 interesting FE trait in selection (see Section 2.4.2). Here, we found limited phenotypic
373 correlations between the TGC measured during FD periods (TGC_{fd1} or TGC_{fd2}) and RFI
374 measured either during basal growth (RFI_{fi1} : $r \leq 0.08$, $P \geq 0.471$) or during the second CG
375 period (RFI_{fi3} : $r \leq 0.18$ $P \geq 0.184$) (Figure 3), raising questions about the interest of such a
376 criterion to evaluate FE in rainbow trout. Indeed, based on our estimates of phenotypic
377 correlations, we can reasonably assume that the genetic correlations between these traits are
378 probably weak. Nevertheless, in Nile tilapia, although de Verdal et al. (2018b) found a weak
379 phenotypic correlation between RFI and TGC during the FD period ($r = 0.09$), the genetic
380 correlation was high ($r = 0.70$), indicating that TGC during FD period could be a promising
381 selection criterion for FE in this species. Such a relationship needs to be confirmed in rainbow
382 trout, and based on current knowledge, there is no strong evidence of the interest in using
383 such an indirect selection criterion for FE in rainbow trout.

384 3.4. Feeding behaviour and its link with FE

385 One of the originalities of this work was the assessment of the relationship between FE traits
386 (FCR and RFI) and feeding behaviour assessed by the number of feed demands over a given
387 period and the proportion of the demands made before noon. The daily profile of feeding
388 behaviour during the three FI measurement periods is presented in Figure 4A; more details on
389 the number of total feed demands per hour per line over the three FI measurement periods are

390 available in the Supplementary Material (Figure A1). Over the three periods, feeding
391 behaviour changed over the hours ($P < 0.001$). Nocturnal demands were only occasional, as
392 expected, because demands were rewarded only during the daylight hours. Even if limited re-
393 rankings were observed between lines, the daily feed demand profiles remained similar
394 between fi_1 and fi_2 , with, on average, 37-72% and 56-80% of the feed demands occurring in
395 the morning. The morning feeding activity of fish is even more pronounced in fi_3 , with 76-
396 90% of demands recorded before noon (Figure 4A). There is limited information on how
397 these seasonal or circannual rhythms influence feeding behaviour in fish, making it complex
398 to give a straightforward conclusion about feeding activities and associated seasonal changes
399 (Assan et al., 2021). Nevertheless, we can reasonably assume that the seasonal difference
400 between the fi periods (autumn for fi_1 and spring-summer for fi_2 and fi_3) may, at least
401 partially, explain the changes observed in the daily feeding profile (Figure A1).

402 Significant differences in the daily profile of feed demands among the ten isogenic lines were
403 found for the first FI measurement periods (fi_1 and fi_2 ; $P \leq 0.001$). Significant interactions
404 between lines and time of the day were found ($P \leq 0.001$), suggesting that the effects of time
405 of day were line-dependent. In fi_3 , daily feeding activity remained similar between lines ($P =$
406 0.421), while the number of feed demands per day remained constant between lines ($P =$
407 0.227, Figure 4B). Mambrini et al. (2004) highlighted, in brown trout, that a line selected for
408 growth over five generations exhibited a more important morning feeding activity than the
409 control line, maintained under the same rearing conditions, even if the variations in feeding
410 activity between lines were not constant over time. Here, we did not find significant
411 correlations between the proportion of the feed demand occurring in the morning and the
412 TGC (Figure 3), suggesting that growth performances in isogenic lines are not related to the
413 feeding profile of the fish.

414 In our study, the daily distribution of feed demands and their number were recorded as
415 phenotypes for feeding behaviour. Indeed, the self-feeders allow continuous recording of feed

416 demands (rewarded or not, as described in Section 2.4.2) without disturbing the behaviour of
417 the fish group in the tank. Interestingly, we found significant positive correlations between
418 RFI calculated from the first feed intake measurement period (RFI_{fi1}) and feeding behaviour,
419 assessed as the number of feed demands (*i.e.* rewarded, unrewarded and both of them) over
420 the same period ($r = 0.42-0.49$, $P \leq 0.022$; Figure 3). It is interesting to note that the fact that
421 the requests are rewarded or not has no influence on the correlations with the RFI. While the
422 number of rewarded demands reflects FI, this is, by definition, not the case for unrewarded
423 demands. Thus, we can hypothesise that this latter phenotype better reflects the motivation of
424 fish for food (*i.e.* appetite). In other words, in the described rearing conditions, the most feed
425 efficient isogenic lines (lower FCR and RFI) were the ones that requested less feed via the
426 self-feeders and presumably had less appetite. In fi_3 , we found significant negative
427 correlations between FCR or RFI and the proportion of the feed demands done in the morning
428 ($r = -0.41$ and -0.38 , $P \leq 0.038$; Figure 3), meaning that the most efficient fish had a higher
429 feeding activity in the morning.

430 The assessment of feeding behaviour in fish is done through various criteria (*e.g.*, number of
431 feed demands, feeding latency, feeding consistency and total feeding time), making
432 comparisons between studies difficult. Nevertheless, our results are in accordance with
433 previous results in African catfish (Martins et al., 2006) and Nile tilapia (Martins et al.,
434 2011a) that found significant positive phenotypic correlations between feeding behaviour
435 (measured as feeding latency, feeding time and the number of feeding acts) and RFI while
436 they did not find significant correlations with FCR. In another study in Nile tilapia, Martins et
437 al. (2011b) found that the correlations between feeding behaviour, measured using the same
438 traits as described above, and RFI depends on the age of the fish. Mas-Muñoz et al. (2011)
439 also highlighted that consistency in feeding activity might be related to FE in common sole
440 *Solea solea*. They found that fish which feed more consistently over time (within the day and
441 over days) showed higher FI and growth but tend to be less feed efficient.

442 Overall, the feeding behaviour differences we observed between isogenic lines highlight the
443 interest to look at the genetic basis of fish feeding behaviour. There is growing evidence of a
444 relationship between FE traits, especially RFI, and feeding behaviour traits in fish, and this
445 study confirms such relationships in rainbow trout while highlighting the need for repeated
446 measurements over time. Therefore, special attention should be paid to feeding behaviour that
447 may be of interest in breeding programs for fish.

448 To conclude, we highlighted, using repeated measurements of FE traits (FCR and RFI), that
449 the growth performances observed during FD periods are not easily linked to variations in FE
450 measured in rainbow trout, suggesting that such indirect criteria for FE are not appropriate in
451 selection. Interestingly, we highlighted some relationships between FE and feeding behaviour
452 (*i.e.* number of feed demands over a period and the proportion of the demands made before
453 noon) while the use of isogenic lines demonstrated the genetic basis of feeding behaviour.
454 Overall, these results support the interest in exploring phenotypes of feeding behaviour as
455 potential proxies of FE for improving RFI in rainbow trout through selective breeding.

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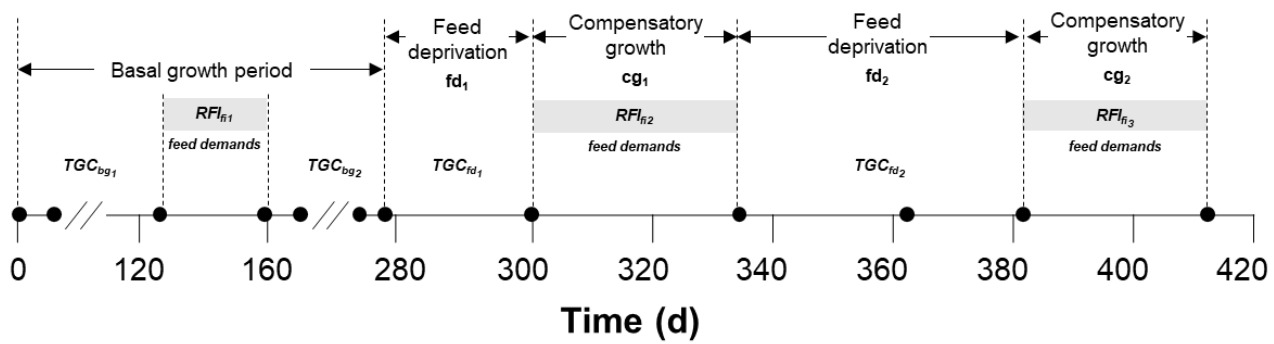
693 **Captions to Figures**

694 Figure 1. Schematic outline and time frame of the experiment performed using ten rainbow
695 trout isogenic lines. All the different experimental periods are indicated: basal growth periods
696 (bg_1 and bg_2), feed deprivations periods (fd_1 and fd_2) and compensatory growth periods (cg_1
697 and cg_2) and the different traits recorded as well: Thermal Growth Coefficients (TGC),
698 Residual Feed Intake (RFI) and feed demands.

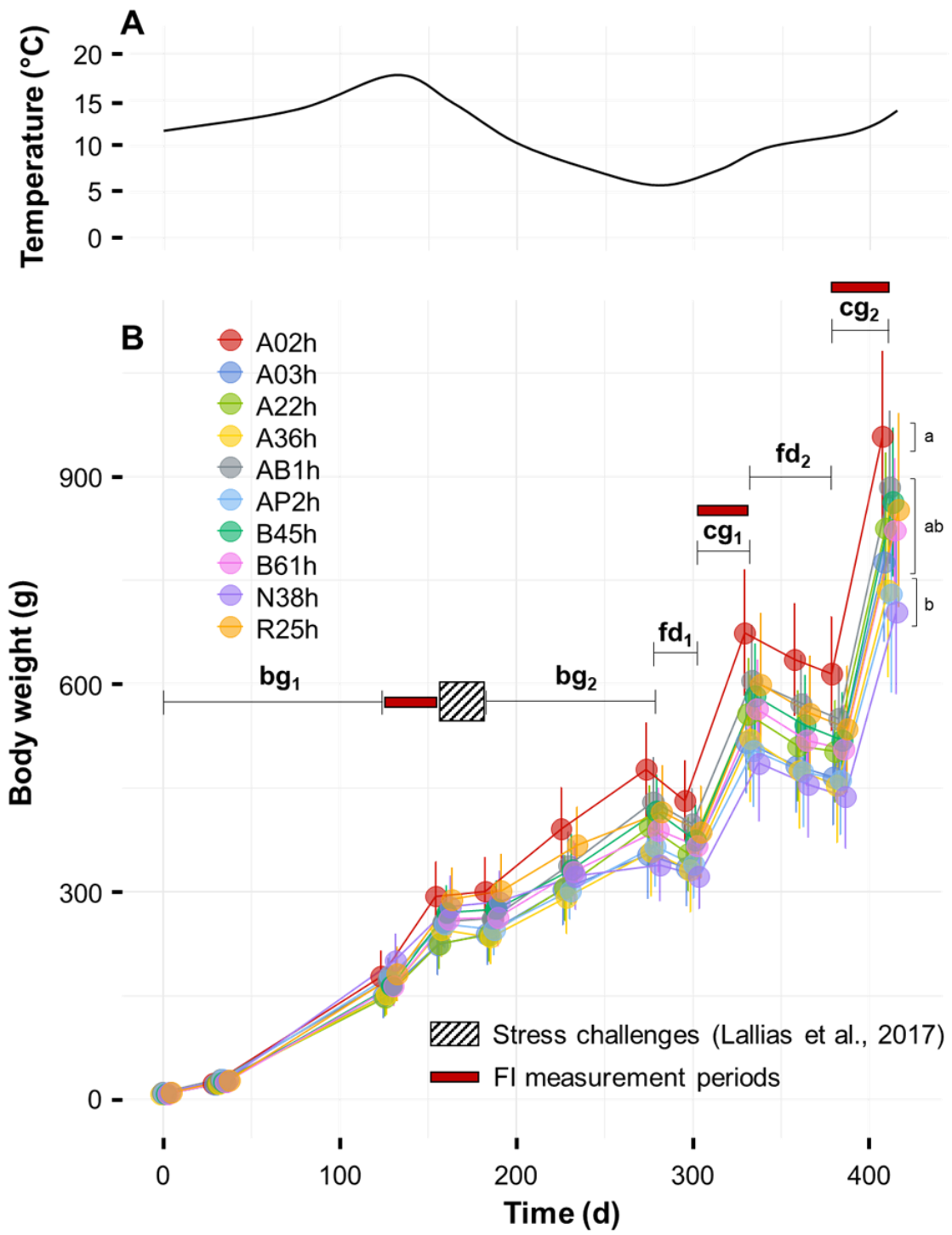
699 Figure 2. Temperature profile (A) and growth kinetics of the ten isogenic lines (B) over the
700 experiment. Values are Means \pm SD ($n = 3$). The different experimental periods are indicated
701 in black: basal growth periods (bg_1 and bg_2), FD periods (fd_1 and fd_2) and CG periods (cg_1
702 and cg_2). Letters denote significant differences in final weights between lines.

703 Figure 3. Correlation coefficients of all the measured phenotypes related to (1) Feed
704 efficiency (FCR and RFI) and feed intake (FI) estimated during the three feed intake
705 measurements periods (fi); (2) Weight assessed as TGC over all the experimental periods (bg ,
706 fd and cg); and 3) Feed demands over the three feed intake measurements periods considering
707 all the demands ("Demands"), the unrewarded demands ("Demands_U"), the rewarded
708 demands ("Demands_R") or the proportion of the demands made before noon
709 ("Morning_%"). The size and the colour gradient of the squares denote the intensity of the
710 correlations. Significant correlations ($p < 0.05$) are highlighted in red.

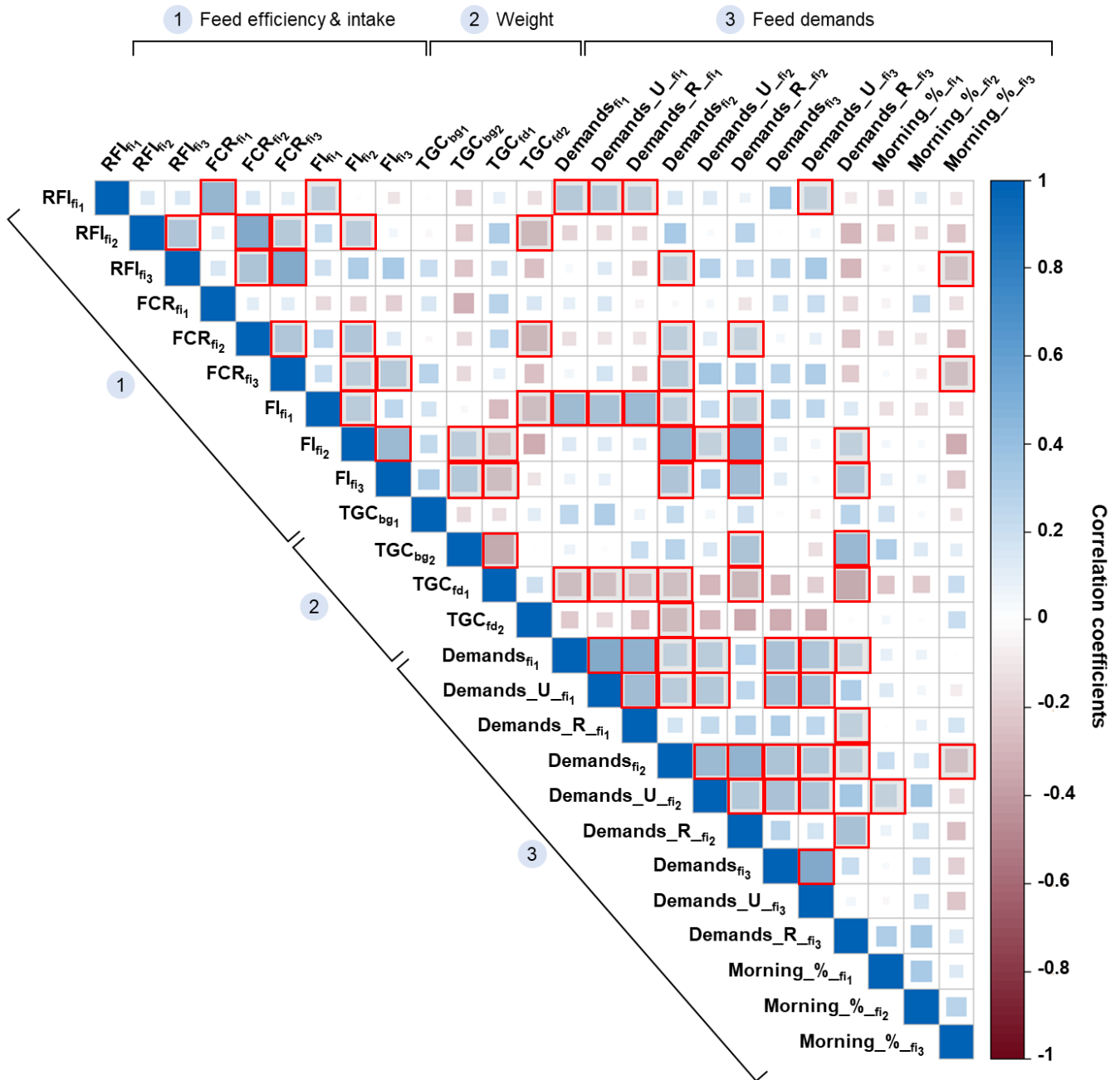
711 Figure 4. (A) Feeding behaviour expressed as the cumulative feed demands ($\% h^{-1}$) in the ten
712 isogenic lines fed using self-feeders: from d 129 to d 161 (fi_1), from d 301 to d 335 (fi_2) and
713 from d 388 to d 415 (fi_3). In order to facilitate reading, values are the means of three replicates
714 and SD were not represented. (B) Daily demands of the ten isogenic lines over fi_1 , fi_2 and fi_3
715 periods. Letters denote significant differences in daily feed demands between lines.



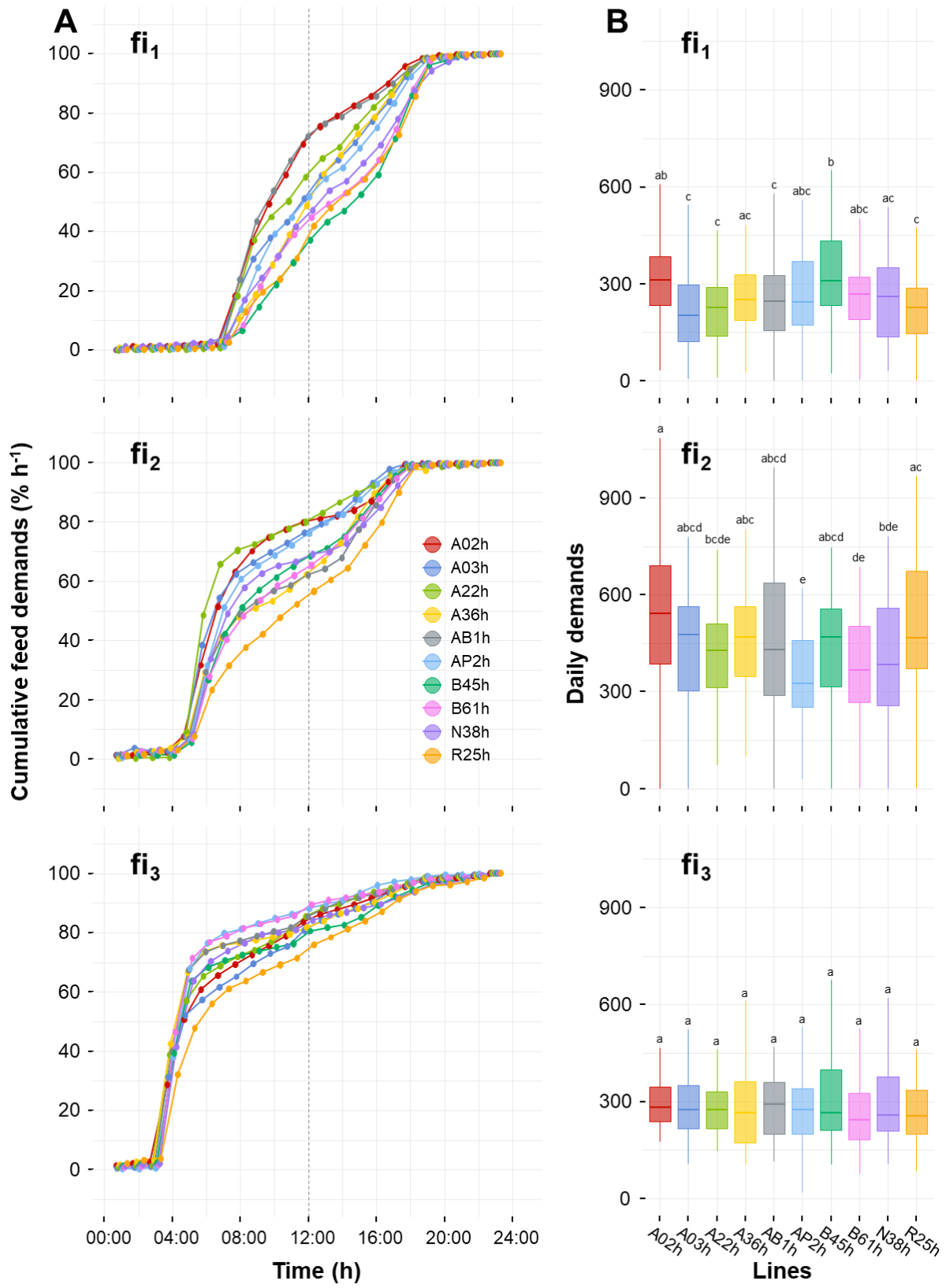
716 Figure 1



717 Figure 2



718 Figure 3



719 Figure 4

720 Table 1. Correlations between body weight variations (BWG; %) over FD periods (fd₁ and
 721 fd₂) and CG periods (cg₁ and cg₂) and Thermal Growth Coefficients (TGC) calculated for the
 722 same experimental periods. Significant correlations are highlighted in bold.

	BWG _{fd1}	TGC _{fd1}	BWG _{cg1}	TGC _{cg1}	BWG _{fd2}	TGC _{fd2}	BWG _{cg2}	TGC _{cg2}
BWG _{fd1}		-	-	-	-	-	-	-
TGC _{fd1}	0.99		-	-	-	-	-	-
BWG _{cg1}	-0.38	-0.37		-	-	-	-	-
TGC _{cg1}	-0.49	-0.53	0.90		-	-	-	-
BWG _{fd2}	0.09	0.05	-0.15	-0.02		-	-	-
TGC _{fd2}	0.20	0.19	-0.23	-0.21	0.96		-	-
BWG _{cg2}	-0.02	0.04	0.16	-0.04	-0.23	-0.14		-
TGC _{cg2}	-0.27	-0.28	0.34	0.39	-0.04	-0.12	0.80	

723

724 Table 2. Thermal growth coefficient (TGC) in 10 rainbow trout isogenic lines during two basal growth periods (bg₁ and bg₂), followed by two
725 periods of FD (fd₁ and fd₂) alternated with two periods of CG (cg₁ and cg₂); Feed intake, FCR and RFI calculated from the three feed intake
726 measurement periods (fi₁, fi₂ and fi₃). Values are Means ± SD. Letters denote significant differences (p < 0.05).

Traits	Isogenic lines									
	A02h	A03h	A22h	A36h	AB1h	AP2h	B45h	B61h	N38h	R25h
Thermal growth coefficients (TGC)										
bg ₁	2.00 ± 0.10 ^a	1.81 ± 0.16 ^a	1.80 ± 0.04 ^a	1.80 ± 0.03 ^a	1.87 ± 0.11 ^a	1.94 ± 0.15 ^a	1.88 ± 0.06 ^a	1.89 ± 0.11 ^a	1.99 ± 0.11 ^a	1.91 ± 0.08 ^a
bg ₂	1.95 ± 0.07 ^a	1.54 ± 0.10 ^{bc}	2.01 ± 0.35 ^{ab}	1.65 ± 0.26 ^{abc}	2.04 ± 0.15 ^a	1.58 ± 0.23 ^{abc}	1.71 ± 0.12 ^{abc}	1.61 ± 0.10 ^{abc}	0.67 ± 0.22 ^c	1.33 ± 0.28 ^c
fd ₁	-1.49 ± 0.07 ^{ab}	-0.87 ± 0.09 ^c	-1.58 ± 0.38 ^{ab}	-1.15 ± 0.35 ^{abc}	-1.17 ± 0.16 ^{abc}	-1.15 ± 0.26 ^{abc}	-1.62 ± 0.22 ^a	-0.97 ± 0.26 ^{bc}	-0.72 ± 0.23 ^c	-1.09 ± 0.10 ^{abc}
cg ₁	3.94 ± 0.22 ^a	3.52 ± 0.29 ^a	3.73 ± 0.20 ^a	3.66 ± 0.06 ^a	3.58 ± 0.03 ^a	3.18 ± 0.48 ^a	3.73 ± 0.31 ^a	3.61 ± 0.11 ^a	3.25 ± 0.52 ^a	3.73 ± 0.17 ^a
fd ₂	-0.49 ± 0.03 ^{ab}	-0.51 ± 0.02 ^{ab}	-0.51 ± 0.01 ^{ab}	-0.68 ± 0.15 ^a	-0.50 ± 0.08 ^{ab}	-0.44 ± 0.03 ^b	-0.59 ± 0.02 ^a	-0.55 ± 0.05 ^{ab}	-0.50 ± 0.01 ^{ab}	-0.58 ± 0.05 ^a
cg ₂	3.52 ± 0.07 ^{ab}	3.75 ± 0.15 ^a	3.72 ± 0.17 ^{ab}	3.50 ± 0.09 ^{ab}	3.66 ± 0.10 ^{ab}	3.30 ± 0.49 ^{ab}	3.86 ± 0.23 ^a	3.64 ± 0.09 ^{ab}	3.40 ± 0.09 ^b	3.53 ± 0.07 ^{ab}
Feed intake (g kg ⁻¹ d ⁻¹)										
fi ₁	14.4 ± 0.81 ^{ab}	13.5 ± 2.39 ^{ab}	12.1 ± 2.11 ^{ab}	15.5 ± 1.15 ^{ab}	11.7 ± 2.78 ^{ab}	11.8 ± 1.94 ^{ab}	16.3 ± 1.73 ^a	15.0 ± 0.50 ^{ab}	10.2 ± 1.63 ^b	14.0 ± 0.84 ^{ab}
fi ₂	14.6 ± 0.96 ^a	14.9 ± 1.74 ^a	13.6 ± 0.64 ^a	16.6 ± 0.82 ^a	13.3 ± 0.54 ^a	12.3 ± 1.94 ^a	14.1 ± 1.41 ^a	13.5 ± 0.31 ^a	13.4 ± 3.12 ^a	15.8 ± 0.95 ^a
fi ₃	20.5 ± 0.80 ^a	24.6 ± 1.55 ^a	22.7 ± 2.07 ^a	23.9 ± 1.66 ^a	21.8 ± 0.95 ^a	20.7 ± 4.37 ^a	23.6 ± 1.81 ^a	22.6 ± 1.75 ^a	22.7 ± 0.71 ^a	22.4 ± 0.90 ^a
Feed conversion ratio (FCR)										
fi ₁	0.78 ± 0.05 ^a	0.94 ± 0.06 ^a	0.79 ± 0.01 ^a	0.83 ± 0.06 ^a	0.82 ± 0.08 ^a	0.90 ± 0.05 ^a	0.83 ± 0.08 ^a	0.82 ± 0.05 ^a	0.88 ± 0.08 ^a	0.81 ± 0.02 ^a
fi ₂	0.86 ± 0.02 ^{abc}	0.90 ± 0.02 ^{ab}	0.79 ± 0.02 ^c	0.96 ± 0.10 ^{ab}	0.84 ± 0.03 ^{abc}	0.84 ± 0.03 ^{abc}	0.83 ± 0.02 ^{abc}	0.82 ± 0.03 ^{abc}	0.87 ± 0.07 ^{abc}	0.94 ± 0.03 ^b
fi ₃	0.95 ± 0.02 ^a	0.95 ± 0.03 ^a	0.91 ± 0.02 ^a	0.99 ± 0.02 ^a	0.93 ± 0.03 ^a	0.92 ± 0.10 ^a	0.93 ± 0.04 ^a	0.94 ± 0.05 ^a	0.96 ± 0.04 ^a	0.99 ± 0.01 ^a
Residual feed intake (RFI)										
fi ₁	-2.85 ± 4.02 ^a	4.18 ± 0.27 ^a	-4.92 ± 2.50 ^a	1.53 ± 5.02 ^a	-2.97 ± 5.08 ^a	2.09 ± 3.45 ^a	3.47 ± 8.08 ^a	0.78 ± 4.36 ^a	-0.58 ± 3.83 ^a	-0.72 ± 1.80 ^a
fi ₂	-3.41 ± 4.74 ^{abcd}	5.73 ± 3.76 ^{abc}	-15.38 ± 4.15 ^d	18.58 ± 19.00 ^{ac}	-4.74 ± 5.81 ^{abcd}	-2.57 ± 4.03 ^{abcd}	-7.05 ± 3.34 ^{abd}	-9.49 ± 5.82 ^{bd}	1.78 ± 11.12 ^{abcd}	16.56 ± 8.07 ^c
fi ₃	-0.90 ± 5.30 ^a	2.49 ± 8.45 ^a	-10.39 ± 5.96 ^a	13.29 ± 5.65 ^a	-6.57 ± 9.88 ^a	-3.17 ± 21.89 ^a	-6.91 ± 11.63 ^a	-3.26 ± 15.71 ^a	4.70 ± 9.75 ^a	10.73 ± 3.03 ^a