

1 **Improving feed efficiency in fish by selective breeding: a review**

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3 Runing title: Improving feed efficiency in fish by selection

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5 Hugues de Verdal<sup>ab\*</sup>, Hans Komen<sup>c</sup>, Edwige Quillet<sup>d</sup>, Béatrice Chatain<sup>e</sup>, François Allal<sup>e</sup>,  
6 John A.H. Benzie<sup>bf</sup>, Marc Vandeputte<sup>de</sup>

7  
8 <sup>a</sup>CIRAD, UMR116 ISEM, TA B-116/16, 73 rue Jean-François Breton - 34398 Montpellier  
9 Cedex 5, France

10 <sup>b</sup>Worldfish, Jalan Batu Maung, Bayan Lepas, 11960, Penang, Malaysia

11 <sup>c</sup>Animal Breeding and Genomics Centre, Wageningen University, P.O. Box 338, 6700 AH  
12 Wageningen, The Netherlands

13 <sup>d</sup>GABI, INRA, AgroParisTech, Université Paris-Saclay, F-78350 Jouy-en-Josas, France

14 <sup>e</sup>Ifremer, Chemin de Maguelone, F-34250 Palavas-les-Flots, France

15 <sup>f</sup>School of Biological Earth and Environmental Sciences, University College Cork, Cork  
16 Ireland.

17 \*Corresponding author

18 Email addresses:

19 HdV: [hugues.de\\_verdal@cirad.fr](mailto:hugues.de_verdal@cirad.fr) ; phone number: +60 4 6202 172

20 HK: [hans.komen@wur.nl](mailto:hans.komen@wur.nl)

21 EQ: [Edwige.Quillet@jouy.inra.fr](mailto:Edwige.Quillet@jouy.inra.fr)

22 BC: [Beatrice.Chatain@ifremer.fr](mailto:Beatrice.Chatain@ifremer.fr)

23 FA: [Francois.Allal@ifremer.fr](mailto:Francois.Allal@ifremer.fr)

24 JB: [j.benzie@cgiar.org](mailto:j.benzie@cgiar.org)

25 MV: [Marc.Vandeputte@jouy.inra.fr](mailto:Marc.Vandeputte@jouy.inra.fr)

26

27 ABSTRACT

28 Improving feed efficiency (FE) is key to reducing production costs in aquaculture and to  
29 achieving sustainability for the aquaculture industry. Feed costs account for 30 to 70 % of  
30 total production costs in aquaculture much work has been done on nutritional and husbandry  
31 approaches to improve FE but only a limited amount of research has been devoted to using  
32 genetics, despite its potential. This paper reviews past work to improve FE in fish by selective  
33 breeding and assess future directions. Direct selection on FE traits requires methods to  
34 measure individual feed consumption and estimate FE efficiently and accurately. This is  
35 particularly difficult to do in fish because of the environment in which they live. Many of the  
36 published studies on FE were found to be inaccurate because of methodological problems.  
37 The relatively low heritability estimates of FE traits in fish published to date are probably  
38 partly as a result of inaccurate measurements of feed intake. Improving ways to measure the  
39 individual feed intake with high accuracy will be critical to the successful application of  
40 genetics to improving FE. Indirect selection criteria that could be used to improve FE  
41 (including growth after starvation/refeeding, body composition, neuropeptides or hormone  
42 levels) are discussed.

43 Promising approaches to measuring feed intake accurately that may enable these studies to be  
44 undertaken are identified. More work using these will be needed prior to assessing the  
45 practicality of the introduction of direct or indirect traits for FE in fish genetic improvement  
46 programs.

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48 Keywords: feed efficiency, genetics, selection, feed conversion ratio, feed intake, fish

49

## 50 **1. Introduction**

51 With an increasing world population predicted to attain 9.6 billion in 2050, the sustainable  
52 increase of food supply, and more specifically animal protein production, is a key challenge.  
53 Animals not only need to become more productive but, more importantly, they also need to  
54 become more efficient. Farmed fish species offer an opportunity in that regard. Compared to  
55 farmed terrestrial species, farmed fish are more efficient in converting feed to biomass (Table  
56 1) using feed amount as the reference. Feed compositions differ significantly amongst  
57 different animals; in terms of protein rates, fish diets contain around 35% protein compared to  
58 around 18-20 % in pigs or chickens.

59 Total fish harvested has grown 2.87 % per year since 1950, essentially through increased  
60 farmed fish production (1.93 % per year; Earth Policy Institute 2013). In 2014, global  
61 aquaculture production (excluding algae and plants) was estimated at 74 million tons, roughly  
62 similar to the global production of beef cattle. At the same time, farmed fish species consume  
63 around six times less feed than beef cattle to produce the same volume of body mass (Table  
64 1). Despite the higher efficiency compared to livestock species, the cost of feed - ranging  
65 from 30 to 70% of the total production costs - is the primary expenditure of intensive fish  
66 farming systems (Doupé and Limbery 2004; Kolstad *et al.* 2004). Improving feed efficiency  
67 (FE) is therefore key to reducing production costs. In salmon for example, a 2 - 5 %  
68 improvement in FE would save 42.9 - 107 million USD feed costs per year, respectively  
69 (following Table 1 and with a feed price of 1.35 USD.kg<sup>-1</sup>).

70 Improving FE would also have a positive effect on the environmental impact of fish farming.  
71 Whatever the species, a FE improvement will result in a reduction of emissions (Pym 1990;  
72 Pinares-Patino *et al.* 2003; Zhang and Aggrey 2003; Hill and Azain 2009; de Verdal *et al.*  
73 2011a, Besson *et al.* 2016). For example, Bouvarel *et al.* (2006) showed that a 4.8%

74 improvement of FE in broiler chicken reduced nitrogen and phosphorus excretions by 9 and  
75 14%, respectively. In aquaculture production, several life cycle assessment (LCA) studies  
76 (Aubin *et al.* 2009; Samuel-Fitwi *et al.* 2012; Mungkung *et al.* 2013) have investigated the  
77 major environmental impacts of improving FE. These studies showed that improving FE will  
78 have less negative impact on eutrophication, acidification, climate change and energy demand  
79 per ton of fish produced, mainly as a results of reduced nitrogen excretion of fish (Aubin *et al.*  
80 2009; Besson *et al.* 2016).

81 In terrestrial species, selective breeding has played an important role in improving feed  
82 efficiency (Table 2). Since 1960 feed efficiency has increased by ~20 to 30% (broilers, laying  
83 hens and pigs respectively). Most of this gain is due to selection, next to improved  
84 management practices and feed formulation. Several studies have estimated genetic  
85 parameters for FE traits in livestock (reviewed by Hoque and Suzuki 2009; Grima 2010;  
86 Willems *et al.* 2013) and found moderate to high heritabilities, ranging from 0.12 to 0.67.  
87 However, direct selection for feed efficiency remains difficult, as it requires the precise  
88 recording of individual feed intake. In terrestrial livestock, it is widely recognized that much  
89 of the historical gain on FE has been obtained indirectly through selection for growth rate  
90 (Emmerson, 1997).

91 In fish, measuring FE implies measuring feed intake, which is highly complex since fish are  
92 generally reared in water and in large groups. In such conditions, it is impossible to measure  
93 individual feed consumption and collect uneaten food. Furthermore, according to the species,  
94 social interactions between fish may modify FE (see section 3), which could lead to large  
95 differences between measurements performed on isolated fish and measurements obtained in  
96 group rearing conditions. As a consequence, most past efforts aimed at improving FE in  
97 aquaculture have focused on feed formulation (Reigh and Ellis 1992; Nematipour and Gatlin  
98 III 1993; Elangovan and Shim 2000; Gaylor and Gatlin III 2001; Lin *et al.* 2008; Tacchi *et al.*

99 2011; Guroy *et al.* 2013; Yao *et al.* 2014) and/or husbandry (Alanära 1996; Bendiksen *et al.*  
100 2003; Imsland *et al.* 2005; Li *et al.* 2008; Magnussen *et al.* 2008; Yilmaz and Arabaci 2010;  
101 Arbelaez-Rojas *et al.* 2011; Zhao *et al.* 2013). These studies have shown strong effects of  
102 nutrition, diet and husbandry on FE. In contrast, little work has been done on genetics. Any  
103 genetic selection approach would need, of course, to pay specific attention to the feeds used  
104 and the age/size of the fish as key aspects of the environment / selection subject that could  
105 influence the genetic outcome.

106 The objective of the present paper is therefore to review the possibilities to improve FE in fish  
107 by selective breeding. In the first part, we will explore the concept of FE and how it can be  
108 measured. In the second part, we review the different ways to measure feed intake in fish,  
109 while in the third part, we focus on the possibilities to directly select for feed intake or FE.  
110 Finally, in the last part, we outline various possibilities to use indirect selection criteria to  
111 improve FE, based on growth and bio-energetics models.

112

## 113 **2. What is feed efficiency and what are the parameters used to measure it?**

114 Improving feed efficiency means reducing feed consumption per kg of fish produced, or  
115 increasing fish production from the same amount of feed. It is important to note that FE will  
116 vary from one species to another, with rearing environment (i.e. temperature, salinity, pH and  
117 feed composition, Árnasson *et al.* 2009) and the developmental stage of the fish (Henryon *et*  
118 *al.* 2002; Árnasson *et al.* 2009). One major aspect determining FE is the level of feed intake  
119 (FI): FE tends to improve up to an optimum when FI increases, and then decreases until  
120 maximum FI is reached (Jobling, 1994). If for some reason FI is less than optimal, increasing  
121 FI will increase FE. Conversely, if FI is higher than the optimum, increasing FI will decrease  
122 FE.

123 A second major point is the relation of FE to fish size, with smaller fish generally having a  
124 better FE than larger fish (Andersen and Riis-Vestergaard, 2003). FE is related to metabolic  
125 rate which is function of fish size. To correct for size differences, weights are scaled to  
126 metabolic weights ( $\text{kg}^{0.8}$ , Clarke and Johnstone, 1999; Jobling, 2002). While improving FE is  
127 the general objective, we need to define ways to measure it. The most used measure of FE is  
128 the ratio of FI to body weight gain (BWG), and is named feed conversion ratio (FCR).  
129 However, its inverse (feed efficiency ratio,  $\text{FER} = \text{BWG} \cdot \text{FI}^{-1}$ ) measures the same trait.  
130 Improving feed efficiency thus means reducing FCR or increasing FER. In these two  
131 measurements of FE, the part of FI allocated for body maintenance is not distinguished from  
132 the part of FI dedicated to growth (Willems *et al.* 2013). Another way to measure FE is thus  
133 to estimate the residual feed intake (RFI).

134 The equation for calculating RFI in a phenotypic approach is given as:

$$135 \quad FI = \beta_0 + \beta_1 * MBW + \beta_2 * BWG + RFI$$

136 with *FI* being the feed intake,  $\beta_0$  the regression intercept,  $\beta_1$  the partial regression coefficient  
137 of animal's FI on metabolic body weight, *MBW* the average metabolic body weight during  
138 the experiment,  $\beta_2$  the partial regression coefficient of animal's FI on body weight gain, *BWG*  
139 the body weight gain, and RFI the residual error of the model. This model allocates the feed  
140 intake according to expected maintenance and growth requirements, the remaining part being  
141 defined as the residual feed intake.

142 RFI is phenotypically independent from growth rate (Koch *et al.* 1963; Kennedy *et al.* 1993;  
143 Doupé and Limbery 2004; Crew Jr. 2005), which is not the case for FCR or FER ratios  
144 (Arthur *et al.* 2001; Martins *et al.* 2011). Used for the first time by Koch *et al.* (1963) on beef  
145 cattle, RFI is defined as the difference between feed consumed by an animal and its predicted  
146 consumption estimated by a regression model taking into account the feed requirements for

147 maintenance and growth as independent variables (Kennedy *et al.* 1993; Doupé and Limbery  
148 2003; Martins *et al.* 2011). Individuals with positive RFI consume more than the average  
149 whereas animals with negative RFI consume less, suggesting the latter are more efficient. RFI  
150 has been widely investigated in terrestrial animals (i.e. pigs, cattle, hens, chicken), and genetic  
151 parameter estimates are generally moderate to high with heritabilities ranging from 0.10 to  
152 0.47 (Johnson *et al.* 1999; Arthur *et al.* 2001; Gilbert *et al.* 2007; de Verdal *et al.* 2011b; Do  
153 *et al.* 2013; Wolc *et al.* 2013).

154 The main issue about RFI estimation is the difficulty of modeling it in the correct parameters.  
155 A lot of different models could be implemented depending on whether nutritional  
156 composition of the feed, coefficient of digestive utilization of metabolizable energy, protein,  
157 lipid or starch, or body composition of the fish is considered. Equations developed on  
158 livestock species, where selection schemes had already been developed using RFI, show that  
159 even more traits could be included (Luiting and Urff 1991; Arthur *et al.* 2001; Robinson and  
160 Oddy 2001; Hoque and Suzuki 2009; Willems *et al.* 2013). As an example, in laying hens, the  
161 RFI model takes into account the egg weight to correct RFI by the energy used to produce  
162 eggs (Luiting and Urff 1991). The same approach is used in dairy cattle for milk production  
163 (Kennedy *et al.* 1993; Connor *et al.* 2013). In this context, the model used is as follows:

$$164 \quad y = \beta_0 + \beta_1 * MBW + \beta_2 * BWG + \beta_3 * PW + RFI$$

165 with  $\beta_3$  being the partial regression coefficient of animal's FI on production weight and  $PW$   
166 the production weight (egg or milk production for example). This type of model could be  
167 interesting to use in fish, for example to correct for visceral and/or intramuscular lipid  
168 content.

169 An important question in terms of selective breeding for feed efficiency is the choice of the  
170 trait(s) to include in the index. As FCR and FER are ratios, they are genetically correlated

171 with the two terms of the ratio, BWG and FI, and so genetic change of FCR or FER cannot be  
172 simply related to underlying genetic variation for growth, feed consumption, or both (Turner  
173 1959; Sutherland 1965). As a consequence, selecting directly on FCR or FER will lead to  
174 poor selection response (Gunsett 1984; Lin 1980) and does not enable an accurate prediction  
175 of genetic gain (Gunsett 1987). However, linear indexes combining body weight gain and FI  
176 can be designed which have optimal properties in terms of accuracy and achieved genetic gain  
177 (Turner 1959; Lin 1980; Gunsett 1984, 1987; Lin and Aggrey 2013). Alternatively, residual  
178 feed intake can also be used as the selection criterion, especially in multiple trait selection  
179 combining RFI and growth (Kennedy *et al.* 1993). When used in single trait models, RFI  
180 should be based on genotypic and not phenotypic regression of feed intake on production, to  
181 avoid a component linked to the genetic variation for one or more elements of production  
182 (Kennedy *et al.* 1993).

183 In any case, in order to develop a selective breeding program to improve feed efficiency  
184 characteristics, it is important to have individual data of the trait under selection. Whatever  
185 the trait used to calculate FE, the crucial issue is to measure both growth and FI. Whilst  
186 growth and growth rate are easily measurable, measuring FI of individual fish is much more  
187 challenging.

188

### 189 **3. How to measure FI for selective breeding in fish?**

190 The simplest way to measure FI in fish is to rear fish in a group and to calculate the FE of the  
191 group. Using separately reared full sib families, it is possible to estimate the genetic  
192 variability of the trait (Henryon *et al.* 2002) and then do between-family selection.



193 A frequently proposed way to measure FI is the use of automatic or self-feeders on family  
194 groups, with recovery of the feed waste to calculate the feed consumption of the aquarium or  
195 the tank (Helland *et al.* 1996; Aknes *et al.* 1997; Lemieux *et al.* 1999; Thodesen *et al.* 2001;  
196 Mambrini *et al.* 2004a; Li *et al.* 2005a; Albrektsen *et al.* 2006; Aknes *et al.* 2006). The main  
197 advantage of this technique is that it enables the estimation of the family FI, and the genetic  
198 variation between families (Kolstad *et al.* 2004). However, this technique is also widely  
199 criticized. First, it leaves unexplored the intra-familial variations for the trait considered,  
200 resulting in overestimated heritabilities (Doupé and Limbery 2004, Kause et al 2006a).  
201 Consequently, this type of selection will be less efficient than selection that also acts on the  
202 within-family component. A way of by-passing the problem is the use of self-feeders with  
203 registration of the triggering individual and the quantity of feed delivered. However, in  
204 practice only some of the fish will activate the self-feeder while the other fish eat the feed  
205 they find in the tank, so this method would be a measurement of the feeding  
206 motivation/behavior rather than a real measurement of individual FI (Brännäs and Alanära  
207 1993; Millot and Bégout 2009). Moreover, the feeding system itself could be responsible for  
208 bias in FE estimation. Individual fish that are fed using self-feeders or with automatic feeders  
209 do not grow with the same rate. Mambrini *et al.* (2004a) showed that brown trout (*Salmo*  
210 *trutta*) fed with self-feeders grew faster and showed an improved FE compared to trout fed in  
211 excess with automatic feeders.

212 Very careful manual feeding to avoid loss of feed is also difficult to manage. There is a large  
213 effect of the “feeder” and, consequently, a low repeatability of the measurement (de Verdal,  
214 pers. comm.).

215 An alternative method in fish to measure FI of “genetic individuals” reared in groups could be  
216 the use of clonal lines, as shown by Grima *et al.* (2008) for rainbow trout. In fish, isogenic  
217 clonal lines are obtained by pair mating unrelated homozygous gynogenetic or androgenetic

218 parents (Komen and Thorgaard 2007, Quillet *et al.* 2007). In such lines, all individuals are  
219 strictly genetically identical but heterozygous and exhibit performance in the range of those of  
220 conventional trout. Isogenic lines are an exceptional tool that allows the measurement of the  
221 genetic variability of traits showing a high environmental variability, as is the case for FE  
222 traits. However, clonal lines can only be used for experimental purposes and consequently,  
223 results are not representative of production conditions, nor can they be used in the  
224 implementation of a breeding program.

225 Another way to estimate individual FI is by rearing animals separately in aquaria. This type of  
226 rearing requires large number of aquaria and confounds the environmental effect of aquarium  
227 with the phenotype of the individual evaluated. More importantly, as stated before, it does not  
228 take into account the social interactions and feeding ranks between fish, which may have a  
229 significant impact on FI and FE. In sunfish, Hayward *et al.* (2000) showed that group rearing  
230 reduces both growth rate and FI probably due to competitive social interactions, which has a  
231 negative impact on FE. McComish (1971) estimated a reduction of more than 50 % for FI and  
232 around 30 % for growth when bluegill are reared in group rather than in isolation, in aquaria  
233 with an *ad libitum* feeding regime. In rainbow trout, Silverstein (2006) demonstrated a  
234 moderate phenotypic correlation ( $r_p = 0.66$ ) between FE estimated in fish held individually or  
235 in a social group, the latter showing greater RFI than isolated fish, in agreement with studies  
236 from Hayward *et al.* (2000) and McComish (1971). Therefore, according to fish species and  
237 their degree of social interactions, the FI measured in isolation will differ from measurements  
238 taken in groups. This implies that it is necessary to consider behavioral aspects and the  
239 impacts it can have on performance traits.

240 Since rearing isolated fish can have an impact on the estimation of FI, it would be more  
241 accurate if FI could be measured on individuals that are kept in groups. Several methods and  
242 techniques have been developed to measure individual FI on fish held in groups (Jobling *et al.*

2001). The simplest method is to analyse the stomach content of each fish obtained by  
dissection (Bromley 1994; Cortés 1997; Rindorf and Lewy 2004). However this method is  
limited to the evaluation of a single meal; it is not suited to follow the feed consumption over  
time.

Another method, much used in the past, is the use of chemical markers integrated in the feed  
(Walsh *et al.* 1987; Morris *et al.* 1990; Johnston *et al.* 1994; Unprasert *et al.* 1999).

Essentially used to study the digestive process and the gastro-intestinal transit time, it requires  
measuring the quantity of a marker in the feces, which is only possible if feces can be  
collected individually, or when done directly in the gastro-intestinal tract, which involves  
sacrificing the fish before analyses or at least handling and anaesthetizing it.

A third method is X-radiography of eaten meals, using X-ray dense markers (generally radio-  
opaque ballotini glass beads) included in pellets (Talbot and Higgins 1983; McCarthy *et al.*  
1993; Silverstein *et al.* 2001; Jobling *et al.* 2001; Boujard *et al.* 2006; Kause *et al.* 2006a;  
Quinton *et al.* 2007a, b; Grima *et al.* 2008). Just after feeding this labeled feed, fish are  
anaesthetized and the number of radio-opaque beads in the gastro-intestinal tract is counted on  
an individual radiography of each fish, allowing the estimate of FI of each fish. This  
technique is highly accurate for one meal but has the disadvantage that it allows only  
measuring the FI of one meal at each time, since recovery can take days or weeks before a  
new measurement can be performed. Furthermore, it seems that some fish can distinguish  
feed with and without radio-opaque beads, which can modify their feeding behavior and their  
ingestion (Chatain, pers. comm.). This method is therefore not suited for measuring FI for a  
long period or for species that show high day-to-day variability in FI as this causes a low  
repeatability of the measurements ( $r=0.09$  to  $0.32$ , Kause *et al.* 2006a, Grima *et al.* 2008).

Kause *et al.* (2006a) estimated that at least three FI measurements were needed to ensure a  
good estimation of the average FI, while 4 to 6 measurements were better.

268 The last method consists in direct observation or video recording of individual daily feed  
269 intake (Adams *et al.* 1995; Tuene and Nordvedt 1995; Smith *et al.* 1995; Hughes and Kelly  
270 1996; Damsgard and Ugedal 1997; Ang and Petrell 1997; Baras *et al.* 2012; de Verdal *et al.*  
271 2016). Feed consumption can be measured for each fish by counting the number of eaten  
272 pellets during a given time span. Video registration of feed consumption for a specific period  
273 (potentially a few consecutive days) is possible without disturbing the fish, but much time is  
274 required to observe the fish or to analyze the video recordings. Duration of the observation is  
275 variable according to the fish species ranging from some minutes to several hours. Whatever  
276 the duration, it should be done at the same time every day, since the feeding response and  
277 behavior may change over the day (Toguyeni *et al.* 1996). Furthermore, the need for external  
278 tagging and individual tracking of each individual limits the group size to 10-20 fish. Such  
279 sizes are not representative of farm rearing conditions.

280

281 It can be concluded that all methods described above have their shortcomings and that there is  
282 still a need for more accurate and tractable methods to help us measure individual variation in  
283 FI and FE. However, in the absence of any better techniques, the methods above have been  
284 used to estimate genetic parameters of FI and FE in different species. The results of these  
285 experiments will be reviewed in the next section.

286

#### 287 **4. What is the variability of FE and can we select for FE directly?**

288 As noted before, there are two levels at which genetic variation in FE can be estimated. The  
289 first one is to rear fish in full sib families, to measure the family mean FI and estimate the  
290 existence of genetic variability between these families (Thodesen *et al.* 2001; Henryon *et al.*  
291 2002; Kolstad *et al.* 2004). The second one is to measure individually each fish and estimate

292 the heritability of the trait considered (Silverstein *et al.* 2001; Kause *et al.* 2006a, b; Quinton  
293 *et al.* 2007a, b; Grima *et al.* 2008). The heritability is a genetic criteria estimating the amount  
294 of variation in a phenotypic trait in a population explained by the genetic variation among  
295 individuals in this specific population. It can be expressed as a ratio of genetic variance over  
296 phenotypic variance (broad sense heritability) or more commonly additive genetic variance  
297 over phenotypic variance (narrow sense heritability).

298 Using family as the measurement unit, it can be concluded that while FE traits do show some  
299 genetic variation (Thodesen *et al.* 2001; Kolstad *et al.* 2004), they present a low coefficient of  
300 variation; ranging from 4.0 to 13.9 % (Henryon *et al.* 2002). Many studies have used the X-  
301 ray method to estimate individual FI and heritabilities of FI or FE (FER or FCR). Whatever  
302 the species and the experimental procedure, estimation of heritability of FE is always low  
303 (ranging from 0 to 0.07) while those of FI are low to moderate ranging from 0.07 to 0.23  
304 (Kause *et al.* 2006b in rainbow trout *Oncorhynchus mykiss*; Quinton *et al.* 2007a, b in  
305 European whitefish *Coregonus lavaretus*). The only exception is the study of Silverstein *et al.*  
306 (2001) who estimated heritabilities of FI of channel catfish *Ictalurus punctatus* to be  
307  $0.37 \pm 0.15$ . The most likely reasons to explain this high value compared to other studies are i)  
308 that the authors performed their experiment with only one meal (without any repetition) and  
309 with only 290 fish, which implies a limited accuracy of the FI measurement, and ii) the full-  
310 sib genetic design confounds the environmental common effects with the additive genetic  
311 variance, which tends to increase heritability estimates.

312 In fish, the only study using RFI to estimate genetic variability of FE was performed on  
313 rainbow trout clonal lines using the X-ray methodology (Grima *et al.* 2008). These authors  
314 showed substantial genetic variability among individual genotypes ( $h^2 = 0.23$ ).

315 According to Quinton *et al.* (2007a), the generally observed low heritability could be  
316 explained by the fact that fish are poikilotherms. Energy intake (by the feed) is used for

317 growth, maintenance or physical activities. The relative share of maintenance requirement is  
318 much lower in fish. For example white grouper (*Epinephelus aeneus*), European sea bass  
319 (*Dicentrarchus labrax*) and gilthead seabream (*Sparus aurata*) use 34.05, 45.38 and 47.89 kJ  
320 of digested energy (DE)  $\text{kg}^{-0.80} \text{day}^{-1}$  respectively which is less than terrestrial animals (e.g.  
321 459.8 kJ of DE  $\text{kg}^{-0.75} \text{day}^{-1}$  in pigs; Martins *et al.* 2011). There is a possibility that  
322 maintenance requirement variability, being relatively lower in fish than in terrestrial animals,  
323 results in a lower variability of FE, as hypothesized by Gjedrem (1983). Another reason that  
324 could explain these low heritability estimates is that measurements were performed during the  
325 exponential growth phase where most of the feed is used for growth (Quinton *et al.* 2007a).  
326 Finally, the low repeatability of the X-ray method itself (range from 0.09 to 0.32) sets an  
327 upper bound for heritability estimates which are consequently also low (Falconer and  
328 Mackay, 1996).

329 It is important to keep in mind that all estimations of FE traits in fish were done at specific  
330 ages, and it is consequently not possible to generalize these results for the global rearing  
331 period. Regarding the age effect, it is known that FE decreases with the age of the fish.  
332 Studying rainbow trout families and using family measurements of FI, Henryon *et al.* (2002)  
333 estimated a higher FER (1.09) during the final period of measurement (i.e. days 186 to 215)  
334 compared to the first phase of measurement (1.68, i.e. days 52 to 76).

335

336 From these studies, it can be concluded that direct measurement of FE is difficult and results  
337 in low estimates of heritability, often with high standard errors. The main reason seems to be  
338 the low repeatability of the methods used to measure FI. Furthermore, none of methods  
339 reviewed here, are suitable for large scale phenotyping as required for selective breeding.  
340 Consequently, finding traits highly correlated with FI and FE that could be used as indirect  
341 criteria for selection could be a better option for selective breeding for FE in fish.

342

## 343 **5. Which indirect criteria could be used to estimate and improve FE?**

344 Different categories of traits have been proposed to account for variations in FE, the major  
345 two categories being traits derived from growth models and traits derived from bio-energetic  
346 models.

### 347 **5.1. Growth model traits**

#### 348 **5.1.1. Growth models**

349 The most widely selected trait in aquaculture is growth rate. Growth can be defined in  
350 different ways (Dumas *et al.* 2010; Jobling 2003):

351 1) body weight gain (BWG), which is the difference in two body weight measurements  
352 taken at time  $t$  and  $t+\Delta t$ :  $BWG = BW_2 - BW_1$ ,

353 2) the specific growth rate (SGR), which is BWG expressed at a logarithmic scale to  
354 reduce the heterogeneity of variance between two body weight measurements, taken at  
355 different ages, and divided by the time between the two measurements  $t$  and  $t+\Delta t$ :

$$356 \quad SGR = (\ln BW_2 - \ln BW_1) / \Delta t * 100$$

357 3) the daily growth coefficient (DGC), which uses the cubic relation between BW and  
358 length to make growth rate linear over time:

$$359 \quad DGC = 100 * ((BW_2^{(1/3)} - BW_1^{(1/3)}) / \Delta t)$$

360 4) the thermal growth coefficient (TGC), which is the same as DGC but now corrected  
361 for the water temperature of the rearing environment during the measurement period:

$$362 \quad TGC = (BW_2^{(1/3)} - BW_1^{(1/3)}) / (T * \Delta t) * 100$$

363

#### 364 **5.1.2 Correlations of growth with FE**

365 In livestock species, it is generally admitted that FE is correlated with growth rate, but in fish,  
366 this is still debatable. Estimations of phenotypic and genetic correlations between growth  
367 traits and FE traits are summarized in Table 3. At the phenotypic level and using X-ray  
368 method, Thodesen *et al.* (1999, 2001) and Kolstad *et al.* (2004) reported positive correlations,  
369 ranging from 0.60 to 0.90, between growth rate (expressed as TGC and BWG, respectively)  
370 and FE (expressed as FER) in Atlantic salmon *Salmo salar*. Using video analyses to record  
371 feed intake, de Verdal *et al.* (2016) found high phenotypic correlation between growth rate  
372 (expressed as BWG) and FCR (of  $0.62 \pm 0.06$ ) in Nile tilapia *Oreochromis niloticus*, which  
373 was in the same range as that estimated in Atlantic salmon.

374 The results from tilapia agree with those of Thodesen *et al.* (1999) who compared wild  
375 Atlantic salmon with a selected strain and concluded that an improvement of growth rate of  
376 around 10 % could result in a 4.6 % improvement in FER by one generation of selection. The  
377 authors explained this high potential impact of selection for growth on FER by the fact that it  
378 could be associated with a reduction of the energy costs per unit of gain, and consequently, an  
379 increase of metabolizable energy available for gain rather than for maintenance requirements.  
380 However this explanation is questionable since the energy needed for maintenance  
381 requirement in fish is low.

382 Ogata *et al.* (2002) compared Japanese flounder selected on growth rate for two generations  
383 with wild individuals and concluded that the selected line had higher growth rate and FI, as  
384 well as a better FE after correction for a phenotypic effect of body size. In both studies  
385 (Thodesen *et al.* 1999; Ogata *et al.* 2002) selected fish were compared with wild-caught fish.  
386 Therefore, the selected and wild groups differed not only for selection for growth, but also for  
387 domestication state, which could bias the results as wild fish are expected to show poor  
388 growth and high FCR in captivity (Millot *et al.* 2010, 2011). The difference for FE or FI



389 between selected and wild fish could therefore be due to domestication, selection, or a  
390 combination of both.

391 In another study on amago salmon (*Oncorhynchus masou*), fish selected for improved growth  
392 on a low fishmeal diet were compared to controls, both on a fishmeal and on a low fishmeal  
393 diet (Yamamoto *et al.*, 2015). The selected fish had a better FER than the controls, especially  
394 on the low fishmeal diet (0.98 vs. 0.84). This seems to be due to a strong increase in feed  
395 intake in the selected fish fed the low fishmeal diet (2.01 vs 1.71 % BW.d<sup>-1</sup>) whereas control  
396 and selected fish had the same feed intake when fed the fishmeal diet. In such a case, it is  
397 likely that the increase in FE is linked to the fact that control fish have a suboptimal feed  
398 intake level when fed a low fishmeal diet, thus increasing the relative cost of maintenance.

399 This also highlights that the type of feed used may have a high impact on the components of  
400 the genetic response (growth and feed intake).

401 The general conclusion of a number of studies comparing FI and FE on brown trout selected  
402 for growth with fish from a control line (Sanchez *et al.* 2001; Mambrini *et al.* 2004a, b;  
403 Mambrini *et al.* 2006; Boujard *et al.* 2006), is that the improvement of growth is only  
404 explained by the increase of feed consumption in selected fish, and that FE is not affected.

405 This lack of response in FE could be explained when we assume that faster growing fish will  
406 most likely be those that feed more, and these are not necessarily the ones that are also more  
407 efficient. This effect is likely to be more pronounced in situations where fish are fed ad  
408 libitum with automated feeders. As discussed earlier, fish fed with automated feeders can  
409 have lower FE than fish fed with self-feeders. This theory is supported by phenotypic  
410 observations on responses to six generations of selection on growth and FCR in Nile tilapia.

411 In this selection experiment, growth rate, expressed as DGC increased from 2.29 to 4.46 while  
412 FCR remained constant at 1.3-1.4 across generations (Komen, personal comm.). In this  
413 experiment, fish were fed with automated feeders, and feeding rate was adjusted each

414 generation to accommodate the higher growth rate as a result of selection. Consequently,  
415 using ad libitum feed ration, selected fish would be fish that are faster growing and feed less,  
416 but also fish that are faster growing because they feed more.

417 Estimates of the *genetic* correlation between FE and growth are scarce in fish. Kause *et al.*  
418 (2006b) and Quinton *et al.* (2007a) found correlations between FI and body weight, ranging  
419 from 0.72 to 0.90 and from 0.93 to 0.97 in full/half sib families of rainbow trout and European  
420 whitefish, respectively. Quinton *et al.* (2007a) concluded from this high genetic relationship  
421 that an indirect selection for FE combining selection for high growth and low FI would be at  
422 least twice as efficient as selection for growth only.

423 Henryon *et al.* (2002) also estimated the genetic correlations between FE (expressed as FER)  
424 and growth (expressed as body weight at a given age) in full-sib families of rainbow trout.  
425 The genetic correlations estimated for seven successive periods of growth between 52 and 215  
426 days of age, and for the cumulative periods, were found ranging from 0.63 to 0.99, with an  
427 average of 0.87 for the cumulative rearing period. The moderate to high genetic correlations  
428 between FER and BW indicate that these two traits share some genetic control. However, it is  
429 important to note that in this study, fish were fed with a restricted amount of feed. Due to this  
430 restricted feeding regime, FER and growth were congruent (fish who grew faster are those  
431 showing higher FER), there was less variation for voluntary feed intake, and consequently  
432 estimates of the genetic correlation between FER and growth traits are high (Henryon *et al.*  
433 2002).

434 The results discussed in this section could be summarized as follows: positive correlations  
435 between growth and FE were observed when selected fish were compared with wild fish.  
436 These correlations are likely biased by domestication effects on behavior which makes fish  
437 less stressed and better adapted to the farming environment. Phenotypic trends in growth and

438 FE within selection lines indicate that selection for higher growth rate alone could favor fish  
439 which have higher FI but these are not necessarily more efficient – and this may depend on  
440 the starting level of FI before selection, and to the type of feed used.

441 There is the risk of a bias if comparisons are done on small and big fish in the same analyses  
442 given the relationship between FE and fish size. However, in nutrition experiments, this bias  
443 is usually dealt with by calculating FE on the basis of metabolic FI and growth rate (i.e FI in  
444  $\text{gr/kg}^{0.8}$  and growth rate in  $\text{gr/kg}^{0.8}$ ). In genetic experiments, fish are compared usually at the  
445 same age rather than same weight/size. Indeed, the aim is to estimate the phenotype of a large  
446 number of fish and it is impossible in practice to measure the feed intake of each fish  
447 individually at the same size even if the experiment is started with fish of similar size.

448 However, from a genetic perspective such experiments should detect those fish that are more  
449 efficient. The relationship between efficiency and fish size does mean that FE needs to be  
450 measured over a series of size/age classes over the production lifetime of the fish (and on a  
451 defined feed) to obtain a practical measure for selection for a given production system.

### 452 **5.1.3 Growth after starvation and refeeding periods**

453 In order to bypass the issues associated with the measure of FI, some authors have  
454 investigated the potential of indirect but tractable criteria linked to growth under specific  
455 conditions to predict FE. Grima *et al.* (2008; 2010a) proposed that body weight loss and gain  
456 during respectively feed deprivation (FD) and re-feeding (RF) periods could serve as possible  
457 proxies of FE (defined as RFI in their work). Figure 1 outlines the general principle of  
458 measuring FD and RF. The loss of weight during FD is assumed to be correlated to the  
459 maintenance requirement of the fish (Lupatsch *et al.* 2003; Grima *et al.* 2008). The RF period  
460 is also known as a compensatory growth period, where an unusually rapid growth follows a  
461 period of starvation (Xie *et al.* 2001, Ali *et al.* 2003). Russel and Woottom (1992) defined this

462 period as “the ability of a dietary restricted animal to achieve its normal body weight and  
463 form by a growth spurt on re-alimentation”. Compensatory growth has been reported in a  
464 large range of fish species (Russell and Wootton 1992; Jobling *et al.* 1994; Nicieza and  
465 Metcalfe 1997; Mélard *et al.* 1997; Boujard *et al.* 2000; Wang *et al.* 2000; Gaylor and Gatlin  
466 III 2000; Chatakondi and Yant 2001; Barreto *et al.* 2003). There is large variability in the  
467 protocols used to measure the weight loss during FD, with measurements performed on  
468 groups or on isolated fish, with different durations of FD period, with repetitive FD periods or  
469 not, and with different sizes and ages of fish at the beginning of the experiment (Li *et al.*  
470 2005b; reviewed in Ali *et al.* 2003). Using a specific procedure with three weeks of FD  
471 followed by three weeks of RF, repeated twice in rainbow trout, Grima *et al.* (2008) found no  
472 significant correlation between RFI and weight loss during FD or growth capacity during RF  
473 considered separately. However, combining both traits increased the proportion of variance in  
474 RFI explained, and the best criterion to estimate RFI was the combination of all the  
475 measurements over the two periods of survey, which explained 60% of RFI variation. More  
476 recently, Grima *et al.* (2010b) observed that European seabass sorted for low weight loss  
477 during FD and high compensatory growth during RF exhibited an improvement of RFI when  
478 compared to groups sorted for opposite characteristics, but that most of the difference came  
479 from the weight loss during FD. However, Daulé *et al.* (2014) did not find any significant  
480 response on FE (FCR or RFI) after one generation of divergent selection of seabass for weight  
481 loss during FD only.

482 Several authors showed significant positive correlations between the increase of growth after  
483 a FD period and the improvement of FE (Russell and Wootton 1992; Barreto *et al.* 2008).  
484 This was considered to be due to a reduction of the basal metabolic rate of the fish during the  
485 FD period which continued for a small period of time after the end of the FD period (Russel  
486 and Wootton 1992). However, this hypothesis is questionable since it is known that the

487 energy needed for maintenance is low in fish (Gjedrem 1983; Martins *et al.* 2011). Using fish  
488 selected for high or low weight loss during starvation, Dupont-Prinet *et al.* (2010) showed no  
489 significant difference in standard metabolic rate during fasting. Other authors proposed that  
490 compensatory growth is only explained by a hyperphagia without any modification of FE  
491 (Hayward *et al.* 2000; Wang *et al.* 2000; Xie *et al.* 2001; Nikki *et al.* 2004).

492

## 493 **5.2. Bio-energetic models**

494 An alternative approach to the use of growth models is to look into the bio-energetics of  
495 growth to identify traits that could be used for selection on FE (Jobling 1993; Karjalainen *et*  
496 *al.* 1997; Cho and Bureau 1998). Growth models do not take into account the available and  
497 digestible energy and nutrients in the feed, nor the energy and proteins retained by the fish.  
498 Both digestibility of nutrients and energy flux can have a large impact on growth and FE of  
499 animals.

500 It is possible to model FI in energetic terms, as described in Figure 2 and in the following  
501 equation (Strand 2005):

$$502 \quad FI = (E_F + E_N + E_M) + (M_S + M_R + M_A + M_F) + (G_S + G_R)$$

503 where *FI* is feed intake;  $E_F$  the faeces excretion;  $E_N$  the urinary loss and gill excretion;  $E_M$   
504 the mucus epidermal cells loss;  $M_S$  the basal metabolism;  $M_R$  the voluntary activity;  $M_A$  the  
505 thermal regulation;  $M_F$  the heat energy;  $G_S$  the somatic growth and  $G_R$  the gamete production  
506 (Figure 2).

507 Such a model takes into account all the energetic components from FI to excretion, growth  
508 and heat production. The interest here is to be able to estimate the optimal feed consumption  
509 and the energy losses with particular attention to different parameters as growth prediction,

510 estimation of the digestible energy needed, determination of digestible energy in the feed and  
511 growth (Cho and Bureau 1998; Kaushik 1998). Using these models could help finding new  
512 measurable traits explaining individual FE differences. It could be potentially important to  
513 estimate the physical activity of the fish or the thermal regulation which are easier to measure  
514 than individual faeces excretion, urinary loss or gill excretion.

515 Lipid and protein are energetically the most important components of body composition. The  
516 ratio between lipid and protein deposition could have an impact on FE (Azevedo *et al.* 1998).  
517 In this section, we will discuss lipid deposition and protein turnover rates in the context of the  
518 bio-energetic model, and show how they could be used in prediction for FE.

519

#### 520 **5.2.1. Lipid deposition**

521 It is well established from terrestrial species like poultry or pigs that FE is linked to body fat  
522 deposition, with leaner individuals exhibiting increased FE. While protein content is mostly  
523 determined by fish size, lipid deposition is highly variable, depending on physiological age  
524 and feed composition (Shearer, 1994). Older fish tend to deposit more fat, resulting in lower  
525 FE. Because of the lower energy content of proteins (17kJ/g) compared to lipids (37kJ/g), the  
526 increased protein deposition and lower fat deposition in leaner animals contributes to the  
527 reduction of metabolic cost of tissue. Faure *et al.* (2013) for instance showed that pigs  
528 selected for low RFI have lower lipid content than pigs from the divergent high RFI line  
529 whatever the body compartment in which the fat was deposited (thinner back fat, less internal  
530 fat and lower intra-muscular fat).

531 Similar relationships between body fat and FE have been recorded in fish. A divergent  
532 selection for muscle fat content has been carried out in rainbow trout (Quillet *et al.* 2005). A  
533 survey after four generations of selection showed that fish from the lean-muscle selected line

534 had lower body and muscle lipid contents, and that FCR was improved by about 6-9%  
535 compared to the fat-muscle selected line irrespective of the carbohydrate content of the diet  
536 (Kamalam *et al.* 2012). The difference in FE among lines was confirmed and enhanced after  
537 seven generations of selection (Quillet, pers. comm.). Similarly, in coho salmon  
538 *Oncorhynchus kisutch*, 16 generations of selection for growth resulted in both higher FE and  
539 body leanness than in the unselected parental stock (Neely *et al.* 2008). In European whitefish  
540 *Coregonus larvaretus*, Quinton *et al.* (2007b) found no significant phenotypic and genetic  
541 correlations between whole-body lipid content and daily FCR. Nevertheless, they calculated  
542 that combining selection for reduced lipid content with selection for high BWG, could  
543 accelerate indirect FCR improvement compared with selection for BWG only. Similar results  
544 were found in rainbow trout (Kause *et al.* 2016). In contrast with those studies, Grima *et al.*  
545 (2010b) concluded in sea bass that the most efficient individuals should be the ones having  
546 the highest muscle fat content. However, in this experiment, the whole body fat content was  
547 not measured, and the correlation was observed on fish that had experienced two fasting-  
548 refeeding periods a few months before, which may have influenced the results.

549 Altogether, these results indicate that relationships between body lipids and FE in fish deserve  
550 further investigations. Traits related to lipid deposition are usually highly heritable (Quillet *et*  
551 *al.* 2005, 2007; Tobin *et al.* 2006; Kause *et al.* 2009). Moreover, it is now possible to estimate  
552 lipid content in different body compartments with non-invasive methods. Muscle fat content  
553 can be efficiently estimated using apparatus like the Distell Fish Fatmeter®. Internal  
554 ultrasound and 2D external imagery allow in vivo prediction of carcass yields (Haffray *et al.*  
555 2014) which in turn is highly correlated to perivisceral fat, another important site of lipid  
556 deposition. Taken together these results suggest that it should be possible to use lipid  
557 deposition as indirect selection criterion to enhance FE. However, care should be given to  
558 selection against muscle fat content as this may interfere with meat quality. The most

559 interesting target to select against is perivisceral fat as this is generally perceived as an  
560 economic loss.

561

### 562 **5.2.2. Protein turn-over rates and nitrogen retention**

563 Another criterion potentially interesting to focus on to improve FE could be the nitrogen  
564 retention (excretion to intake ratio). In chicken, this trait was previously described with a  
565 heritability of 0.29 and with a genetic correlation with FCR equal to 0.95 (de Verdal *et al.*  
566 2011a). In pig strains, Saintilan *et al.* (2013) estimated genetic correlations ranging from 0.97  
567 to 0.98 and from 0.38 to 0.83 between nitrogen retention and FCR and RFI, respectively,  
568 indicating that the nitrogen retention could be a good criterion in view to improve FE.  
569 However, despite its relatively easy measurement in terrestrial animals, this trait is highly  
570 complex to measure in fish since the ability to estimate the nitrogen retention of each  
571 individual reared in groups is difficult, reducing the practicality of this trait as a selection  
572 criterion in fish species. In European sea bass (*Dicentrarchus labrax*), McKenzie *et al.* (2014)  
573 found that the differences between fasting tolerant and sensitive phenotypes was more  
574 probably explained by differences in the use of dietary lipids and proteins, fasting tolerant fish  
575 using less proteins as metabolic fuel than fasting sensitive fish.

576

### 577 **5.2.3. Oxygen consumption**

578 The rate of oxygen consumed increases after feeding in fish. The first study using oxygen  
579 consumption to estimate FE was done by Kinghorn (1983) on young rainbow trout.  
580 According to this author, a high FI associated with high genetic growth capacity will lead to  
581 improved FE by increasing the availability of metabolizable energy for body weight gain



582 relative to maintenance requirement costs. By measuring the metabolized energy, more  
583 specifically the oxygen consumption, and the energy required for growth, Kinghorn (1983)  
584 showed that oxygen consumed was highly negatively correlated with gross feed efficiency  
585 ratio. Furthermore, variation in oxygen consumption was highly heritable ( $0.51\pm 0.12$ ) with  
586 moderate coefficient of variation ( $CV=18.3\%$ , Kinghorn 1983). It is interesting to note that  
587 the family mean heritability of gross FER was very low ( $0.03\pm 0.10$ ), which is in the same  
588 range as reported from direct estimations of FER by X-ray techniques (ranging from 0 to 0.07,  
589 see section 2.2). Furthermore, feed consumption showed a moderate to high family mean  
590 heritability ( $0.41\pm 0.13$ ), but this trait was moderately correlated with FER (Kinghorn 1983).  
591 These results should be interpreted with care since calculations were based on a number of  
592 assumptions (oxygen consumption as an indirect measure of FI, a constant maintenance  
593 requirement, and heritability was estimated from family means-Thodesen *et al.* 1999).

594

### 595 **5.3. Other traits**

#### 596 **5.3.1. Neuropeptides and hormones**

597 It is well known that many neuropeptides and hormones are involved in the FI and digestive  
598 processes, as illustrated in Figure 3. Feeding activities are regulated by a multitude of  
599 hormones and neuropeptides produced by the brain and other peripheral organs as the liver,  
600 the gut or the stomach. Complete reviews of the role of these neuropeptides and hormones in  
601 fish were written by de Pedro and Björnsson (2001) and Volkoff *et al.* (2010). There is no  
602 doubt that the regulation of FI in fish involves orexigenic and anorexigenic signals at the brain  
603 level (Lin *et al.* 2000; Bernier and Peter 2001; Volkoff *et al.* 2010). Feed deprivation  
604 generally causes an up-regulation of the expression of orexigenic factors and a down-  
605 regulation of the expression of anorexigenic factors (Volkoff *et al.* 2010).

606 Consequently, it would be interesting to study the potential regulation processes of these  
607 hormones and neuropeptides on FI and FE, and estimate the relationship between FE traits  
608 and the level of these hormones and neuropeptides. For example, it was previously shown that  
609 the level of plasmatic growth hormone (GH) in Nile tilapia tends to be negatively correlated  
610 with the increase in food ration (Toguyeni *et al.* 1996). Furthermore, regulatory hormone  
611 levels are heritable in humans ( $h^2$  ranging from 0.34 to 0.67 for ghrelin, amylin, insulin and  
612 leptin; Fisher *et al.* 2007).

613

### 614 **5.3.2. Gastro-intestinal tract morphology and functioning**

615 The upper limit of FE is related with the digestive tract capacity to assimilate nutrients from  
616 feed (Lemieux *et al.* 1999). Consequently, FE is dependent on the digestive tract morphology  
617 and functioning. According to Volkoff *et al.* (2010), variations in fish feeding habits are  
618 linked with different morphologies and physiologies. These authors illustrated this by the  
619 development of teeth and stomach, generally poorly developed in omnivorous or herbivorous  
620 fish species but well-developed in carnivorous fish species (e.g. salmon, seabass). In Nile  
621 tilapia, Charo-Karisa *et al.* (2007) showed that selection for growth on a herbivorous diet for  
622 three generations in low input earthen ponds resulted in an increase of gut length index (GLI:  
623 gut length/ standard length) from 3.1 to 4.2. Heritability of GLI was low, 0.09, but the genetic  
624 correlation with body weight was 0.22. In chickens, genetic relationships were found between  
625 FE and the development of the gastro-intestinal tract in terms of weight, length and weight to  
626 length ratio (de Verdal *et al.* 2010, 2011b). In those two studies, chickens had been selected  
627 on the ability to digest a low quality diet. It was previously shown in chicken that difference  
628 in FE linked to increases in digestibility were apparent only when using the low quality diet,  
629 while they were not significant using a highly digestible diet (Mignon-Grasteau *et al.*, 2010).

630 Feed efficiency is also dependent on the availability of digestive enzymes and on their  
631 capacity to degrade and transport nutrients from the digestive tract to the blood (Lemieux *et*  
632 *al.* 1999). For example, pepsin is the main enzyme in the stomach and is active in protein  
633 digestion, and alkaline phosphatase is involved in the transport and absorption of lipid and  
634 carbohydrates. However, it is complex to identify if the enzyme activities are based on gastro-  
635 intestinal digesta (from the feed) or on gastro-intestinal tissues (from the gut).

636 Several studies on proteolytic enzymes in fish have provided the evidence that trypsin and  
637 chymotrypsin are key enzymes for feed utilization and growth through their involvement in  
638 the processes of protein digestion (Lemieux *et al.* 1999; Belanger *et al.* 2002; Rungruangsak-  
639 Torrissen *et al.* 2006; Chan *et al.* 2008). In two salmonid species (Atlantic salmon and  
640 rainbow trout), a strong linear correlation was found between trypsin activity and protein  
641 digestibility (Krogdahl *et al.* 1994; Rungruangsak-Torrissen *et al.* 2006). Trypsin and  
642 chymotrypsin are the major protease enzymes secreted by the pancreas in the anterior part of  
643 the intestine (Dabrowski 1983). Trypsin activity is also correlated with FER, while  
644 chymotrypsin was not, according to Lemieux *et al.* (1999) in a study on Atlantic cod *Gadus*  
645 *morhua*. This link can be as strong as the relation with growth rate [trypsin activity expressed  
646 in U. g of fish<sup>-1</sup> exhibited a significant relationship with growth rate, FI and FER ( $r^2 = 0.58,$   
647  $0.38$  and  $0.19$ , respectively)], which supports the hypothesis of trypsin activity in feed  
648 utilization. In the same way, the protease activity ratio of trypsin to chymotrypsin (T/C ratio)  
649 was shown to be linked with growth rate (Rungruangsak-Torrissen *et al.* 2006) and FER  
650 (Sunde *et al.* 2001) in Atlantic salmon. Considering the correlation between FER and pyloric  
651 caecal T/C ratio, it would be interesting to use this last trait as an indicator of FE  
652 (Rungruangsak-Torrissen, 2007; Sunde *et al.* (2004).

653

654 While these traits might be useful to estimate FE, a lot of work is still needed from a genetic  
655 point of view. Most correlations described are phenotypic and estimates of genetic  
656 correlations are in almost all cases lacking. It is necessary to have an accurate idea of the  
657 correlations between each of these traits before including them in a selection process. Since  
658 some of these traits show common pathways, there is a possibility that selecting on one trait  
659 could result in negative correlations with other traits in the same pathway. It should be also  
660 noted that the measurement of almost all these indirect metabolic traits is lethal, which  
661 reduces their potential efficiency and increases the cost of selective breeding, as in this case  
662 recording of additional slaughtered sibs would be necessary to implement a breeding program.  
663 Finally, genomic tools could be useful as was previously highlighted that some genomic  
664 regions were linked with FE characteristics in livestock species (Chen et al. 2011; Wolc et al.  
665 2013; Tran et al. 2014; Al-Husseini et al. 2014). However, nothing has been reported to date  
666 on fish to our knowledge. The rapid development of new sequencing technologies in  
667 aquaculture (Robledo et al. 2017) will allow improving quicker FE traits when these will be  
668 well measured or estimated.

669

## 670 **Conclusion**

671 Improving FE in fish by the selective breeding will have high positive economic and  
672 environmental impacts. Many methods have been suggested and tested to improve FE using  
673 genetics, but results in terms of response to selection are often inconclusive as FE-related  
674 traits show little genetic variation. Furthermore, many results are questionable due to flawed  
675 experimental protocols, especially for measuring individual feed intake. There is an urgent  
676 need for sound experimental procedures that are economically and practically feasible at  
677 production scales. The primary issue appears to be improving methods to measure individual  
678 FI with high accuracy. Increasing the repeatability of the measurements over time and

679 environments, and the assessment of FE over the whole rearing period, are two other critical  
680 elements that require a lot more attention.

681 Nevertheless, while FE improvement by selective breeding in fish will not be easy, it is likely  
682 to be feasible. One way forward would be to combine different traits showing a correlation  
683 with FE and implement a multitrait selection using BLUP (Best Linear Unbiased Prediction).  
684 The development of genomic tools for FE, as was recently done for livestock animals where  
685 some genomic regions were found linked with FE could also be investigated in fish. Since it is  
686 difficult to measure FI, the identification of molecular markers linked to QTLs (quantitative  
687 trait loci) or metabolism pathways associated with genes controlling FI or FE, would be  
688 valuable. In the event of a trait under highly polygenic control, the development of genomic  
689 selection may allow significant increases in the precision of estimated breeding values, as  
690 well as easier selection if the association of genomic markers and phenotype can be done in  
691 controlled reference populations, while selection itself would rely solely on the multilocus  
692 genotype of selection candidates (Meuwissen *et al.* 2016).

693

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696

697

698 **References**

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1231 **Appendix**

1232 *List of abbreviations used in the present review*

1233 FE – Feed Efficiency

1234 FI – Feed Intake

1235 FCR – Feed Conversion Ratio

1236 FER – Feed Efficiency Ratio

1237 RFI – Residual Feed Intake

1238 BWG – Body Weight Gain

1239 SGR – Specific Growth Rate

1240 BW – Body Weight

1241 DE – Digested Energy

1242 DGC – Daily Growth Coefficient

1243 TGC – Thermal Growth Coefficient

1244 L – Initial specific growth rate

1245 K – Maturation rate

1246  $T_i$  – Age of inflexion

1247 FD – Feed deprivation

1248 RF – Refeeding

1249

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1251 **Tables**

1252 *Table 1 – Feed efficiency and feed consumption of the main livestock and fish species at the*  
 1253 *world scale*

Species	FCR <sup>1</sup>	World production (in 2011; 10 <sup>6</sup> tons)	Feed consumption (estimated, 10 <sup>6</sup> tons)
Beef cattle	8 – 12.7 <sup>2</sup>	63 <sup>6</sup>	504 – 800
Sheep and lamb	5 – 16.9 <sup>3</sup>	13 <sup>6</sup>	65 – 220
Pig	5-6.5 <sup>2</sup>	110 <sup>6</sup>	550 – 715
Broiler chicken	2-2.5 <sup>2</sup>	95 <sup>6</sup>	190 – 237.5
Fish species	1-2.68	62 <sup>6</sup>	62 – 166.2
- Carps and other cyprinids (10 major species) <sup>5</sup>	1.40-2.68 <sup>7</sup>	22.95 <sup>4</sup>	32.1 – 61.5
- Nile tilapia ( <i>Oreochromis niloticus</i> )	1-1.32 <sup>8</sup>	2.81 <sup>4</sup>	2.81 – 3.71
- Atlantic salmon ( <i>Salmo salar</i> )	0.65-0.92 <sup>9</sup>	1.73 <sup>3</sup>	1.12 – 1.59
- Rainbow trout ( <i>Oncorhynchus mykiss</i> )	1.01-1.29 <sup>10</sup>	0.77 <sup>4</sup>	0.78 – 0.99

1254 <sup>1</sup>FCR (Feed Conversion Ratio) = Feed intake \* Body weight gain<sup>-1</sup>

1255 <sup>2</sup>Cassidy *et al.* 2013

1256 <sup>3</sup>United States Department of Agriculture (USDA) 2013

1257 <sup>4</sup>FAO yearbook. 2012

1258 <sup>5</sup>*Cyprinus carpio, Ctenopharyngodon idellus, Carassius carassius, Megalobrama*

1259 *amblycephala, Mylopharyngodon piceus, Catla catla, Labeo rohita, Cirrhinus mrigala,*

1260 *Hypophthalmichthys molitrix, Hypophthalmichthys nobilis*

1261 <sup>6</sup>Earth Policy Institute 2013

1262 <sup>7</sup>Másílko *et al.* 2014; Abidi *et al.* 2014

1263 <sup>8</sup>Crovatto Veras *et al.* 2013; Koumi *et al.* 2011; Wang *et al.* 2009

1264 <sup>9</sup>Mundheim *et al.* 2004; Kolstad *et al.* 2004; Sunde *et al.* 2004; Quinton *et al.* 2007a

1265 <sup>10</sup>Farhangi and Carter 2007; Grima 2010; Henryon *et al.* 2002; Sanchez *et al.* 2001

1266 *Table 2 – Improvement in productivity and efficiency due to selective breeding*

Species	Trait	Performance		
		1960	2005	Δ (%)
Pigs <sup>1,2</sup>	Growth g/d	629	925	47
	FCR	3.24	2.65	18
Broilers <sup>3</sup>	Growth g/d	10	40	400
	FCR	2.85	1.98	30
Laying hens <sup>4</sup>	# eggs per year	230	315	30
	FCR (g/ g egg)	3.13	2.28	27
Nile tilapia <sup>5</sup>	Growth g/d	0.61	4.75	780
	FCR	1.58	1.45	8

1267 <sup>1</sup>Rauw *et al.* 1998

1268 <sup>2</sup>Saintilan *et al.* 2013 (estimates for 2005 from average of data collected between 2000 and  
1269 2009)

1270 <sup>3</sup>Zuidhof *et al.* 2014

1271 <sup>4</sup>Leenstra *et al.* 2016

1272 <sup>5</sup>Omasaki and Komen (unpublished data from a domesticated and unselected Kenyan strain  
1273 and from the GIFT strain, generation 5 of growth selection, commercial results from 2005).

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1277 *Table 3 – Estimations of phenotypic and genetic correlations between growth traits and feed intake and FE traits<sup>1</sup>.*

	Species	Growth trait <sup>2</sup>	Feed trait <sup>3</sup>	Correlations	Results
Thodesen <i>et al.</i> (1999)	Atlantic salmon ( <i>Salmo salar</i> )	TGC	FER	Phenotypic	r = 0.90
Thodesen <i>et al.</i> (2001)	Atlantic salmon ( <i>Salmo salar</i> )	TGC	FER	Phenotypic	r = 0.79
Silverstein (2006)	Rainbow trout ( <i>Oncorhynchus mykiss</i> )	TGC	RFI	Phenotypic	Fed at satiation (r = -0.31) 5% BW ration (r = -0.57)
Kolstad <i>et al.</i> (2004)	Atlantic salmon ( <i>Salmo salar</i> )	BWG	FI FER	Phenotypic	Between FCE and BWG (r = 0.6) Between FCE and FI (r = 0.45) Between BWG and FI (r = 0.98)
Doupé and Limbery (2004)	Black bream ( <i>Acanthopagrus butcheri</i> )	BWG	FI	Phenotypic	After 42 days (r = 0.78) After 56 days (r = 0.69)
Kause <i>et al.</i> (2006b)	Rainbow trout ( <i>Oncorhynchus mykiss</i> )	DWG BW	DFI	Phenotypic	Between DFI and BW : 0.48 to 0.54 Between DFI and DWG : 0.51 to 0.74
				Genetic	Between DFI and BW : 0.72 to 0.90 Between DFI and DWG : 0.86 to 0.96
Quinton <i>et al.</i> (2007a)	European whitefish ( <i>Coregonus lavaretus</i> )	DWG	DFI	Phenotypic	r = 0.86 to 0.88
				Genetic	r = 0.93 to 0.97
Henryon <i>et al.</i> (2002)	Rainbow trout ( <i>Oncorhynchus mykiss</i> )	BW	FER <sup>4</sup>	Genetic	0.63 to 0.99
de Verdal <i>et al.</i> (2016)	Nile tilapia ( <i>Oreochromis niloticus</i> )	BWG	FI FCR RFI	Phenotypic	Between BWG and FI : 0.74 Between BWG and FCR : -0.62 Between BWG and RFI : -0.03

1278 <sup>1</sup>All the measurements were done with the X-ray methods or by measuring directly the feed intake of the family group.

1279 <sup>2</sup>TGC=Temperature Growth Coefficient; BW= Body Weight; BWG=Body Weight Gain; DWG=Daily Weight Gain (=BWG. number of experimental days<sup>-1</sup>);

1280 <sup>3</sup>FER=Feed Efficiency Ratio; RFI= Residual Feed Intake; FI=Feed Intake; DFI=Daily Feed Intake (=FI. number of experimental days<sup>-1</sup>)

1281 <sup>4</sup>FER estimated as the cumulative FER for all the grow out period

## Figures

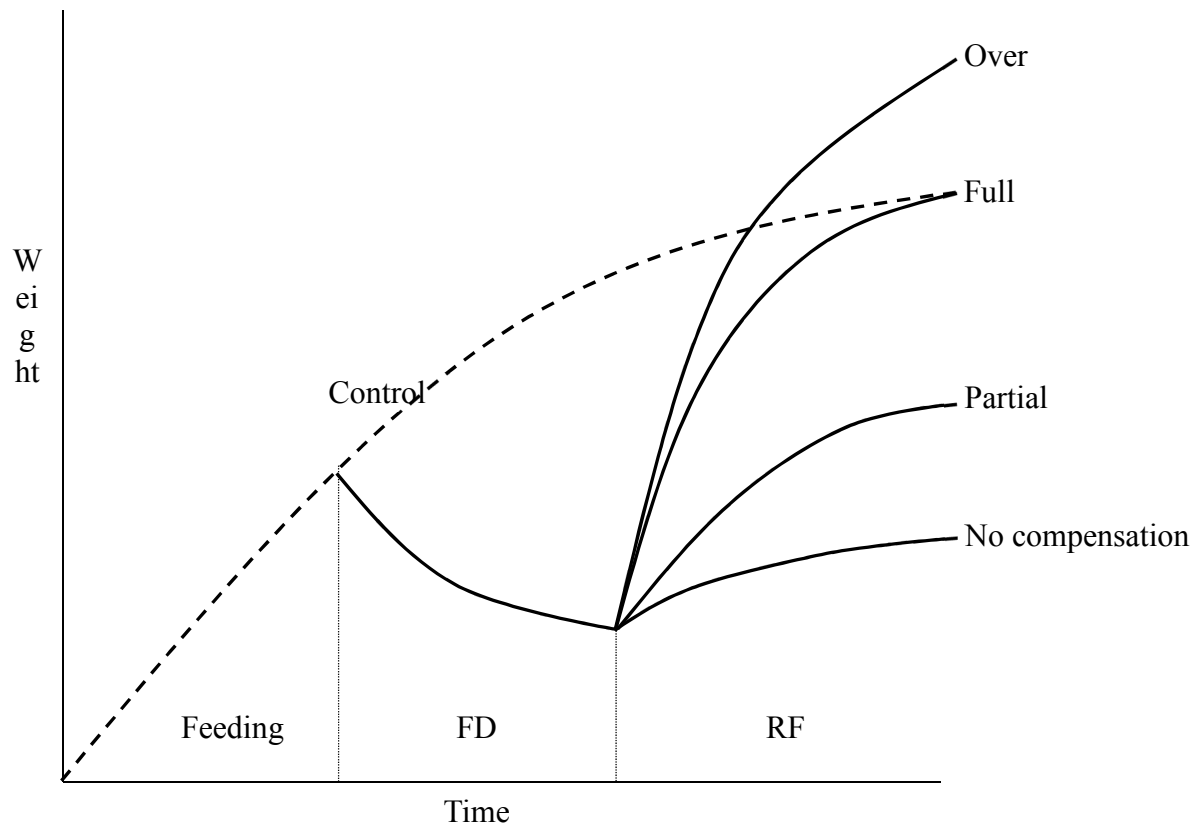
*Figure 1- Variation of body weight after feed deprivation (FD) and re-feeding (RF) period, based on Jobling (1994), modified from Ali et al. (2003).*

*Figure 2– Energy flux in fish, criteria used in the bio-energetic models (from Strand 2005, modified from Bailey 2003)*

*Figure 3 – A model for FI regulation by hormones and neuropeptides in fish (modified from de Pedro and Björnsson 2001)*

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*Figure 1- Variation of body weight after feed deprivation (FD) and re-feeding (RF) period, based on Jobling (1994), modified from Ali et al. (2003).*

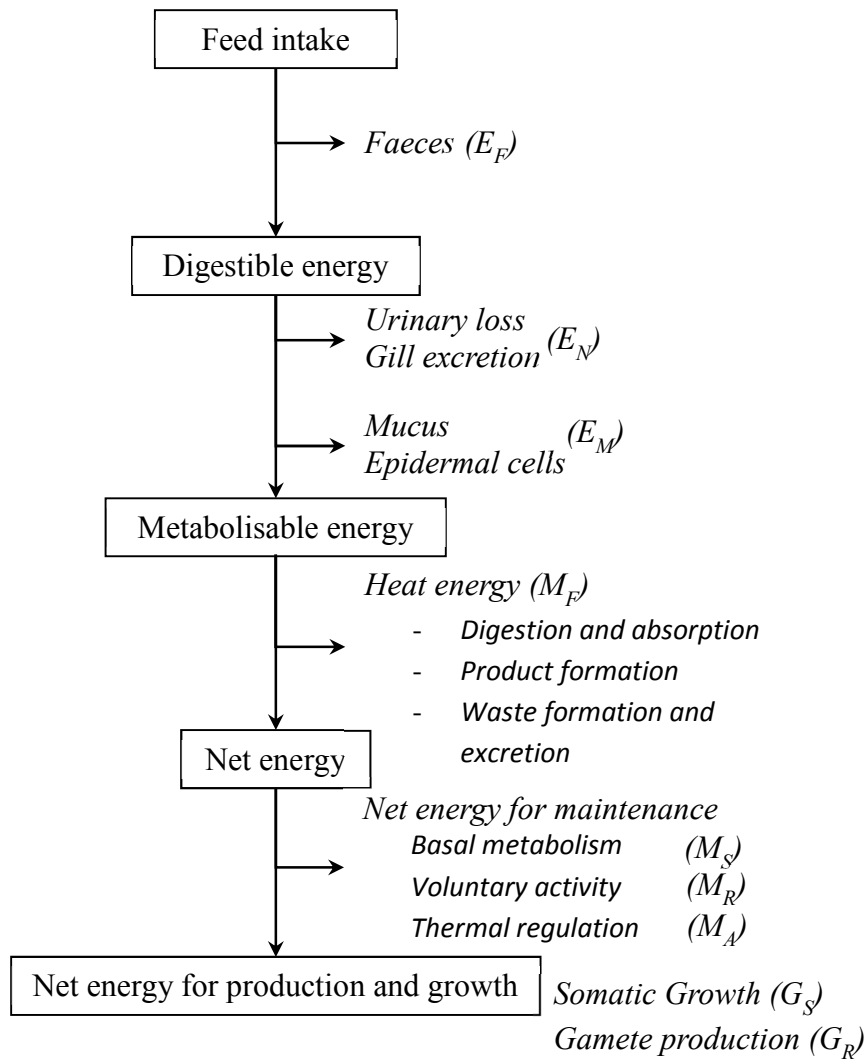


Figure 2 – Energy flux in fish, criteria used in the bio-energetic models (from Strand 2005, modified from Bailey 2003)

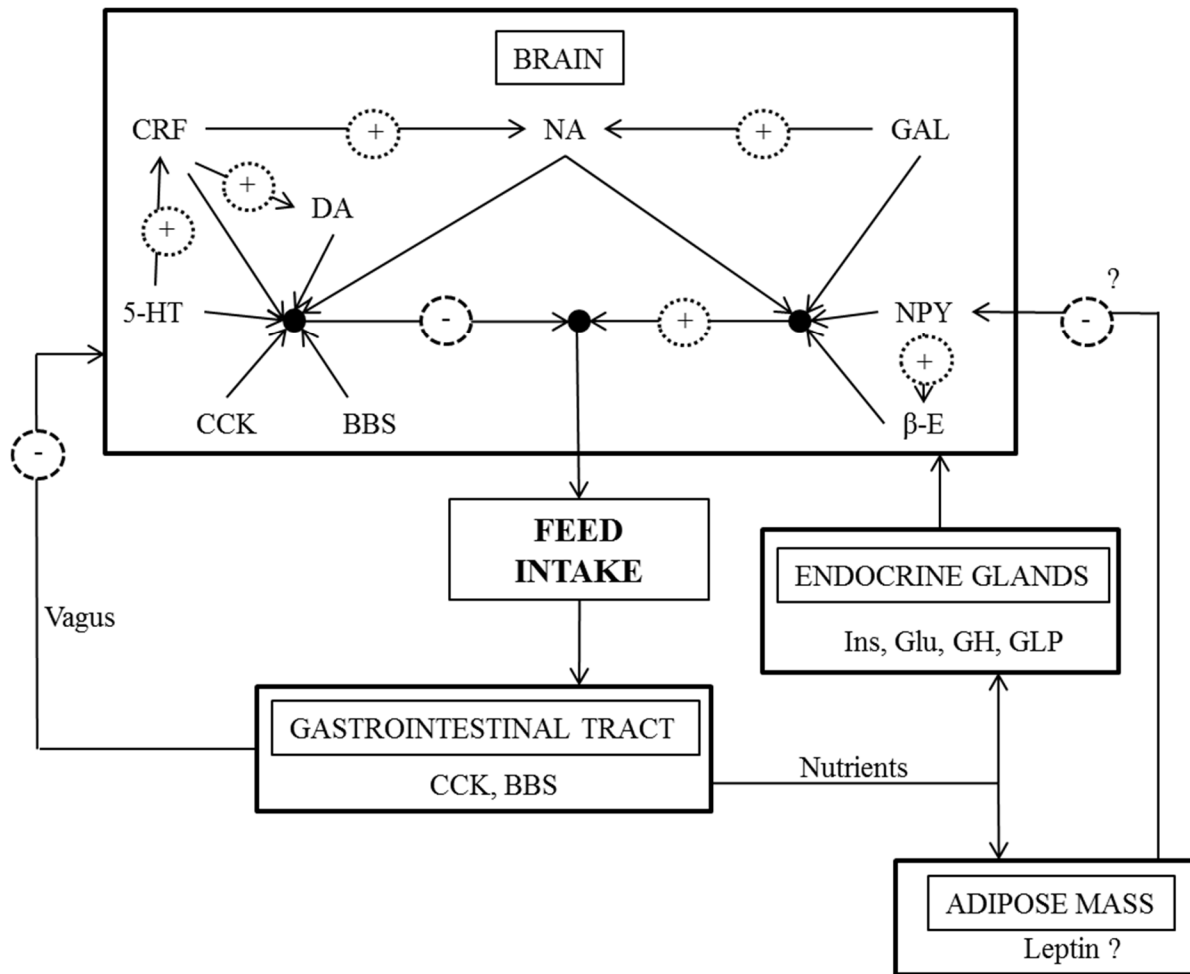


Figure 3 – A model for FI regulation by hormones and neuropeptides in fish (modified from de Pedro and Björnsson 2001) with CRF, corticotrophin-releasing factor; NA, noradrenaline; GAL, galanin; DA, dopamine; 5-HT, serotonin; CCK, cholecystokinin; BBS, bombesin; NPY, neuropeptide Y;  $\beta$ -E,  $\beta$ -endorphin; Ins, insulin; Glu, glucagon; GH, growth hormone; GLP, glucagon-like peptide; +, stimulatory input; -, inhibitory input.