Feed efficiency of Rainbow trout *(Onchorynchus mykiss)* kept at high and low stocking density

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ABSTRACT

Feed efficiency is a trait of high economic importance in fish production, and is highly related to feeding regimes employed and stocking density. However, feed efficiency is difficult to estimate because measurements of individual feed intake are generally not available in fish that are usually reared in groups in tanks. An alternative is to estimate feed efficiency using tank as the unit of measurement. The objective of this study was to investigate tank residual feed intake in rainbow trout kept at high (HD) and low (LD) stocking density during 42 days (Day 0-14 and Day 14-42) and the consequences of subsequently reducing density in the HD treatment between 42 and 78 days (Day 42-61 and Day 61-78). HD fish weighed less at all times than LD fish ($P < 0.05$). LD fish grew faster than HD fish ($P < 0.05$) but not between Day 42-61. The coefficient of variation of body weight was larger in HD fish than in LD fish ($P < 0.05$) at Day 14 and Day 42. LD fish ate more than HD fish between Day 14-78 ($P < 0.01$). HD fish were less food efficient than LD fish between Day 0-14 but more food efficient between Day 42-61. A higher coefficient of variation of body weight in the HD tanks suggests that growth and feed intake were inhibited because of dominance relationships at a high stocking density and possibly competition for food. After relocating HD fish to a low density treatment, HD fish showed compensatory growth and compensatory feed efficiency. Although it is not practical to estimate residual feed intake individually in fish, this research shows that calculation of tank residual feed intake can be used as an alternative, especially when used to compare families for family trait selection.

Keywords: growth, feed efficiency, fish, residual feed intake, stocking density, trout

1. Introduction

According to the World Fish Centre, global per capita fish consumption has doubled over the past 50 years, and production would need to double again to meet the projected demand over the next 25 years. Since supply from capture fisheries is static, with most stocks already heavily depleted, overfished or fully exploited, the increased demand has to be met by an increase in aquaculture production (Muir, 2005). Only about 10% of todays global aquaculture production is based on genetically improved stocks; some of the breeding programs consist only of the most basic components of a breeding scheme, while others are more advanced, including multi-trait breeding value estimation and molecular marker information (Gjedrem et al, 2012). Traits of high economic importance in fish production are growth rate,

feed efficiency, resistance to disease, meat quality, and age at maturation (Gjedrem, 1983). In farmed fish species, as in terrestrial animals, feed represents at least 50% of production costs; in addition, it is responsible for a substantial part of environmental loading (Grima, et al, 2008). However, despite its importance, measurement of feed efficiency requires advanced methods. Therefore, in contrast with terrestrial livestock species, knowledge on feed efficiency in fish is limited.

Residual Feed Intake (RFI) is widely used as a selection criterion in genetic selection programs of terrestrial livestock animals, where low values indicate high feed efficiency (e.g. Rauw, 2012). In aquaculture species, individual feed efficiency is difficult to estimate, because measurements of individual feed intake are generally not available in fish that are reared in groups in tanks. Alternatively, individual feed efficiency can be recorded using one fish reared per tank (Silverstein et al, 2005) or feed

efficiency can be estimated using the X-ray technique (Grima, et al, 2008). Whereas those methods are valuable in an experimental setting, they are difficult and costly to carry out routinely in fish production systems. A third alternative is to estimate feed efficiency using tank as the unit of measurement (Mambrini et al., 2004).

Feed intake and efficiency are highly related to feeding regimes employed and stocking density which directly influence social interactions and competition for food (Thorpe and Cho, 1995; Cutts et al, 1998). Increasing stocking density can negatively influence feed efficiency in fish through increased levels of stress and activity. For example, Larsen et al. (2012) observed similar feed intakes but higher resting metabolic rates and therefore reduced feed efficiencies in rainbow trout in high density groups compared with low density groups. In addition, Laursen et al. (2013) observed that farmed rainbow trout in a high stocking density group had elevated stress levels and higher oxygen consumption than those in a low stocking density group.

The objective of this study is to evaluate a method that involves measurement of residual feed intake by tank in Rainbow trout *(Onchorynchus mykiss)*. In addition we investigate tank residual feed intake in fish kept at high and low stocking density and the consequences of reducing stocking density after a period of high stocking density.

2. Materials and Methods

2.1. Animals and their management

A total of 2,000 rainbow trout *(Onchorynchus mykiss)*, with an average weight of 48 g, originating from a commercial trout farm, were transported to the facilities of the Zamarramala Aquaculture Centre (Segovia, Spain). The fish were randomly placed into one of two independent recirculation units in two separate adjacent rooms; each room consisted of 10 identical tanks of 500 l each. After 15 days, in each room, 495 fish were allocated to one high density tank (HD treatment) and five groups of 99 fish each were allocated to five low density tanks (LD treatment); the four remaining tanks in each room were left empty for later use. The initial densities were 37 kg/m^3 for the high-density tanks and 6 kg/m^3 for the low-density tanks. Fish had four weeks to acclimatize before the start of the experiment at Day 0.

Water came from a well with a constant temperature of 14.6 °C in a recirculation system, therefore, fish in tanks kept within the same room share the same water. Fish were kept at a photoperiod of 12 hr. light - 12 hr. dark. During the experiment, the average dissolved oxygen was greater than 7.4 ppm. The pH hovered between 7.5 and 8.5, and levels of NH4+ between 0.1 and 0.2 ppm at all times. Fish were fed with a commercial diet using feeding tables recommended by the manufacturer (DIBAQ DIPROTEG). Fish were provided with a starter diet until reaching 100 g weight (43.7% protein, 16.0% fat) and with a finisher diet (43.3% protein, 19.7% fat). Feeding was carried out twice daily by hand and was *ad libitum* until fish stopped eating.

At the beginning of the acclimatization period, a white spot infection *(Ichthyophthirius multifiliis)* was observed that affected all tanks in both rooms. Dead fish were removed from each tank daily and diagnosis was confirmed by microscopic examination of small superficial scrapes of skin. Tanks were instantly treated with formalin at a dose of 250 ppm and contaminated water replaced every two days. Skin analysis showed that the infection was eliminated within 12 days of the acclimatization period. To assure that the infection did not return, small scrapes of skin were collected on a sample of 8 fish per tank during all the weight measurements.

2.2. Feeding experiment

At Day 0, the experiment started with 56 to 65 animals per tank in the ten tanks assigned to the LD treatment, and 401 and 416 animals per tank in each of two tanks assigned to the HD treatment. At Day 42, the average density in the tanks was 55 and 11 kg/m^3 for the HD and LD treatments, respectively. At that point, the fish in each room belonging to the high-density tank were divided into five equal groups and redistributed over five tanks, with an average density of 11 kg/m^3. The trial ended on Day 78, at which the average density in the tanks was 17 and 16 kg/m^3 for the HD and LD treatments, respectively.

Body weight (BW) and fork length (FL) were individually recorded five times at Day 0, 14, 42, 61, and 78 after anaesthetization with tricaine methanesulfonate (MS222®). Cumulative feed intake and biomass gain was calculated for each tank for Period 1 (Day 0-14), Period 2 (Day 14-42), Period 3 (Day 42-61) and Period 4 (Day 61-78). Feed intake (FI), body weight and body weight gain (BWG) of an average fish were calculated for each tank by dividing total feed intake, biomass and biomass gain for each tank by the number of fish. Specific rate of increase in weight (SGR) and length (SLR) were calculated as $SGR = (Ln(weight_{end}) - Ln(weight_{start}))/(time)(100\%)$, and $SLR = (Ln(length_{end}) - Ln(length_{start}))/(time)(100\%)$, where the weight and length at the end and start correspond to those of Period 1, 2, 3 and 4 (Hopkins, 1992). The coefficient of variation of body weight (CVBW) was calculated as $CVBW = ([sd/mean]100)$ of body weight.

An overview of the experimental procedures is given in Table 1. The experiment had approved animal care protocols from the Instituto Tecnológico Agrario of Junta de Castilla y León (Spain).

2.3. Feed efficiency: residual feed intake

The equation used to estimate residual feed intake (RFI) for each tank was based on the following multiple linear regression of food intake on metabolic weight and body weight gain of an average fish in each tank:

Day of Experiment	Procedure
-45	Rainbow trout arrive at Zamarramala Aquaculture Centre
-30	Fish are allocated to high and low density experimental tanks
0	First weight and length measurement
14	Second weight and length measurement
42	Third weight and length measurement. Fish of the high density treatment are reallocated to low density tanks.
61	Fourth weight and length measurement
78	Fifth weight and length measurement

Table 1

$$FI_i = b_0 + (b_1 BW_i^{0.80}) + (b_2 BWG_i) + e_i \qquad (1)$$

Where FI_i = feed intake of an average individual in tank i (kg); $BWi^{0.80}$ = metabolic body weight of an average individual in tank i ($kg^{0.80}$); BWG_i = body weight gain of an average individual in tank i (kg); b_0 = the population (tank) intercept; b_1, b_2 = partial regression coefficients representing maintenance requirements per metabolic body weight and feed requirements for growth, respectively; and e_i = the error term, which represents the RFI of an average individual in tank i. Metabolic body weight was estimated as the average value of body weight of an average individual at the beginning and at the end of each period to the power 0.80 (Grima, et al, 2010). Animals with a negative RFI are more feed efficient than the average of the population on which the model is formed, whereas animals with a positive RFI are less feed efficient.

2.4. Statistical analysis

The SAS program (SAS Inst. Inc., Cary, NC) was used for the statistical analysis of all traits. The analysis of variance model used to describe individual body weight and fork length was:

$$Y_{ijk} = \mu + Room_i + Treatment_j \\ +(Room)(Treatment)_{ij} + e_{ijk} \qquad (2)$$

where $Room_i$ = the effect of the room i (2 rooms; fixed effect), $Treatment_j$ = the effect of the stocking density j (HD, LD; fixed effect), $(Room)(Treatment)_{ij}$ = the interaction effect of Room i with Treatment j, and $eijk$ = the error term of animal k, $e_{ijk} < NID(0, \sigma_e^2)$. Body weight and fork length tested under this model were denoted by Y_{ijk}, as measured on animal k situated in room i, allocated to treatment j. Initially, the effect of tank was also included, but because this effect was

not significant, it was excluded from further analysis. The same model, but excluding the non-significant interaction effect of $(Room)(Treatment)_{ij}$, was used to analyze CVBW.

Feed intake, RFI, BWG, SGR, and SLR are not estimated individually but for each tank, expressed as the values of an average fish in each tank. The analysis of variance model used to describe these traits in each period was:

$$Y_{ijkl} = \mu + Room_i + Treatment_j + Period_k \\ +(Treatment)(Period)_{jk} + e_{ijkl} \qquad (3)$$

where $Room_i$ = the effect of the room i (2 rooms; fixed effect), $Treatment_j$ = the effect of the stocking density j (HD, LD; fixed effect), $Period_k$ = the effect of the period k (Period 1 to 4; fixed effect), $(Treatment)(Period)_{jk}$ = the interaction effect of Treatment j with period k, and e_{ijk} = the error term of an average animal l, $e_{ijk} < NID(0, \sigma_e^2)$. Average daily FI, RFI, BWG, SGR, and SLR tested under this model were denoted by Y_{ijk}, as measured on an average animal l situated in room i, allocated to treatment j in period k. Initially, the interaction effects of room with treatment and period were also included, but because these effects were not significant, they were excluded from further analysis.

Values are presented as least squares means and phenotypic correlations are estimated after adjusting for the effects included in models (2) or (3). Post hoc statistical power was computed using the means and standard deviations within treatment (low or high density) observed in this experiment and together with the software Gpower (Faul et al., 2007). The power for significance levels of 0.05 and 0.01 was 0.75 and 0.49, respectively.

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3. Results

Fig. 1

3.1. BW, FL, BWG, SGR, SLR, CVBW and FI

Figure 1 presents least squares means of body weight (a), fork length (b) and the coefficient of variation of body weight (c) at Day 0, 14, 42, 61, and 78 for each treatment. Fish in the high density stocking treatment weighed less at all times than fish in the low stocking treatment ($P < 0.05$ at Day 0, $P < 0.01$ at Day 14, and $P < 0.0001$ at Day 42 to 78; Figure 1a), and shorter between Day 14 and 78 ($P < 0.01$ at Day 14, and $P < 0.0001$ at Day 42 to 78; Figure 1b). LD fish grew faster than HD fish in Period 1 (0.90 ± 0.03 vs 0.71 ± 0.06 g/d, respectively; $P < 0.05$), Period 2 (10.4 ± 0.03 vs 0.73 ± 0.06 g/d, respectively; $P < 0.0001$) and Period 4 (12.0 ± 0.03 vs 10.4 ± 0.03 g/d, respectively; $P < 0.0001$), but growth rate was not significantly different between LD and HD fish in Period 3 (12.2 ± 0.03 vs 12.0 ± 0.03 g/d, respectively). The specific rate of increase in weight was higher in LD fish than in HD fish in Period 1 (1.68 ± 0.03 vs $1.42 \pm 0.07\%$, respectively; $P < 0.01$) and Period 2 (1.40 ± 0.03 vs $1.13 \pm 0.07\%$, respectively; $P < 0.01$), but was lower in Period 3 (1.21 ± 0.03 vs $1.39 \pm 0.03\%$, respectively; $P < 0.001$) and similar in Period 4 (0.98 ± 0.03 vs $0.97 \pm 0.03\%$, respectively). The specific rate of increase in length was higher in LD fish than in HD fish in Period 1 (0.34 ± 0.009 vs $0.25 \pm 0.02\%$, respectively; $P < 0.0001$) and Period 2 (0.43 ± 0.009 vs $0.39 \pm 0.02\%$, respectively; $P < 0.05$), but was similar in Period 3 (0.49 ± 0.009 vs $0.48 \pm 0.009\%$, respectively) and in Period 4 (0.35 ± 0.009 vs $0.35 \pm 0.009\%$, respectively). The coefficient of variation of body weight was significantly higher in HD fish than in LD fish at Day 14 ($P < 0.05$) and at Day 42 ($P < 0.01$).
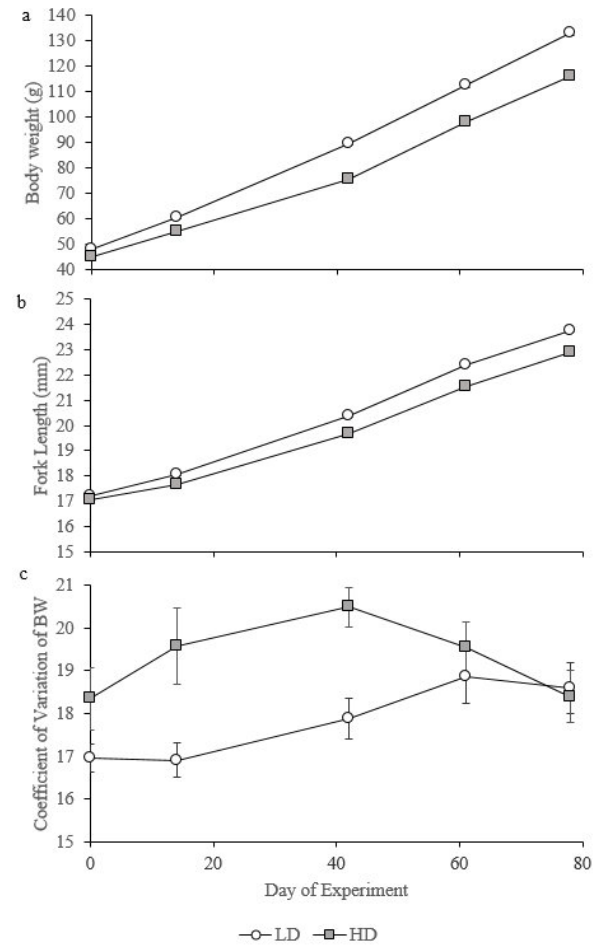
The relationship between cumulative feed intake and body weight of an average fish is given in Figure 2, for each tank in each of the four periods. Animals that ate more, grew faster ($R = 0.90, P < 0.0001$). LD fish ate more than HD fish in Period 2 (1.05 ± 0.02 vs. $0.84 \pm 0.05 g/d$; $P < 0.01$), Period 3 (1.05 ± 0.02 vs $1.17 \pm 0.02 g/d$; $P < 0.0001$) and Period 4 (1.41 ± 0.02 vs. $1.21 \pm 0.02 g/d$; $P < 0.0001$), but the difference was not significant in Period 1 (0.79 ± 0.02 vs. $0.73 \pm 0.05 g/d$).
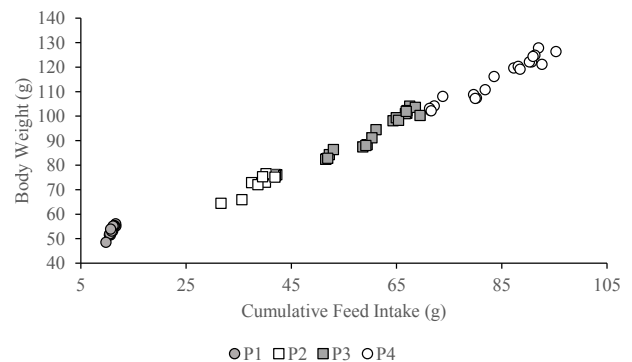

Fig. 2

3.2. Feed efficiency

The relationship between feed intake, and metabolic body weight and body weight gain of an average fish in each tank is given in Figure 3a and 3b, respectively. The R^2 of equation (1) indicated that 65% of the variation observed in FI could be attributed to variation in metabolic body weight and body weight gain.
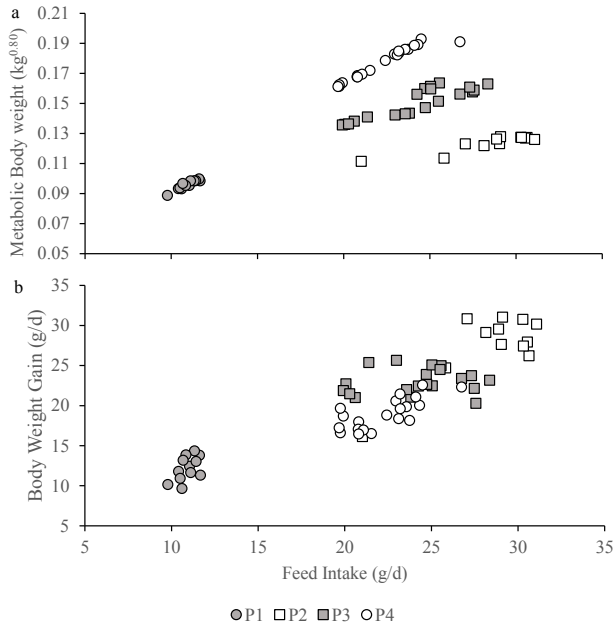

Fig. 3

Average residual feed intake for each tank in each period is given in Figure 4. HD fish had a higher RFI (were less feed efficient) than LD fish in Period 1 ($P < 0.0001$). The difference had decreased and was no longer significant in Period 2. After relocation, HD fish had a lower RFI (were more feed efficient) than LD fish ($P < 0.01$). In Period 4, the differences had disappeared and RFI was no longer significantly different from zero ($P = 0.9985$).
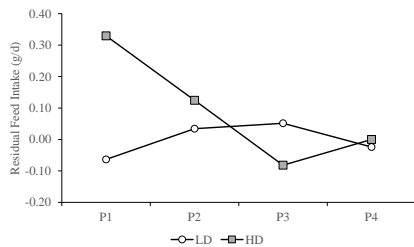

Fig. 4

4. Discussion

Aquatic production systems are unique in that the animals utilize a three-dimensional medium, where density is defined as the number of animals confined in a given three-dimensional space as influenced by the number of fish or weight of fish per volume (Conte, 2004). At high densities, inter-individual competition increases possibly as the result of the formation of dominance hierarchies (Adams et al., 1998; North et al, 2006). However, as densities further increase, the formation and maintenance of hierarchies may actually become more difficult (North et al, 2006). When resources are limited within the group, the most competitive individuals will gain a disproportionate share of these resources, thus lowering the average success of group members; the more restricted and defensible a food supply, the greater the competition (Canario et al, 1998; Gilmour et al, 2005; North et al, 2006).

Competition between individuals in particular and fish to fish interactions in general may result in concomitant levels of activity and stress (Conte, 2004). Metcalf et al. (1995) and Sloman et al (2000) demonstrated that social status is strongly related with standard metabolic rate in juvenile Atlantic salmon and brown trout, respectively. Factors such as physical disturbance and social domination of one fish by another can act as powerful stresses with an obvious and major influence on growth rate and food conversion efficiency, partly as a result of the catabolic or gluconeogenic effects of corticosteroids (e.g. Barton and Iwama, 1991; McCormick et al., 1998). As a consequence, high stocking density may lead to a decrease in overall weight, length, growth rate and feed efficiency (Fagerlund et al, 1981). The feeding regimes employed in commercial fish farming thus influence the level of competition for feed resources amongst fish and subsequently the productive output (Thorpe and Cho, 1995; Cutts et al, 1998).

Li and Brocksen (1977) indicated that dominant trout in a group grew faster and more efficiently than the rest of the population. As a result, it was observed that the variance of growth rate, consumption rate and growth efficiency tended to increase with density; this was suggested to be a good indication of intraspecific competition. Also, Jobling (1995) suggests that rapid and homogeneous growth rates, and uniform body weights at harvest, must result from a social environment that is favorable, whereas the opposite holds when interindividual competition increases. Rapid and homogeneous growth is expected to be accompanied by a more favorable feed efficiency (Jobling, 1995).

In the present study, between Day 0 and Day 42, when fish were kept at distinct stocking densities, animals in the high stocking density treatment weighed significantly less and were significantly shorter, had slower growth rates and lower specific rates of increase both in weight and in length. In addition, fish were less feed efficient (had higher residual feed intake) than LD fish, which was significant in the first period. The coefficient of variation of body weight (and of fork length; data not presented) was larger in HD individuals than in LD fish at Day 14 and at Day 42. These results suggest that in the present experiment, growth was negatively influenced by the occurrence of dominance relationships and stress at a high stocking density. Although feed was given to satiety, since feed was provided only two times a day, competition for food may still have

occurred when the group was thought to be nutritionally satisfied (and feeding was stopped), whereas submissive fish may still not have eaten satisfactorily. Therefore, it is possible that the reduction in efficiency and growth during this period may have become counteracted by increasing the feeding rate. Indeed, whereas the stocking density in the HD group reached an average of 55 kg/m^3, stocking density practices on commercial trout farms can be successful varying from < 20 to > 80 kg/m^3 (North et al, 2003).

When an unfavorable resource situation is corrected, compensatory growth has been described in terrestrial farm animals such as cattle and sheep (Ryan, 1990), and chickens (Zubair and Leeson, 1996), but also in fish (Ali et al, 2003). Compensatory growth is described as accelerated growth after a period of growth depression resulting from a limited resource availability due to undernutrition, stress or disease. Refstie and Kittelsen (1976) showed in brown trout that a high stocking density can depress growth and that subsequently reducing the density induces compensatory growth. In the present study, the difference in growth rate between LD and HD disappeared in Period 3 when fish in the high density group were relocated to a low density treatment. The specific rate of increase in weight now became *larger* in HD than in LD fish. In the last period, in Period 4, LD fish again grew significantly faster than HD fish while the specific rate of increase both in weight and in length was similar between the treatments. It should be noted that the results could not be tested against a control group maintained at high density.

Weight gain during compensatory growth can be attributed to the accumulation of protein and fat as well as water. Dobson and Holmes (1984), in rainbow trout, conclude that weight gains are due to growth rather than to an increase in gut fat deposits or water uptake. It is unclear whether fish are eating more feed during compensatory growth or whether they are processing it more efficiently, or a combination of both. In the present study, HD fish ate less food per individual per day in each period than LD fish. The higher coefficient of variation of body weight in the HD group suggests that the coefficient of variation of food intake may also have been higher (but this could not be estimated) resulting in some animals that were able to eat (considerably) more than other tank mates. To our knowledge there are no reports in the literature regarding compensatory feed efficiency in response to a reduction in stocking density, after a period of stocking at high density. Results of the present study show that fish in the HD treatment became significantly more feed efficient than LD fish, in the first period (Period 3) after relocation. This suggests that the compensatory growth observed in Period 3 corresponds to a compensatory feed efficiency. Interestingly, the coefficient of variation in BW was no longer significantly different between HD and LD fish after Day 42 (relocation) and the difference reduced up to Day 78, indicating that body weights became more homogeneous after relocation.

Two methods are used to evaluate feed efficiency in animal production: feed conversion ratio (FCR) and residual feed in-

take (RFI). Feed conversion, the traditional measure of feed efficiency, is defined as the inputs (food) per unit of outputs (weight gain). However, it shows significant phenotypic and genetic correlations with feed intake, growth rate, and mature size, moreover, the outcome of selecting for a ratio, when efficiency is included in the selection index, cannot be predicted. In contrast, RFI is defined as the difference between the actual feed intake and that predicted from a linear regression of feed intake on maintenance (metabolic body weight) and growth, and is therefore phenotypically independent of growth rate and body weight (size) (Rauw, 2012). Variation in RFI can be caused by variation in partial efficiencies for maintenance and growth and by variation in metabolic food demanding processes not included in the model, such as behavioral activities, responses to pathogens and responses to stress. Indeed, animals that are more active are found to be less food efficient (Rauw, 2012). Herd and Arthur (2009) indicate that, in beef cattle divergently selected for RFI, 9% of the proportions of variation in RFI could be explained by physical activity, and 37% by tissue metabolism and stress. Also in fish, activity rates can be a large and variable component of an individuals energy budget (Boisclair and Sirois, 1993). According to Petrell and Jones (2000), energy expenditure in salmon due to power requirements for swimming explained over 20% of the observed difference in feed conversion ratio. Martins et al. (2001) reported that high glucose responding African catfish, i.e., animals that show a higher stress response, seem to be the less efficient fish in terms of resource utilization for production. In a later study in juvenile Nile tilapia they showed that individual differences in feeding activity and stress response explained part of the differences in feed efficiency by explaining variance in maintenance energy expenditure (Martins et al., 2011). Trenzado et al (2006) showed that selection for a high stress response in rainbow trout affected feed efficiency negatively. These results were confirmed by Øverli et al (2006).

Heritabilities of RFI are estimated to be moderate (Crews, 2005) which has resulted in RFI to be included in the breeding goal of several livestock species (Herd, 2009). Feed efficiency is of high economic importance in livestock and aquaculture species alike, however, measurement of feed efficiency in fish is complicated since individual intake is very difficult to measure. As Grima, et al (2010) indicate, improving feed utilization efficiency in aquaculture production systems is crucial. This requires both fundamental research into the phenotypic and genetic background of feed efficiency in different fish species and how this correlates with other production and welfare traits, and research into the practical application of techniques to measure feed efficiency in commercial situations and implement these in the breeding objective. Although individual feed recording by evaluating fish independently or by using methods such as the X-ray technique deliver useful fundamental information, these methods are not practical in commercial situations. Therefore, in the present experiment, we evaluated RFI by tank. Using tank residual feed intake as a measure of feed efficiency allows for the estimation of feed efficiency of a group of fish without regis-

tering individual feed intake. The draw-back is that there is one recording per tank (feed intake and body weight) so a great deal of information is lost when compared to individual recording. Also, if applied in selection programmes, then all selection must be based on group statistics, and consequently includes losing within-group information (Kolstad et al, 2004). However, this method may be particularly useful for selection within families. Family selection is more efficient compared with individual selection for traits with low heritability, while it is less efficient for traits with high heritability (Gjedrem, 2000). Family selection is particularly useful for traits that are not practical to measure individually but that are possible to record in groups.

5. Conclusion

In the present study, fish in a high density treatment had reduced average body weights, growth, feed intakes and were less food efficient. A higher coefficient of variation of body weight in the HD tanks suggests that growth and feed intake was inhibited because of dominance relationships at a high stocking density and competition for food. After relocating HD fish to a low density treatment, HD fish showed compensatory growth and compensatory feed efficiency and the difference in coefficient of variation of body weight between HD and LD fish decreased. The commonly reported effects of group competition on reductions in food efficiency, nutritional condition and growth and increase in fin erosion may be indicative of reduced welfare status. Increasing stocking density may be successful with additional measures, such as increased oxygen administration and continuous feeding. Research is needed for prescribing acceptable levels of health, nutritional condition and behavioral indicators of intensively farmed fish (Ellis et al, 2005; 2008). With heritabilities that are moderate, residual feed intake is included in the breeding goal of several livestock species. Although it is not practical to estimate residual feed intake individually in fish, this research shows that calculation of tank residual feed intake can be used as an alternative, especially when used to compare families for family trait selection.

6. Acknowledgements

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