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Deriving breeding goals and expected selection responses for a breeding program that limits the environmental impacts of rainbow trout farming

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Abstract

With the growing societal concerns about the sustainability of the food production systems, there is an increasing interest at considering not only economic gains but also environmental impacts in the selection of farmed species. In this study, we compared predicted selection responses for alternative breeding programs aiming to limit environmental impact of the production of rainbow trout, one of the most important fish species in European aquaculture. The environmental consequences of genetic improvement based on an optimal index selection were instigated in a theoretical rainbow trout fry production farm under a constant annual production volume. The tested breeding goals included three different traits: the body weight at 110 days post hatching (BW), the feed efficiency (FE) measured through the feed conversion ratio and the survival rate (SR) while we tested several correlations scenarios between the traits. A cradle-to-farm-gate life-cycle assessment was performed to evaluate the environmental value of each trait that have been used in the breeding goals defined in order to maximize selection responses while minimize environmental impacts. We explored different impact categories, such as acidification, climate change, cumulative energy demand, eutrophication, land occupation and water dependence. Annual genetic gains using optimal selection indexes were ranging from 0.9 to 1.4% for the different impact categories while the annual genetic gains were ranged from 0.4 to 4.6 % for BW, 0.0 to 2.8 % for FE and -11.0 to 0.9 % for SR. We demonstrated the interest of using ENV in breeding goals to minimize environmental impacts at the farm level while maintaining high genetic improvements in growth and feed efficiency related traits. Nevertheless, another selection strategy should be considered to avoid negative consequences on SR when considering possible negative correlations between traits. Although our results are promising, their interpretations have to be qualified by the lack of considerations for the economic repercussions of such selection strategy.

Keywords: Breeding objective, Fish farming, Life-Cycle Assessment, Optimal index selection, Salmonid, Sustainability

1. Introduction

Rainbow trout (*Oncorhynchus mykiss*) is the main fish species farmed in France and one of the major salmonid species farmed worldwide (960,000 t in 2020; FAO, 2022). Production is historically performed in flow-through systems, in which inlet water is diverted from a river, passed once through the rearing tanks and then returned to the river. In trout production systems, all nutrients are provided by exogenous formulated feed containing fish meal, fish oil and plant-based ingredients in various proportions. The entire production cycle is not necessarily ensured on the same site. Thus, the farms producing from a few to several hundred tons annually have different production objectives responding to different markets. For instance, some farms produce fry, pan-sized trout and/or large trout for fillets (fresh or smoked), while others produce fish for restocking rivers or ponds for angling (Chen et al., 2015). These different production strategies imply different practices (e.g., feed type, feeding management, oxygen supply, rearing densities, and water treatment) and also drive breeding programs. Rainbow trout breeding programs are currently mainly focused on the increase of productivity (growth, disease resistance, processing yield), but also on answering consumer demands (fish morphology, product quality; Chavanne et al., 2016).

Breeding objectives always involve consideration of multiple traits, even in situations where output of a single trait is dominant (Sölkner et al., 2008). In the optimal selection index derived to maximize the expected selection response on the breeding objective (Hazel, 1943), the relative importance of each trait is scaled by its weight defined for the multi-trait breeding goal. When considering that the aim of the breeding program is to maximize farm profit, the weights used in the breeding objective are economic values derived using profit equations (Brascamp et al., 1985; Dekkers and Gibson, 1998; Gunia et al., 2013). The economic value (EV) of the trait is then derived as the marginal profit related to a change in trait expression of one physical unit (Hazel et al., 1994).

Deriving the optimal selection index corresponds to calculate the index weights for all the traits included in the selection index based on EV as well as on the phenotypic and genetic correlations between all traits considered in the breeding program. Using this optimal selection index will lead the direction and magnitude of the expected responses in the considered traits to maximize the economic return of genetic improvement. However, EV might not be the best weights to use in a breeding objective oriented towards the improvement of the environmental sustainability of fish production (Olesen et al., 2000).

With the growing societal concerns about the sustainability of animal and plant production, there is an increasing interest at considering not only economic gains but also environmental impacts in the selection of farmed species. This aspect of selective breeding remained, nevertheless, an open field of research with only few studies on cattle (e.g., Cantalapiedra-Hijar et al., 2020; van Middelaar et al., 2014), pigs (e.g., Ali et al., 2018) and fish (e.g., Besson et al., 2020, 2016). Recently, Besson et al. (2020) compared the use of EV or environmental values (ENV) as weights in a breeding goal combining thermal growth coefficient (TGC) and feed conversion ratio (FCR) in European sea bass (*Dicentrarchus labrax*). Such ENV can be used as weights in the breeding goal to derive a selection index that maximizes the reduction of the environmental impacts of fish production. They found that using ENV in the breeding goal generated an annual reduction of, at least, 0.92% in eutrophication per ton of fish produced. Integrating ENV into a breeding goal requires properly assessing the environmental impacts at the farm level which can be achieved using a life-cycle assessment (LCA).

LCA is an international standardized holistic method (ISO, 2006) designed to evaluate the global impact of a product or a process on the environment. Such evaluation implies the assessment of all the different phases required for or caused by the product's existence; it includes raw material uses and energy production, manufacturing, transport, and emissions to the environment at each stage until the product's end of life.

For the two last decades, LCA has been regularly used to assess the environmental impacts of aquaculture production through different environmental impact categories including mainly acidification, climate change, energy demand, eutrophication, land competition and water dependence. These categories are usually chosen for relevance to the known principal impacts of aquaculture systems and to enable comparison with previous seafood LCA studies (Bohnes et al., 2019; Henriksson et al., 2012; Pelletier et al., 2007). Salmonid production has been extensively studied through LCA with some investigations focused on rainbow trout production (e.g., Aubin et al., 2009; d'Orbcastel et al., 2009; Dekamin et al., 2015; Samuel-Fitwi et al., 2013).

The aims of our study were: i) to define various breeding goals based on ENV derived from different LCA impact categories and ii) to predict the expected selection responses for all those breeding objectives as well as for the three main traits (growth rate, feed conversion ratio and fry survival) of interest in a rainbow trout farm producing fry.

2. Materials and Methods

2.1. Farm design and operations

All the data (i.e. zootechnical performances, farm management, infrastructures and equipment inventory, nature and quantities of inputs...) were derived from four interviews of fish farmers and visits to production sites in Brittany, the leading region for trout production in France, performed in February 2022. A theoretical commercial French fish farm producing rainbow trout fry in a flow-through system was considered in this study (see **Table 1** for details). In trout farming, production volume in a given site is under strict regulations, so the production was constrained to a quota of 12 tons of fry sold annually.

Three cohorts of trout were reared on the site throughout the year. The first two cohorts, each consisting of 400,000 eyed eggs from a French breeder, entered the site in December (cohort 1) and March (cohort 2). They will be sold at a commercial size of 10 g. The last cohort (cohort 3) consisted of 200,000 eyed eggs that entered the site in August and will be reared up to size of 40 g. We defined a production cycle as the duration from the entrance of the eggs of cohort 1 on the farm to the exit of the fish of cohort 3.

The flow-through production system was divided into a 200-m² indoor facility where trout are reared from eggs to 1-2 g and outdoor rearing structures where fish were then reared up to the commercial sizes. In addition, two other buildings (30 and 50 m²) were used for equipment and feed storage).

Table 1. Production data and inputs used for the rainbow trout fry production in a theoretical commercial French fish.

| | Cohort 1 | Cohort 2 | Cohort 3 | All combined |
|---|-----------------|-----------------|-----------------|---------------------|
| Date in | December 1 | March 1 | August 1 | - |
| Date out | April 23 | June 27 | February 5 | - |
| Duration for one cycle de production | - | - | - | 431 |
| Number of eggs in | 400000 | 400000 | 200000 | 1000000 |
| Number of fries out | 361919 | 361916 | 180959 | 904794 |
| Size after indoor phase (g) | 1.1 | 1.1 | 2.2 | - |
| Size after outdoor phase (g) | 10 | 10 | 40 | - |
| Rearing duration (d) | 144 | 119 | 189 | 452 |
| Indoor rearing duration (d) | 64 | 55 | 54 | 173 |
| Outdoor rearing duration (d) | 80 | 64 | 135 | 279 |
| Mortality over the indoor phase (%) | 7 | 7 | 7 | 7 |
| Mortality over the outdoor phase (%) | 3 | 3 | 3 | 3 |
| Total volume of water used (m ³) | 289550 | 202848 | 443654 | 936053 |
| Water used during the indoor phase (m ³) | 132710 | 114048 | 111974 | 358733 |
| Water used during the outdoor phase (m ³) | 156840 | 88800 | 331680 | 577320 |
| Total electricity used (kWh) | 4838 | 13020 | 2654 | 20513 |
| Electricity used during the indoor phase (kWh) | 1382 | 2340 | 2654 | 6377 |
| Electricity used during the outdoor phase (kWh) | 3456 | 10680 | 0 | 14136 |
| Total feeds used (kg) | 2368 | 2407 | 5351 | 10127 |
| Feed 1 (kg) | 81 | 76 | 47 | 204 |
| Feed 2 (kg) | 705 | 666 | 413 | 1784 |
| Feed 3 (kg) | 1582 | 1666 | 798 | 4045 |
| Feed 4 (kg) | 0 | 0 | 4094 | 4094 |
| Feed conversion ratio (FCR; kg kg ⁻¹) | 0.66 | 0.66 | 0.74 | 0.70 |

In the indoor facility, rearing structures consisted of thirty-six 0.38-m³ fibre-glass tanks under artificial light. The water supply was by gravity from a surrounding stream, and the average monthly temperature varied from 7 to 19 °C throughout the year, while the water flow ranged from 10 to 110 m³ h⁻¹. During low water periods (in April and August), a 4-kWh pump was used for water recirculation, and a 1-kWh blower supplied air. When the density of fish became limiting in the indoor system (i.e. 30 kg m⁻³) without air or oxygen supply, fish were sorted and transferred in outdoor rearing facilities consisting of four 32-m² raceways and two 85-m² raceways. Fish first transferred into two 32-m² raceways were sorted and distributed into the other raceways once the stocking density reaches 30 kg m⁻³. Up to eight 0.75-kWh aerators were used during this rearing phase during low water periods. Another river provided the water supply throughout the outdoor rearing to reach the commercial size. Over the production cycle (i.e. 3-6 months), fish were fed using four different diets, and their rationing was adjusted according to fish size and water temperature.

Daily growth of the fish was modelled using a model developed by Muller-Feuga (1990), considering the fluctuating temperatures occurring during the rearing phase:

$$\frac{dBW}{dt} = \Gamma f_1(BW) f_2(\theta)$$

Expression dBW/dt is the body weight increase, $f_1(BW)$ is the weight function, and $f_2(\theta)$ is the thermal function. Parameter Γ is exogenous and incorporates all other factors influencing growth.

The weight function is assumed to be log-linear (Ricker, 1979). Thus, an increase in weight is positively related to fish weight (BW), but with a smaller percentage as the size rises. That is:

$$f_1(BW) = C BW^m$$

Where C is the log-linear regression parameter. The parameter m has been estimated for hot blood vertebrates, obtaining a value of 0.7 (Brett and Groves, 1979).

$$f_2(\theta) = D(e^{\alpha(\theta_M - \theta)} - e^{\beta(\theta_M - \theta)})$$

Function $f_2(\theta)$ is based on exponential form, and it includes maximum and minimum water temperature limits beyond which growth is impossible. D is a temperature adjusting parameter, while α and β are the first and the second temperature function parameters, respectively (Muller-Feuga, 1990). The variable $\theta = \theta(t)$ represents water temperature in time t . Parameter θ_M is the maximum temperature for possible growth under culture conditions.

On this farm, the mortality rate was estimated at 7% for the indoor rearing (M_{in}), the most sensitive phase and 3% over the outdoor rearing (M_{out}). Thus, the number of eggs or fish for a given day (Nb_n) can be calculated as follows:

$$Nb_n = Nb_{n-1} - ((Nb_{n-1} M_{in \text{ or } out})/d)$$

Where Nb_{n-1} is the number of eggs or fish the day before and d is the duration of the rearing phase (i.e. indoor or outdoor) in days.

Rearing density (RD) was calculated as the product of the individual weight (BW) and the number of eggs or fish (Nb) divided by the volume of the rearing structure (V):

$$RD \text{ (kg m}^{-3}\text{)} = \frac{BW \text{ (kg)} Nb}{V \text{ (m}^3\text{)}}$$

Feed conversion ratio (FCR) was calculated as the ratio between the feed distributed per production cycle and the fish production (i.e. the biomass of fry at the exit of the farm minus the biomass of eggs at the entrance):

$$FCR \text{ (kg kg}^{-1}\text{)} = \frac{\text{Feed distributed (kg)}}{\text{Fry out (kg)} - \text{eggs in (kg)}}$$

All combined, this information allowed us to model each rearing step on a daily basis using Excel® version 2019 software. The outputs of this model were used to generate inventory data for the LCA. Two limiting factors were considered in this step: (1) the annual production should stay constant, and (2) without providing O₂ addition, the rearing density should not exceed 30 kg m⁻³.

2.2. Life cycle assessment

2.2.1. Goal and scope

An LCA was conducted according to the steps described in **Figure 1** and general requirements of the methodology proposed by ILCD standards (Joint Research Centre, 2010). The methodology was adapted to the characteristics of fish farming. The goal and scope of this study is the environmental assessment of trout farming in a theoretical farm producing rainbow trout fry. Effects of changes in performances of several traits (see Section 2.4) on the environmental impacts have been investigated. The system was defined from cradle-to-farm-gate and included five distinct sub-systems (**Figure 2**): (1) production of purchased feed, including cultivation of ingredients, processing, and transportation; (2) production of energy expended at farm level (electricity and diesel); (3) production of farming facilities and equipment used; (4) fish farming, including nutrients emission from the biological transformation of feed after onsite treatment of wastewater. The functional unit, basis for the environmental calculation, was one ton of fry produced at the farm gate.

2.2.2. Life cycle inventory

Life cycle inventory (LCI) was conducted on the basis of the data collected on production farms and using Agribalyse® version 3.0 and EcoInvent® version 3.8 databases.

(1) Production of purchased feed - Crop-derived ingredients used in fish feed mainly originated from Brazil and France (e.g. soybean meal from Brazil and wheat bran from France). In contrast, fish-derived ingredients originated from the Peruvian and the Norwegian fish milling industry (e.g. fish meal from Peru and fish meal from fish trimming from Norway). The exact composition of the different feeds used and their nutritional values were given by the feed manufacturers. The transport of feed ingredients to feed manufacturers in France was by trans-oceanic ship and by lorry (>32 t), whereas the transport of feed from France to the fish farm in Brittany was by lorry (>32 t). Transport distances and other data required to compute the environmental impact of feed ingredients were based on the literature (Boissy et al., 2011; Pelletier et al., 2009).

Figure 1. The general methodological framework for life cycle assessment (LCA).

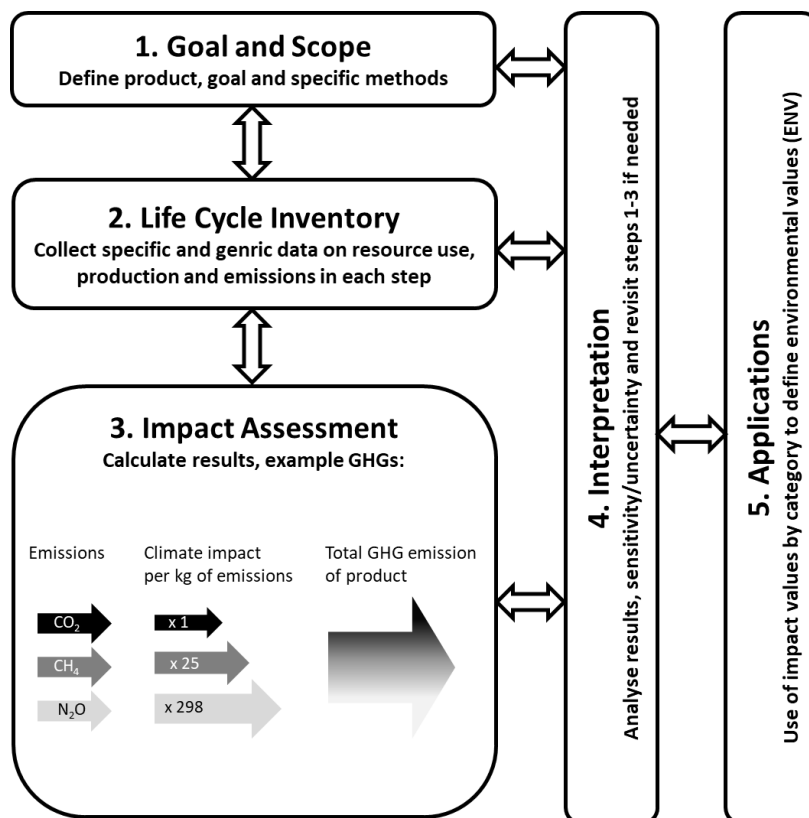
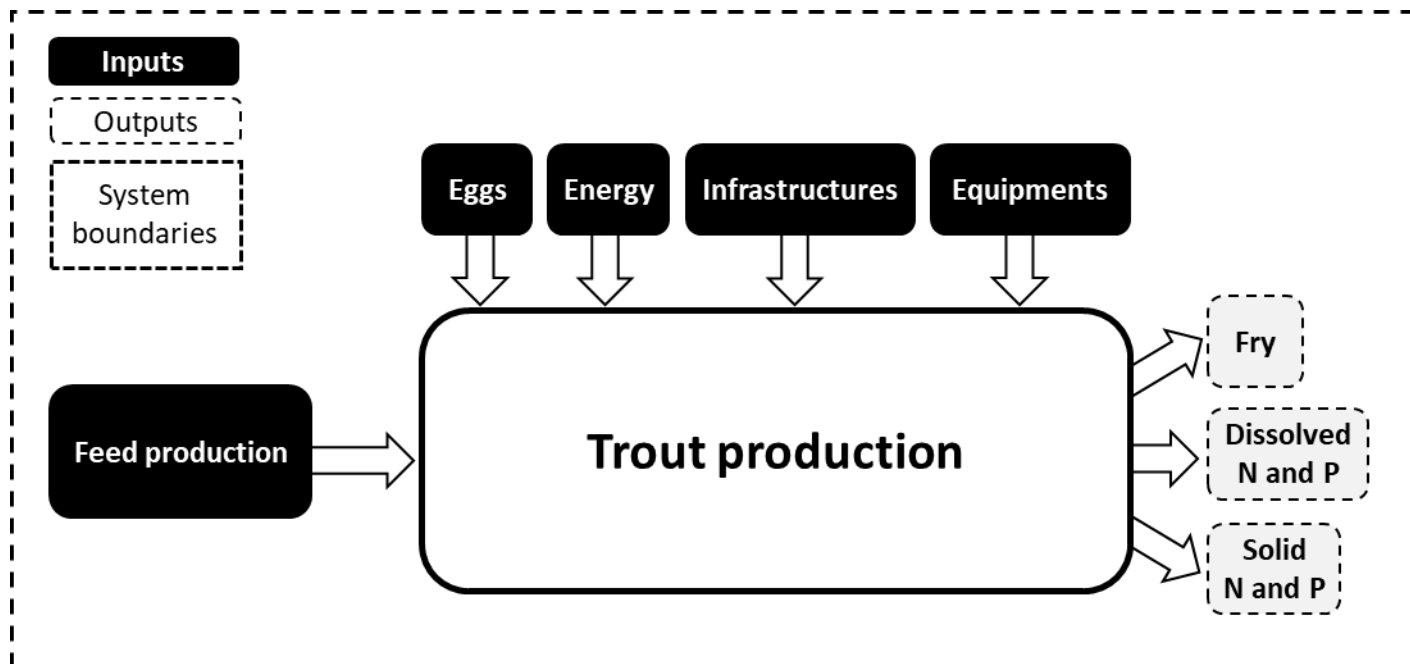


Figure 2. System boundaries and flows of rainbow trout *Oncorhynchus mykiss* fry production.



- (2) Production of energy expended on the farm - Most of the water circulation in the farm is done by gravity flow. So, the farm's electricity consumption was estimated at 20,500 kWh over one production cycle, while diesel and gasoline consumption were limited to 200 L. The electricity used by the farm was coming from the French energy mix proposed by the Ecoinvent version 3.8 (Wernet et al., 2016).
- (3) Production of farming facilities and equipment used - We considered the construction of three different buildings of 30, 50 and 200 m² with a life span of 30 years. The production of equipment used (i.e. pump, tanks) was calculated using data from INRAE. The use of building and equipment was adjusted to consider the period of the year and the size of the fish. The surface of the rearing structures has been adjusted to the optimal to include possible effects of changes in performances of several traits (see Section 2.4) in rearing structures' occupancy.
- (4) Farm operation - The farm operation sub-system included the use of energy, facilities and equipment and the emission of pollutants from the biological transformation of the feed distributed to the fish. The amount of nitrogen (N), phosphorus (P) and chemical oxygen demand (COD) of the dissolved organic matter excreted by the fish in effluent water were calculated through mass balance considering the onsite treatment capacity of the sludge settling pond. Sludge produced by the farm was used for neighbourhood agricultural purposes and was not included in the analysis.

2.2.3. Life cycle impact assessment

Each flow observed in the system was assigned to different impact categories relatively to its potential environmental effects. The six environmental categories investigated were: acidification, climate change, cumulative energy demand, eutrophication, land competition, water dependency (CML2 Baseline 2000 version 2.04) (Guinée, 2002) and cumulative energy demand (Frischknecht et al., 2015). These six impact categories were chosen because they represent the main environmental impacts aquaculture contributes (Bohnes et al., 2019; Henriksson et al., 2012; Pelletier et al., 2007). Acidification refers to the negative effects of acidifying pollutants, such as SO₂, NO_x, HCL and NH₃, on the environment and is expressed in kg SO₂-equivalents. Climate change is the potential impact of gaseous emissions, such as CO₂ and CH₄, on the heat radiation absorption in the atmosphere. Climate change was calculated according to the GWP100 factors (potential effect at a 100-year time horizon) and expressed in kg CO₂-equivalents. Cumulative energy demand (CED) expresses the depletion of energy resources, expressed in GJ. Eutrophication is mainly the consequence of nitrogen (N) and phosphorus (P) emissions to the air, water and soil and is expressed in kg PO₄³⁻-equivalents. Land competition (m² yr⁻¹) corresponds to the ground surface used directly (land occupied by ponds) and indirectly (land used to grow feed) by the production system, while water dependency (m³) corresponds to the water flowing into the production system. The environmental impacts were calculated using Simapro® version 8.0 software.

2.3. Simulated breeding program

We simulated a simple breeding program using R freeware version 4.0.3 (R Development Core Team, 2020) derived from current breeding schemes in rainbow trout in France that can be described in four different steps (see **Figure 3**):

- (1) Families are created by artificial fertilization according to a partial factorial mating design of sires and dams: 10 independent full factorial designs of 10 sires and 10 dams are thus considered to produce about 400,000 eyed eggs from which 50,000 are randomly chosen to be reared. Therefore, 1,000 full sibs' families are produced, corresponding to 100 paternal and 100 maternal families. The age at reproduction is two years for males and three for females.
- (2) Mass selection is then performed on the candidates ($n = 2000$) randomly chosen among the 50,000 descendants.
- (3) Assignment of the kinship of the candidates and indexing on lethal characteristics (such as disease resistance) measured on collaterals ($n = 1200$) randomly chosen for a derived batch in parallel to the choice of the batch of selection candidates.
- (4) In a last step, selection of brooders ($n = 200$) is normally performed.

2.4. Breeding goals

The breeding goal (H) combined three traits covering key aspects of trout production. In trout farming, the market is segmented with products sold mainly at constant weight while regulations limit the production of farms. So, growth rate plays an important role in trout rearing by reducing the duration of production cycles. For this reason, the first trait included in the breeding objective was the body weight at 110 days post hatching (BW).

Because commercial feeds are the most important inputs in fish farming and have both economic and environmental consequences, the feed efficiency (FE) measured through the feed conversion ratio was added to the breeding objective. The last trait we included in H is the survival rate (SR). The breeding goal can be expressed as follows:

$$H_X = ENV_{BW}^X A_{BW} + ENV_{FE}^X A_{FE} + ENV_{SR}^X A_{SR}$$

where A_i is the breeding value (or true additive genetic value) of the trait i ; ENV_i of trait i is calculated as the marginal impact in H_X (impact variation per physical unit) and based on the difference in environmental impact values before and after changing the average performance of the trait by one genetic standard deviation, while maintaining the other traits at constant values.

We calculated the ENV in the same way for each of the impact category (X) from LCA (i.e. acidification, climate change, CED, eutrophication, land occupation and water dependency). In order to describe the importance of traits, we estimated the relative environmental weights (RWs) by multiplying trait's ENV by its genetic standard deviation (σ_g).

We obtained six different breeding goals, so-called H_{acid} , $H_{climate}$, H_{CED} , H_{eutro} , H_{land} and H_{water} , whose responses we seek to maximize by selecting on the corresponding optimal selection indexes.

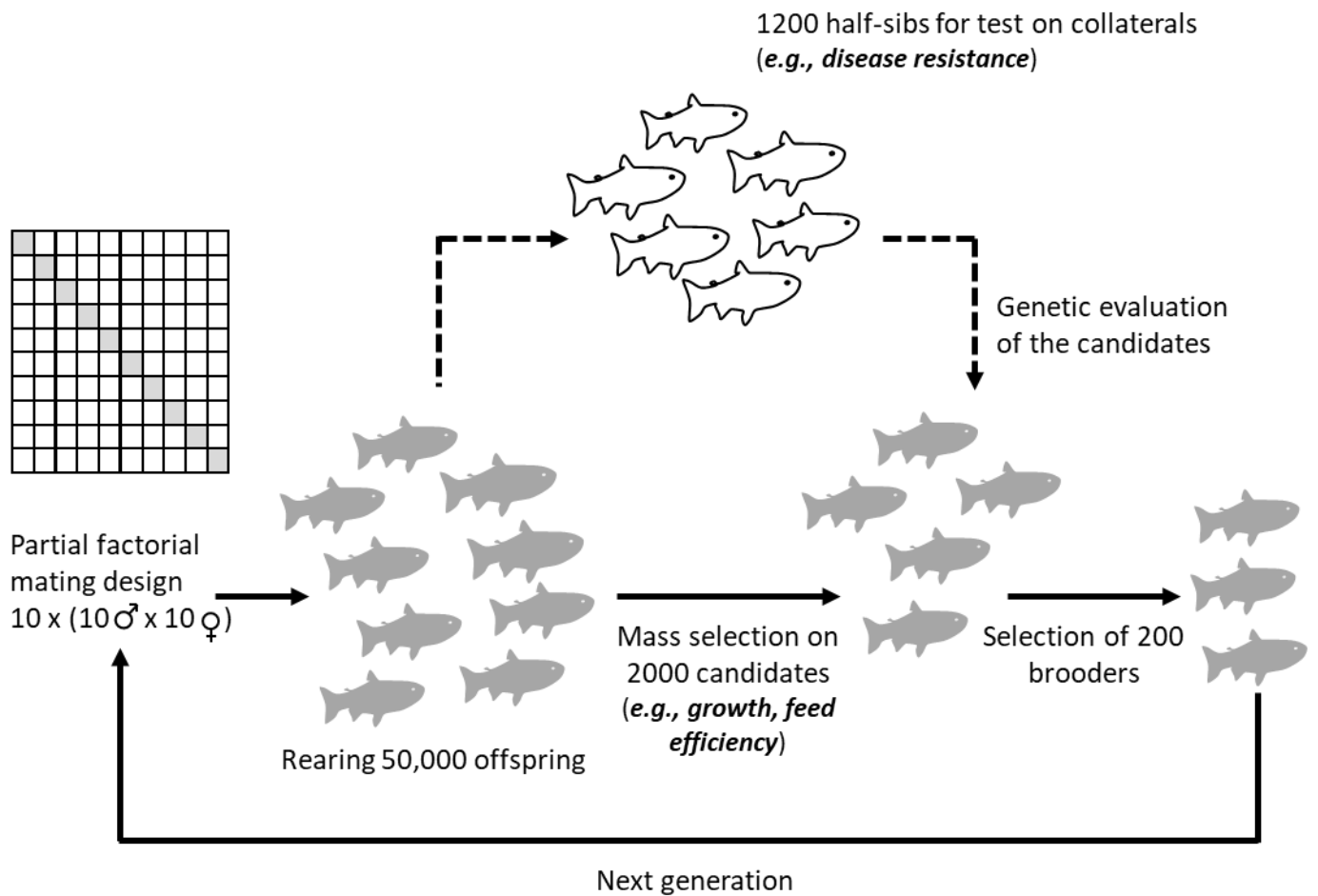


Figure 3. Modelled rainbow trout breeding scheme. We assumed non-lethal measurements on candidates such as growth and efficiency related traits while survival rate from disease resistance was tested on collaterals.

2.5. Selection indexes and responses to selection

The response to selection under each scenario was assessed by means of an optimal selection index (I). The same traits were considered in the breeding goal (H_X) and in the selection index (I_X):

$$I_X(z) = b_{BW}^X Y_{BW}(z) + b_{FE}^X b_{FE} Y_{FE}(z) + b_{SR}^X Y_{SR}(hs)$$

where Y indicated phenotype observed on candidates (z) or half-sibs (hs). Non-lethal measurements for BW and FE were performed on candidates. Here, we assumed that SR is mostly influenced by the occurrence of the cold-water disease and rainbow trout fry syndrome caused by the bacteria *Flavobacterium psychrophilum*. In France, these two diseases are reported as among the major bacteriosis affecting rainbow trout farming (Siekoula-Nguedia et al., 2012). Here, we assumed SR was measured through challenges to *F. psychrophilum* infection performed on collaterals (**Figure 3**) while all candidates for selection have the same number of half-sibs in the challenge (hs = 23) so that we can estimate the performances on SR (Y_{SR}) for a candidate for selection as follows:

$$Y_{SR} = \frac{1}{hs} \sum_{i=1}^{hs} SR_i$$

The vector of coefficients (**b_x**) containing index weights for each trait of the optimal index is given by:

$$\mathbf{b}_X = \mathbf{P}^{-1} \mathbf{G} \mathbf{ENV}^X$$

where **ENV^X** is the vector containing the **ENV** values of the three traits of interest included in H_X; **P** is the matrix denoting the variances and covariances among the predictors Y in I and **G** is the matrix denoting the variances and covariances between the predictors Y in I and the true additive genetic values A in H_X. Derivation of **P** and **G** is provided in **Appendix A1**.

We calculated the variance of the selection index I (σ_I²) as:

$$\sigma_{I_X}^2 = \mathbf{b}_X' \mathbf{P} \mathbf{b}_X$$

and the genetic variance of the breeding objective (H) as:

$$\sigma_{H_X}^2 = \mathbf{ENV}^{X'} \mathbf{V}_H \mathbf{ENV}^X$$

where **V_H** is the matrix denoting the genetic variances and covariances across traits in H with r_g the genetic correlations between traits:

$$\mathbf{V}_H = \begin{pmatrix} \sigma_{g1}^2 & \cdots & r_{g13} \sqrt{\sigma_{g1}^2 \sigma_{g3}^2} \\ \vdots & \ddots & \vdots \\ r_{g31} \sqrt{\sigma_{g3}^2 \sigma_{g1}^2} & \cdots & \sigma_{g3}^2 \end{pmatrix}$$

Accuracy of index selection (ρ_x) was calculated as:

$$\rho_x = \frac{\sigma_{Ix}}{\sigma_{Hx}}$$

The genetic gain (AGG_{Hx}) can be calculated as follows:

$$AGG_{Hx} = \frac{1}{2} \frac{(i_f + i_m) \rho_x \sigma_{Hx}}{L}$$

where, for female (f) and male (m), $i_f = i_m = i$ the selection intensity derived for the same selection rate (i.e. 10%) in male and female candidates for selection. L is the average generation interval of 2.5 years (3 years for females and 2 years for males).

Annual genetic gains for each trait have been calculated as follows:

$$AGG_{X,trait} = \frac{AGG_{Hx}}{\sigma_{Ix}^2} \mathbf{G}' \mathbf{b}_X$$

We estimated the selection accuracy (ρ_x) and annual genetic gains (AGG_{Hx}) for the breeding goals corresponding to the different impact categories: climate change (kg CO₂ eq), cumulative energy demand (CED; GJ), land competition (m² yr⁻¹) and water dependence (m³).

In order to assess the consequences of a selection to maximize responses on a given breeding objective Hx on the responses for the other impact categories ($Y \neq X$), we calculated:

$$\Delta R_{Y \neq X} = \sum ENV_{trait}^Y AGG_{X,trait}$$

2.6. Genetic parameters

The genetic parameters of the three traits are presented in **Tables 2** and **3**. Heritability (h^2) values were extracted from literature in rainbow trout: 0.15-0.55 for body weight at different ages (e.g., Evenhuis et al., 2015; Haffray et al., 2012; Kause et al., 2016), 0.10-0.23 for feed efficiency traits (Grima et al., 2008; Kause et al., 2006a, 2016; Knap and Kause, 2018) and 0.23-0.35 for resistance to *F. psychrophilum* (Fraslin et al., 2019; Vallejo et al., 2017).

Genetic standard deviations (σ_g) were calculated as follows:

$$\sigma_g = \sqrt{h^2 \sigma_p^2}$$

where σ_p^2 is the phenotypic variance of each trait.

For BW and FE, σ_p^2 as calculated assuming a coefficient of variation of 0.20 and knowing the phenotypic mean of the traits (i.e. 10 g and 0.70 kg kg⁻¹ for BW and FE, respectively, **Table 1**). For SR, $\sigma_p^2 = p(1-p)$ was estimated considering that $p = 10\%$ of mortality in the theoretical farm (**Table 1**).

Table 2. Genetic parameters of body weight at 110 days post-hatching (BW), feed efficiency (FE), and survival rate (SR) used to predict the responses to selection.

| Trait | Heritability | Genetic standard deviation |
|--------------|---------------------|-----------------------------------|
| BW | 0.30 | 1.10 |
| FE | 0.15 | 0.08 |
| SR | 0.30 | 0.16 |

Table 3. Genetic (above diagonal) and phenotypic (below diagonal) correlations between body weight at 110 days post hatching (BW), feed efficiency (FE) and survival rate (SR).

| Trait | BW | FE | SR |
|--------------|-------------------|-----------|--------------------|
| BW | | 0.0 | {-0.3, -0.15, 0.0} |
| FE | {-0.4, -0.2, 0.0} | | 0.0 |
| SR | 0.0 | 0.0 | |

Based on the literature estimates, genetic correlations between BW and FE were assumed to be null, while phenotypic correlations remained uncertain, but probably negative in rainbow trout; thus, we tested values at -0.4, -0.2 and 0. For the same reason, we also tested genetic correlations of -0.3, -0.15 and 0 between BW and SR, while the phenotypic correlation was assumed to be null between these two traits. As no information was available in the literature, both genetic and phenotypic correlations were assumed to be null between FE and SR (**Table 3**).

3. Results

3.1. Environmental impacts and contribution analysis

Among fry trout-production stages, feed (i.e., feed production, milling, and transport) was among the main contributors to the environmental impacts related to climate change (36% of 2381 kg CO₂ eq), acidification (33% of 12.7 kg SO₂ eq) and cumulative energy demand (CED; 25% of 65.3 GJ) (**Figure 4**). Farm functioning (i.e., farm operations and on-farm emissions) was the main contributor to eutrophication (65% of 50.5 kg PO₄³⁻ eq) and water dependence (58% of 112,103 m³) and influenced land competition (24% of 703 m²). Eggs (i.e., production and transport of trout eggs) were highly contributing to water dependence (43%), eutrophication (28%) and CED (24%). Electricity consumption was the main contributor to the CED (28%), while buildings and rearing structures, depending on the impact category, accounted for 0-14% of the environmental impacts at the farm level. Chemicals (i.e., production and transport of medicines, cleaning products and other chemicals) had a negligible contribution (<3%) (**Figure 4**).

A summary of the environmental impacts of the visited rainbow trout farms is available in **Appendix A2**.

3.2. ENV determination

LCA was used to determine environmental values (ENV) used as weights in the three-trait breeding goals. ENV estimated from the different impact categories were provided in **Table 4**. While for SR, the relative weight of the ENV remained low in all the breeding goals H_X (i.e. from 0% in H_{acid} to 2.4% in H_{water}) RW for BW and FE (i.e. RW_{BW} and RW_{FE}, respectively) were highly variable for the different H_X. For instance, RW_{BW} varied from 0.0 to 97.6% in H_{eutro} and H_{water} respectively. Nevertheless, in all H_X excepted H_{water}, the highest RWs were for FE with values ranging from 52.2% to 99.6% in H_{CED} and H_{eutro} respectively, while RW_{BW} varied from 5.9% to 47.1%. The only situation where RW of these two traits tended to be equilibrated was in H_{CED} with RW_{FE} = 52.2% and RW_{BW} = 47.1% (**Table 4**). Interestingly, H_{water} was the only breeding goal whose RWs were distinctly different from others. Indeed, while for the others H, RWs were ranging according to the following ascending order: RW_{SR} < RW_{BW} < RW_{FE}, in H_{water} we estimated RW_{FE} < RW_{SR} << RW_{BW}.

Given the similarities in weighing between H_{acid} and H_{climate}, and then H_{eutro} and H_{land}, we focused on four breeding goals only: H_{climate}, H_{CED}, H_{land} and H_{water} (**Table 4**) for the subsequent analysis.

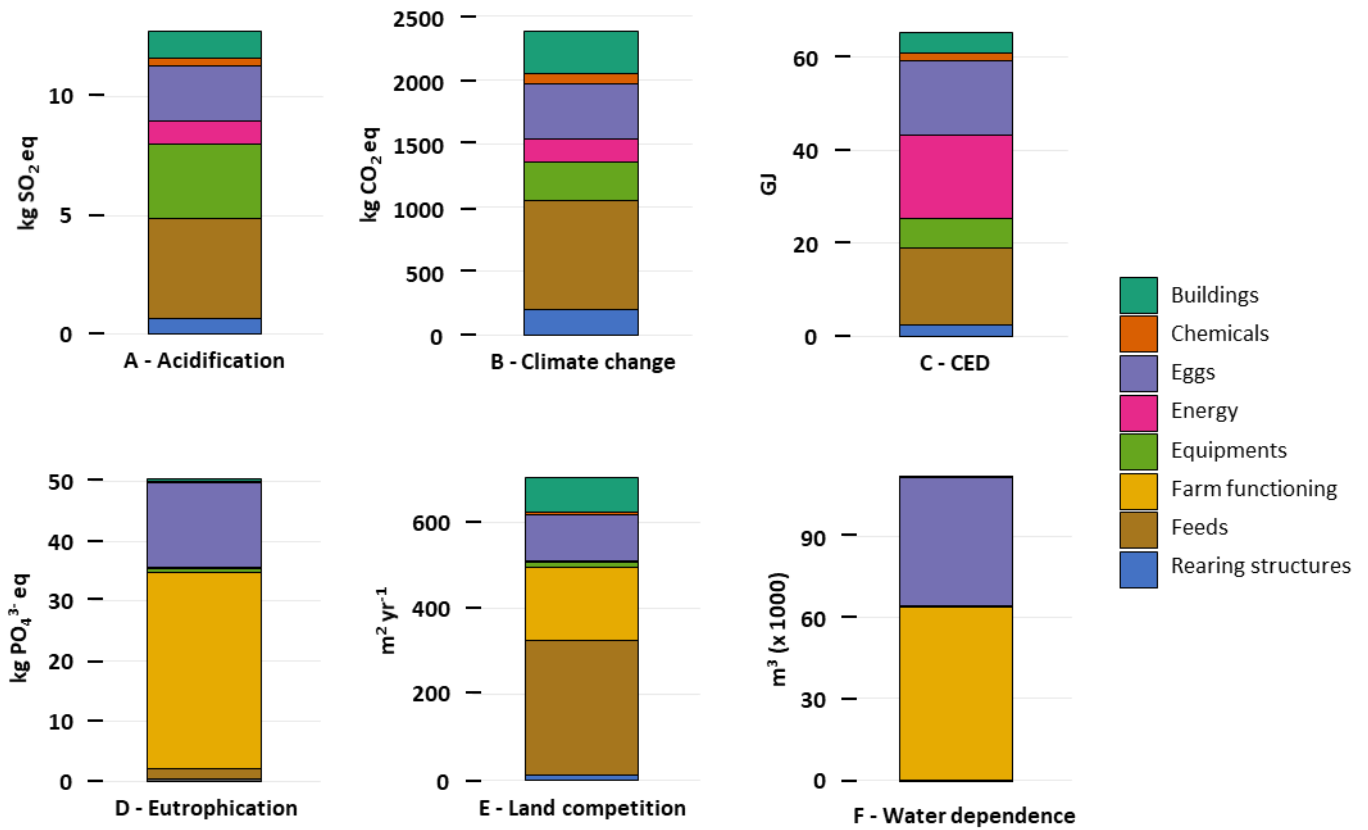


Figure 4. Environmental impacts of the rainbow trout fry production at the level of the theoretical farm for (A) acidification, (B) climate change, (C) cumulative energy demand (CED), (D) eutrophication, (E) land competition and (F) water dependence. Results are expressed per ton of fish produced.

Table 4. Environmental values (ENV) for the three traits: body size at 110 days post hatching (BW), feed efficiency (FE), and survival rate (SR) expressed in physical units (see Section 2.2.3) and relative weights of the ENV (RW, %) in the breeding goal (H) with traits standardized by their genetic standard deviation.

| Impact category | Breeding goal name | ENV (physical units) | | | RW (%) | | |
|--|----------------------|----------------------|-------------------|-------------------|------------------|------------------|------------------|
| | | ENV _{BW} | ENV _{FE} | ENV _{SR} | RW _{BW} | RW _{FE} | RW _{SR} |
| Acidification (kg SO ₂ eq) | H _{acid} | 0.1 | 5.0 | 0.0 | 22.22 | 77.78 | 0.00 |
| Climate change (kg CO ₂ eq) | H _{climate} | 20 | 1250 | 5 | 18.48 | 80.83 | 0.69 |
| Cumulative energy demand (GJ) | H _{CED} | 1.5 | 23.75 | 0.15 | 47.10 | 52.20 | 0.71 |
| Eutrophication (kg PO ₄ ³⁻ eq) | H _{eutro} | 0.00 | 83.75 | 0.15 | 0.00 | 99.62 | 0.38 |
| Land competition (m ² yr ⁻¹) | H _{land} | 2 | 450 | 1 | 5.94 | 93.61 | 0.45 |
| Water dependence (m ³) | H _{water} | 3000 | 0 | 500 | 97.56 | 0.00 | 2.44 |

3.3. Genetic gain and changes in environmental impacts

In a three-trait breeding goal, the responses to selection results from a complex interaction between weights assigned to each trait and the genetic and phenotypic parameters between the three traits. Overall, the selection accuracy ranged from 0.39 to 0.62. The accuracy of index selection was the highest for the breeding goal H_{CED} with values ranging from 0.50 to 0.63 while the lowest accuracy was found for H_{land} (0.39-0.45) (**Table 5**). Annual genetic gains expected for H (AGG_H), expressed for one ton of fry produced at the farm level, ranged from 20.3 to 26.0 kg CO₂ eq for $H_{climate}$, 0.73 to 0.91 GJ for H_{CED} , 7.0 to 8.9 m² yr⁻¹ for H_{land} and 1264 to 1385 m³ for H_{water} .

To assess the phenotypic significance of such gains compared to the environmental impacts calculated in the hypothetical farm before selection, we calculated annual relative gains when considering the optimal selection indexes (**Table 6**). We found that relative gains were ranging from 0.9% to 1.4% for the different breeding goals. The highest relative gains were obtained for H_{CED} (i.e. 1.2% to 1.4%) and, to a lesser extent, H_{land} (i.e. 1.0% to 1.3%), while breeding goals targeting limitations for climate change ($H_{climate}$) or water dependence (H_{water}) led to lower relative gains (i.e. 0.9-1.2%). Relative gains varied depending on correlations between traits, with the lowest relative gains obtained when considering a null phenotypic correlation between BW and FE and a negative genetic correlation between BW and SR ($r_{p12} = 0$ and $r_{g13} = -0.3$) while the highest relative gains were observed when $r_{p12} = -0.4$.

When looking at the genetic gains for each trait, AGG_{BW} greatly differed among H_x with values ranging from 0.04 to 0.23 g/year in H_{land} while AGG_{BW} reached 0.42-0.46 g/year in H_{water} . Overall, AGG_{BW} increased when considering a negative phenotypic correlation between BW and FE (r_{p12}) and a negative genetic correlation between BW and SR (r_{g13}). For instance, in H_{CED} , AGG_{BW} increased from 0.34 g/year when r_{p12} and r_{g13} were null to 0.43 g/year with $r_{p12} = -0.4$ and $r_{g13} = -0.3$ (**Table 5**).

For FE, the annual gains were positive in $H_{climate}$, H_{CED} and H_{land} with AGG_{FE} ranging from 0.01 to 0.02 kg kg⁻¹/year, the highest AGG_{FE} being estimated in H_{land} . Nevertheless, when considering water dependence (H_{water}), AGG_{FE} was null when the phenotypic correlation between BW and FE was null ($r_{p12} = 0$) while the response became slightly favourable ($AGG_{FE} < 0.01$ kg kg⁻¹/year) when r_{p12} was negative. As for BW, AGG_{FE} were particularly affected by the r_{p12} and r_{g13} values with the highest values estimated when $r_{p12} = 0$ and $r_{g13} = 0$ while AGG_{FE} gradually decreased when both genetic and phenotypic correlations decreased (**Table 5**).

Whatever the breeding goal considered, AGG_{SR} was null when r_{p12} and r_{g13} were null, but became negative when negative correlations were assumed. The most unfavourable response to selection was obtained at the stronger negative correlations tested ($r_{p12} = -0.4$ and $r_{g13} = -0.3$), and it was especially true for H_{CED} and H_{water} with respective expected annual survival rate decreasing by -0.8%/year ($AGG_{SR} = 0.008$) and -1.0%/year ($AGG_{SR} = 0.010$) (**Table 5**).

Figure 5 displayed the genetic gains for the four impact categories depending on which impact category was considered as the breeding goal (i.e., the impact used to define the optimal selection index). We focused on the comparison between two scenarios of correlations: (1) the reference scenario where both phenotypic and genetic correlations are nulls ($r_{p12} = 0$ and $r_{g13} = 0$) and (2) a scenario with moderate phenotypic and genetic correlations ($r_{p12} = -0.2$ and $r_{g13} = -0.15$) that we assumed being the most realistic scenario.

Table 5. Index accuracy (ρ_H), annual genetic gains (AGG) expressed in physical units for the different breeding goals (i.e. H_{climate} , H_{CED} , H_{land} and H_{water}) and for the three traits under selection according to scenarios based on phenotypic (r_p) and genotypic correlations (r_g) between BW (1), FE (2) and SR (3).

| Breeding goal name | Estimate | Scenarios | | | | | | | | |
|----------------------|-------------------|------------------------------|---------------------------------|---------------------------------|----------------------------------|-------------------------------------|------------------------------------|---------------------------------|-------------------------------------|------------------------------------|
| | | $r_{p12}: 0$ $r_{g13}: 0$ | $r_{12}: 0$ $r_{g13}: -0.15$ | $r_{p12}: 0$ $r_{g13}: -0.3$ | $r_{p12}: -0.20$ $r_{g13}: 0$ | $r_{p12}: -0.2$ $r_{g13}: -0.15$ | $r_{p12}: -0.2$ $r_{g13}: -0.3$ | $r_{p12}: -0.4$ $r_{g13}: 0$ | $r_{p12}: -0.4$ $r_{g13}: -0.15$ | $r_{p12}: -0.4$ $r_{g13}: -0.3$ |
| H_{climate} | ρ_H | 0.46 | 0.46 | 0.41 | 0.44 | 0.44 | 0.44 | 0.50 | 0.50 | 0.46 |
| | AGG _H | 26.0 | 26.0 | 20.3 | 22.2 | 22.2 | 22.2 | 25.2 | 25.2 | 25.2 |
| | AGG _{BW} | 0.137 | 0.137 | 0.178 | 0.239 | 0.240 | 0.241 | 0.314 | 0.314 | 0.315 |
| | AGG _{FE} | 0.019 | 0.019 | 0.013 | 0.014 | 0.014 | 0.014 | 0.015 | 0.015 | 0.015 |
| | AGG _{SR} | 0.000 | -0.002 | -0.004 | 0.000 | -0.002 | -0.004 | 0.000 | -0.002 | -0.004 |
| H_{CED} | ρ_H | 0.50 | 0.51 | 0.50 | 0.54 | 0.55 | 0.55 | 0.62 | 0.62 | 0.63 |
| | AGG _H | 0.79 | 0.79 | 0.73 | 0.80 | 0.80 | 0.80 | 0.91 | 0.91 | 0.91 |
| | AGG _{BW} | 0.339 | 0.340 | 0.374 | 0.386 | 0.387 | 0.391 | 0.424 | 0.425 | 0.428 |
| | AGG _{FE} | 0.012 | 0.012 | 0.007 | 0.009 | 0.009 | 0.009 | 0.012 | 0.012 | 0.012 |
| | AGG _{SR} | 0.000 | -0.004 | -0.010 | 0.000 | -0.004 | -0.009 | 0.000 | -0.004 | -0.008 |
| H_{land} | ρ_H | 0.45 | 0.45 | 0.39 | 0.41 | 0.41 | 0.41 | 0.44 | 0.44 | 0.44 |
| | AGG _H | 8.9 | 8.9 | 6.7 | 7.0 | 7.0 | 7.0 | 7.7 | 7.7 | 7.7 |
| | AGG _{BW} | 0.040 | 0.040 | 0.054 | 0.136 | 0.136 | 0.136 | 0.229 | 0.229 | 0.228 |
| | AGG _{FE} | 0.020 | 0.020 | 0.015 | 0.015 | 0.015 | 0.015 | 0.016 | 0.016 | 0.016 |
| | AGG _{SR} | 0.000 | 0.000 | -0.001 | 0.000 | -0.001 | -0.001 | 0.000 | -0.001 | -0.002 |
| H_{water} | ρ_H | 0.55 | 0.55 | 0.56 | 0.56 | 0.56 | 0.57 | 0.60 | 0.60 | 0.60 |
| | AGG _H | 1264 | 1265 | 1273 | 1290 | 1291 | 1298 | 1379 | 1379 | 1385 |
| | AGG _{BW} | 0.421 | 0.422 | 0.426 | 0.430 | 0.431 | 0.435 | 0.459 | 0.460 | 0.463 |
| | AGG _{FE} | 0.000 | 0.000 | 0.000 | 0.003 | 0.003 | 0.003 | 0.006 | 0.006 | 0.006 |
| | AGG _{SR} | 0.001 | -0.005 | -0.011 | 0.001 | -0.005 | -0.011 | 0.001 | -0.005 | -0.010 |

Table 6. Overall annual relative gains when considering the optimal selection indexes expressed as % of the hypothetical farm for the different impact categories: climate change (kg CO₂ eq), cumulative energy demand (CED; GJ), land competition (m² yr⁻¹) and water dependence (m³). We considered different scenarios based on phenotypic (r_p) and genotypic correlations (r_g) between BW (1), FE (2) and SR (3).

| Impact category | Scenarios | | | | | | | | |
|------------------|------------------------------|---------------------------------|---------------------------------|----------------------------------|-------------------------------------|------------------------------------|---------------------------------|-------------------------------------|------------------------------------|
| | $r_{p12}: 0$ $r_{g13}: 0$ | $r_{12}: 0$ $r_{g13}: -0.15$ | $r_{p12}: 0$ $r_{g13}: -0.3$ | $r_{p12}: -0.20$ $r_{g13}: 0$ | $r_{p12}: -0.2$ $r_{g13}: -0.15$ | $r_{p12}: -0.2$ $r_{g13}: -0.3$ | $r_{p12}: -0.4$ $r_{g13}: 0$ | $r_{p12}: -0.4$ $r_{g13}: -0.15$ | $r_{p12}: -0.4$ $r_{g13}: -0.3$ |
| Climate change | 1.1% | 1.1% | 0.9% | 0.9% | 0.9% | 0.9% | 1.1% | 1.1% | 1.1% |
| CED | 1.2% | 1.2% | 1.1% | 1.2% | 1.2% | 1.2% | 1.4% | 1.4% | 1.4% |
| Land competition | 1.3% | 1.3% | 1.0% | 1.0% | 1.0% | 1.0% | 1.1% | 1.1% | 1.1% |
| Water dependence | 1.1% | 1.1% | 1.1% | 1.2% | 1.2% | 1.2% | 1.2% | 1.2% | 1.2% |

Overall, as demonstrated earlier, adding negative phenotypic (r_{p12}) and genetic correlation (r_{g13}) tended to reduce the gains. The gains for a given impact category decreased when using a non-optimal selection index for this category. Thus, a drastic ten-fold decrease in gains was observed for land competition and water dependence where gains dropped from 8.9 to 0.8 m² yr⁻¹ and from 1264 to 120 m³ in the reference scenario when considering the less-efficient selection index (i.e. based on ENV_{water} and ENV_{land}, respectively). Interestingly, such decrease was less drastic in the realistic scenario considering the negative correlations. Altogether, results displayed in **Figure 5** showed that selection based on optimizing response on H_{water} tended to greatly differed from the others.

4. Discussion

To our knowledge, this study is the first investigating the efficiency of a breeding program that limits the environmental impacts of rainbow trout farming. We focused on rainbow trout fry production stage through a theoretical farm designed based on surveys from French fish farmers. Several breeding goals (H) linearly combining three traits of major interest (BW, FE and SR) weighted by their environmental values (ENV), which express the marginal changes in environmental impacts due to improvement in trait performances, have been evaluated. ENV have been derived from six LCA impact categories previously highlighted as the main environmental impacts in aquaculture production systems from past LCA studies (Bohnes et al., 2019; Henriksson et al., 2012; Pelletier et al., 2007). A cradle-to-farm-gate LCA was carried to avoid over estimation of ENV of traits decreasing environmental impacts at farm level, but increasing environmental impacts at sector level (van Middelaar et al., 2014).

Regarding the environmental impacts estimated at the farm level, the results are relatively different from previous LCA studies conducted on rainbow trout production. Among the observed differences, we highlighted a higher relative contribution of eggs/fish inputs in the eutrophication and water dependence of the theoretical farm compared to other studies while relative contribution of feeds is lesser for the others impact categories. These differences are mainly due to the fact that the theoretical farm considered only the fry production phase, whereas LCA studies were generally conducted using data from farms performing grow-out period or the rearing cycle from eggs to very large trout (e.g., Chen et al., 2015; Samuel-Fitwi et al., 2013). Thus, the comparison with literature must be made cautiously because the fry production phase is less dependent on some inputs known to strongly affect the environmental impacts of fish farming. This is particularly true for feeds with FCR generally >1 kg kg⁻¹ during grow-out period while, for fry production, FCR are usually ~0.7 kg kg⁻¹ as highlighted by the surveys we performed. The logic is the same for oxygen supply, that is generally not used during the fry production phase. The environmental balance sheet available in **Appendix A2** shows great differences in environmental impacts between the farms performing the grow-out period and the farm producing fry. Overall, the consistency of the results obtained by our impact assessment method, also used to generate the environmental balance of the four existing farms (**Appendix A2**), with the existing literature validated the impact estimation approach carried out at the scale of the theoretical farm and, consequently, the estimation of the ENV.

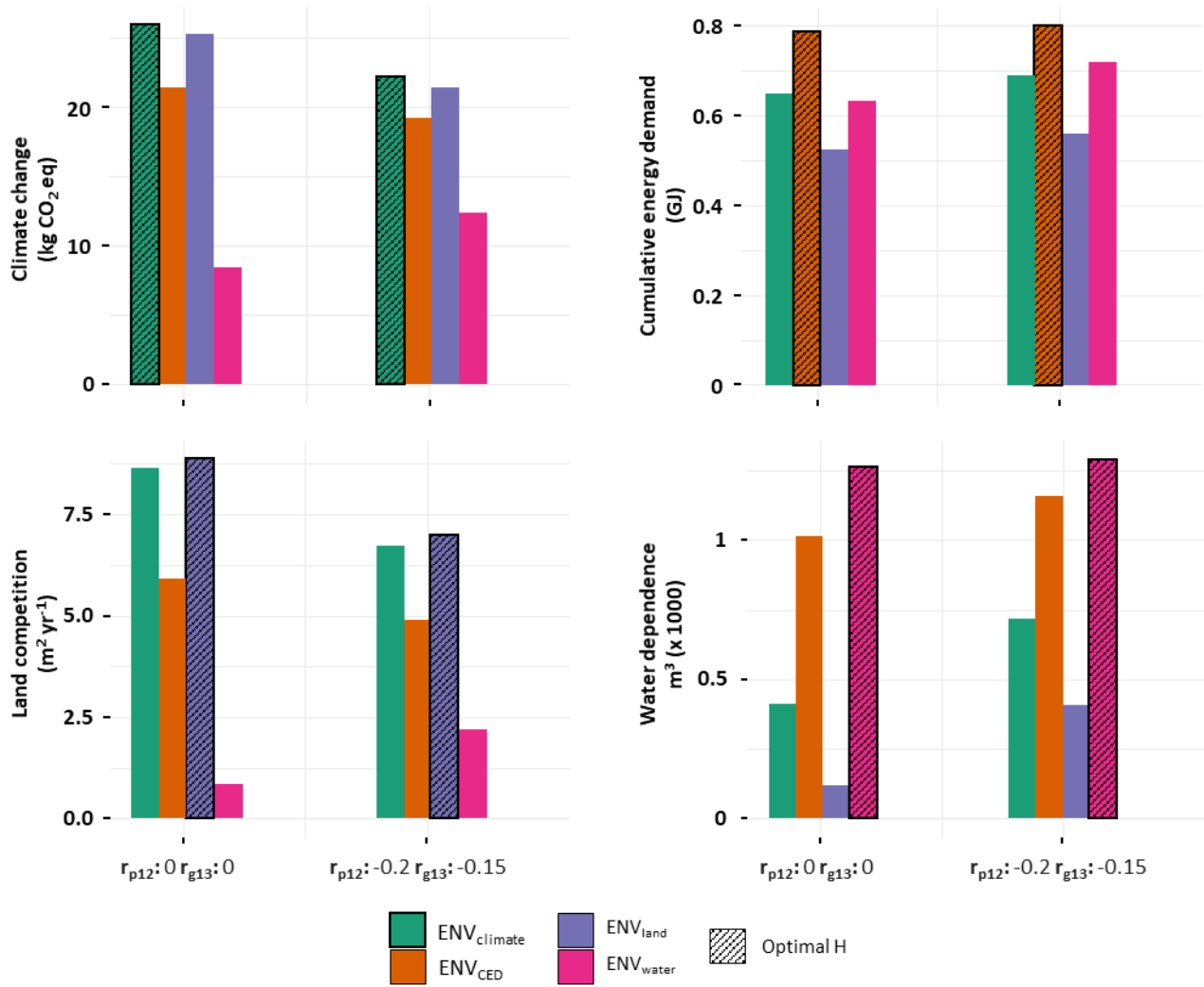


Figure 5. Annual gains (in physical units) for the different impact categories according to two different scenarios of correlations: (1) a reference scenario where both phenotypic and genetic correlations are nulls ($r_{p12} = 0$ and $r_{g13} = 0$) and, (2) a realistic scenario with moderate negative phenotypic and genetic correlations ($r_{p12} = -0.2$ and $r_{g13} = -0.15$). Responses on H_x for the optimal selection index I_x for each impact category are black dashed.

In this study, we considered three major traits of interest for farmers, highlighted from surveys, i.e. growth rate, expressed as the body weight at 110 days post-hatching, feed efficiency, expressed as FCR and survival rate. These traits were also identified as key traits in breeding in a previous investigation aiming to study breeding trait preferences among rainbow trout farmers (Sae-Lim et al., 2012). The relative weight of ENVs for different traits in breeding goals is highly variable depending on the impact category for which selection response is being maximized. Nevertheless, it appears that feed efficiency weighs heavily in the majority of environmental breeding goals, and this is particularly true for limiting eutrophication and land competition. Conversely, when selection is performed to reduce water dependence, the ENV_{FE} was null and the breeding goal was then mainly weighted by ENV_{BW} . Overall, we estimated very low ENV_{SR} in the different breeding goals (H_X) considered.

In order to understand the relative weights of the ENVs, it is necessary to analyse the consequences of a change of one genetic standard deviation in the performances observed for the three traits under the constraint of a constant annual production at the farm scale. Indeed, an improvement in survival, at constant annual production, mainly allows a reduction in the number of eggs at the entrance and the environmental impacts at this level will be reduced. Nevertheless, this reduction remains small since in the scenario considered, the reduction in the number of eggs at entry is less than 1%. The logic is the same for FE, where again, a better feed efficiency mainly results in a reduction of feed inputs while the environmental impacts of other items remain fixed. However, as feed is a major source of environmental impacts in aquaculture (Bohnes et al., 2019), the ENV_{FE} was very high compared to the other traits. These results are consistent with other studies conducted in African catfish *Clarias gariepinus* and European sea bass (Besson et al., 2020, 2017, 2016). The effects of a gain in growth rate on the environmental impacts of the farm are more complex to understand. Indeed, an improvement in growth rate, at constant production, will lead to a reduction in rearing times and, consequently, to changes in the use of rearing infrastructures and different equipment. However, the consequences of these changes rely on temperature and water availability. Indeed, the increase in early growth rate, leading to a faster exit of fry from the rearing indoor facility, will affect the use of equipment related to water recirculation or air supply. Nevertheless, this reduction in equipment use will be seasonally dependent. While in low water periods the effects will be marked (cohort 3), this will be less true in winter periods (cohort 1) where water abundance and low temperatures do not require water recirculation and air supply. Overall, it is not surprising to find that the relative weight ENV_{BW} is intermediate in a majority of the H 's but becomes much larger when selection is aimed at reducing water and electricity dependence (H_{water} and H_{land} , respectively). There are very few studies that have quantified the ENV of growth-related traits by considering CED. To our knowledge, only Besson et al. (2014) found that for the thermal growth coefficient (TGC), the highest ENVs (expressed as %/ton of production) observed were for CED among four impact categories considered. Nevertheless, any comparison with the literature must be qualified by the fact that the production systems studied are very different and do not operate under the same constraints. Here, we have chosen a scenario with constant annual production (production quotas). Thus, the environmental impacts are not diluted by an increase in annual production.

Given the similarities observed in the ENVs of some H_X , we decided to focus on the H aiming at impact reduction by considering four impact categories among the six initially assessed: climate change, CED, land and water. This arbitrary choice between H_{acid} vs. $H_{climate}$ and H_{eutro} vs. H_{land} was made considering that there was no need to prioritize certain impact categories over others, the proximity of the H s being such that it is possible to transpose the responses to the selection on one or the other impact category. Overall, we have demonstrated that the selection aimed at reducing environmental impacts is effective. The different H_X tested allow an improvement of growth but in variable proportions. After one generation of selection, the growth gains expected for H_{CED} and H_{water} (between 7 and 9% of the mean before selection) are comparable with genetic gains achieved on the same species in production in Chile and Norway with breeding goals weighted by EV on the traits (7-13% per generation; Lhorente et al., 2019). The gains are, however, lower for $H_{climate}$ and H_{land} . The same is true for feed efficiency where the gains are low in H_{water} but quite comparable for the other H (7- 9% per generation) to the values predicted by Kause et al. (2006b). The annual environmental gains ranging from 0.9% to 1.4% are comparable to the reduction of 0.9% per year of eutrophication observed by Besson et al. (2020) in European sea bass in a breeding goal with TGC and FCR weighted by ENV.

The responses to selection on H_X were conditioned by the phenotypic and genetic correlations between the traits considered in the selection indexes. In rainbow trout, and more generally in fishes, although there are more and more studies on this subject, there is still a lot of uncertainty about the amplitude of the correlations between certain traits, the majority of studies being focused on growth and yield traits (e.g., Blay et al., 2021; Haffray et al., 2012). Faced with some discrepancies in previous studies or in the absence of data, we explored different scenarios, by varying phenotypic correlations between BW and FE between -0.4 and 0 and genetic correlations between BW and SR between -0.3 and 0. We have shown that the responses to selection differ greatly according to the intensity of correlations between traits, and the same is true for the precision of selection indices. So far, in fish, there are strong indications that the genetic correlation between growth and feed efficiency is weak (between 0 and - 0.4; e.g. Kause et al., 2016). Hence, growth and feed-related traits should be included in the breeding goal and in the index to maximize the environmental responses (Besson et al., 2020). Nevertheless, it is interesting to note that environmental gains tend to decrease for H_{land} and $H_{climate}$ when negative phenotypic correlations were considered between BW and FE. Such a correlation implies that the largest individuals are also those with the highest FCR. The results are therefore consistent given the importance of feed in these impact categories. Considering a negative genetic correlation between BW and SR results in a marked reduction in environmental gains for $H_{climate}$ and H_{land} in particular. Here, we considered identical heritability between these two traits ($h^2 = 0.30$). Selection through optimal index where these two traits are included tended to decrease their respective responses leading to a negative response to selection for SR. In addition to a logical reduction of environmental gains, such a situation raises questions about the relevance of an optimal index based on all these traits. In this respect, if the genetic correlation between BW and SR is proven, it would seem wiser to adopt a threshold-based approach to ensure that selection on growth does not deteriorate the survival rate.

By considering a scenario of correlations that seemed the most realistic, we were able to estimate genetic gains for the four impact categories depending on which impact category was considered as the breeding goal. This approach allowed us to study the indirect effects of a selection strategy on the other impact categories evaluated in LCA. Logically, for a given impact category, the gains decrease when the optimal index is not used. Nevertheless, it is important to note that this reduction in gains never leads to an extreme situation where the environmental impacts after one year would be higher than those observed at generation 0 of selection. Overall, it is the selection for a reduction in water dependency that appears to be the least relevant for targeting the other impact categories as well, and this is particularly true for climate change and land competition. This point may help in making a choice among the tested breeding goals.

The question of choice among the tested H_X is central, but the interpretation of our results should not hide the absence of economic considerations in our study. Indeed, currently, it is difficult to establish a direct relationship between breeding goals weighted by EV or ENV in fish. Besson et al (2020) were able to demonstrate that only minimal differences were observed between two-trait breeding goals based on EV or ENV when the genetic correlation between the two traits (FCR and TGC) was strongly negative (< -0.5). Nevertheless, such conclusions remained not consistent at other correlation intensities. In a context where feed cost is the first production cost in fish farming, representing up to 70% of production costs, and given the preponderant contribution of feed in the environmental impacts of farms, it seems coherent to prioritize breeding goals maximizing the response of FE. However, such an approach would require more studies to be validated by combining an economic approach. A relevant approach could be the combination of EV and ENV in the same breeding goal to take into account both the environmental and the economic impacts in selection similarly to Kariuki et al. (2019). These authors developed breeding goals on dairy cattle weighted by both economic and non-market values of the traits. Furthermore, one of the limitations of our study is the consideration of a single flow-through production system from egg to fry that does not include grow-out, the longest and most input-dependent rearing phase. This choice is not necessarily reflecting the evolution of trout production in France with a gradual shift towards RAS production systems (Martins et al., 2010). It is therefore logical to question the relevance of the breeding goals we studied. However, the evaluation of the environmental impacts of very contrasted trout farms (see **Appendix A2**) confirmed the interest of maximizing the response on FE because the feed remains a major source of impacts in, at least, four of the six categories of impacts evaluated, whatever the production system considered.

5. Conclusion

This study demonstrated the efficiency of using ENV in breeding goals to minimize environmental impacts at the farm level while maintaining high genetic improvements in growth and feed efficiency related traits in rainbow trout production. Although our results have to be qualified by the lack of considerations for the economic repercussions of such selection strategy, the significant weight of feeds in both the economic and the environmental performances of rainbow trout farms suggests that there is a real interest in integrating weights based on ENVs to balance growth and feed efficiency traits in breeding goals. However, care should be taken to avoid any risk of degradation of survival rate.

This approach opens the way to designing selection indexes, in animal breeding, to include, in addition to EVs, ENVs but also other weightings based on current societal considerations related to ethics and animal welfare.

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Appendix 1. Derivation of **P** and **G** matrices.

For the P-matrix:

Information sources: Y_1 = performances on candidates (z) for BW

Y_2 = performances on candidates (z) for FE

\bar{Y}_3 = mean performance from 23 half-sibs (*hs*) for SR

$Var(Y_1) = \sigma_{p1}^2$ for the phenotypic variance of measurements of BW
 $Var(Y_2) = \sigma_{p2}^2$ and FE on candidates

$Var(\bar{Y}_3) = \frac{\sigma_{p3}^2 + \frac{1}{4} \sigma_{a3}^2 n - 1}{n}$ for the phenotypic variance of a mean of SR records
 from $n = 23$ half-sibs per candidate

$Cov(Y_1, Y_2) = r_{p12} \sqrt{\sigma_{p1}^2 \sigma_{p2}^2}$ where r_{p12} is the phenotypic correlation between BW
 and FE

$Cov(Y_1, \bar{Y}_3) = \frac{1}{4} r_{a13} \sqrt{\sigma_{a1}^2 \sigma_{a3}^2}$ where r_{a13} is the genetic correlation between BW and
 SR

$Cov(Y_2, \bar{Y}_3) = \frac{1}{4} r_{a23} \sqrt{\sigma_{a2}^2 \sigma_{a3}^2}$ where r_{a23} is the genetic correlation between FE and
 SR

$$\mathbf{P} = \begin{pmatrix} Var(Y_1) & Cov(Y_1, Y_2) & Cov(Y_1, \bar{Y}_3) \\ Cov(Y_2, Y_1) & Var(Y_2) & Cov(Y_2, \bar{Y}_3) \\ Cov(\bar{Y}_3, Y_1) & Cov(\bar{Y}_3, Y_2) & Var(\bar{Y}_3) \end{pmatrix}$$

For the G-matrix:

$Cov(Y_1, A_1) = \sigma_{a1}^2$ for the genetic variance of measurements of BW
 $Cov(Y_2, A_2) = \sigma_{a2}^2$ and FE on candidates

$Cov(\bar{Y}_3, A_3) = \frac{1}{4} \sigma_{a3}^2$ for the genetic variance of a mean of n records of
 SR from $n = 23$ half-sibs per candidate

$Cov(Y_1, A_2) = r_{a12} \sqrt{\sigma_{a1}^2 \sigma_{a2}^2}$ where r_{a12} is the genetic correlation between BW
 and FE

$Cov(Y_1, A_3) = \frac{1}{4} r_{a13} \sqrt{\sigma_{a1}^2 \sigma_{a3}^2}$ where r_{a13} is the genetic correlation between BW
 and SR

$Cov(Y_2, A_3) = \frac{1}{4} r_{a23} \sqrt{\sigma_{a2}^2 \sigma_{a3}^2}$ where r_{a23} is the genetic correlation between FE
 and SR

$$\mathbf{G} = \begin{pmatrix} Cov(Y_1, A_1) & Cov(Y_1, A_2) & Cov(Y_1, A_3) \\ Cov(Y_2, A_1) & Cov(Y_2, A_2) & Cov(Y_2, A_3) \\ Cov(Y_3, A_1) & Cov(Y_3, A_2) & Cov(Y_3, A_3) \end{pmatrix}$$

Appendix A2. Summary of the environmental impacts of four rainbow trout farms considering economic allocations of impacts.

- Farm 1: production of pan-size (250-300 g) and very large trout (> 3 kg) from eggs in flow-through and recirculating aquaculture system (RAS).
- Farm 2: production of fry (10 g and 40 g) from eggs in flow-through system.
- Farm 3: production of pan-size (250-300 g) and large trout (1.5-2.0 kg) from eggs with fry production in RAS and growing in flow-through system.
- Farm 4: production of large (1 kg) and very large trout (> 3 kg) from eggs in flow-through system.

