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*Flesh quality recovery in trout after spawning*

1 **Flesh quality recovery in female rainbow trout (*Oncorhynchus mykiss*) after**  
2 **spawning**

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5

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9 **Highlights**

- 10 • Evolution of quality after spawning is described for the first time in trout  
11 • Fish adiposity increased after spawning  
12 • Raw and smoked fillet color is recovered after spawning  
13 • Raw and smoked fillet mechanical resistance decreased after spawning  
14 • Flesh quality is recovered after about six months post-spawning rearing period

15

1 **Abstract**

2 In fish rearing industry, sexual maturation results in loss of profit or at least in a delay to  
3 valorize spawning fish. Indeed, many edible fish display poor fillet quality after sexual  
4 maturation and as such cannot be processed immediately after spawning. So, a post-spawning  
5 rearing period may allow the recovering of an acceptable fillet quality. So far, flesh quality  
6 restoration after spawning has received little attention. In the present study, the evolution of  
7 technological and organoleptic qualities was investigated in diploid autumnal strain female  
8 rainbow trout (24 months of age) after spawning. Immediately after spawning, nine groups of  
9 trout (n = 25) from the same cohort were placed separately into circular tanks and fed *ad*  
10 *libitum*. Fish were then sampled at 0, 1, 2, 4, 8, 13, 16, 24, and 33 weeks after spawning (PS0,  
11 PS1, PS2, PS4, PS8, PS13, PS16, PS24, and PS33). Immature (no egg produced) female trout  
12 from the same cohort were also sampled as controls at the beginning (C0) and at the end  
13 (C33) of the experiment. Immediately after spawning, PS0 trout showed a significantly lower  
14 raw fillet yield than control (C0). Furthermore, raw fillet from these trout was less colored  
15 (lower redness a\*) and presented higher lightness L\* value than raw fillet from C0 trout while  
16 their fillet mechanical resistance was similar. Raw fillet yield increased after the 16<sup>th</sup> week  
17 post-spawning. The fillet lightness steadily decreased from the 4<sup>th</sup> week to the 24<sup>th</sup> week post-  
18 spawning and did not change afterwards, whereas fillet redness increased from the 8<sup>th</sup> week to  
19 the 24<sup>th</sup> week after spawning. Fillet mechanical resistance declined progressively after  
20 spawning with a significant change from the 13<sup>th</sup> week. Concerning the smoked fillet, the  
21 smoking yield of PS0 trout was significantly lower than that of C0 trout. Thereafter the  
22 smoking yield of post-spawning trout slowly increased until reaching a significantly higher  
23 value at the 24<sup>th</sup> week. The evolution of smoked fillet color and mechanical resistance after  
24 spawning was similar to that of raw fillet. At the end of the experiment, most quality  
25 parameters of PS33 trout fillet were similar to those of C33 trout. We discuss the post-

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1 spawning quality parameters recovery in three sequential phases. On the whole, our study  
2 reports that the technological and organoleptic properties of the flesh were recovered in  
3 female trout 24 weeks after spawning ( $\approx 1400^{\circ}\text{C}\cdot\text{day}$ ).

4 **Keywords:** salmonids; yields; color; texture; post-spawning evolution.

5

1        **1. Introduction**

2        Flesh quality is a set of muscle characteristics conferring the ability to meet market  
3 preferences. Sanitary, technological, nutritional and organoleptic properties account for flesh  
4 quality (Lefevre and Bugeon, 2015). Technological quality is related to carcass characteristics  
5 during primary processing (gutting, filleting, skinning/trimming) and further processing  
6 (cooking, salting, smoking...). Organoleptic qualities include flesh color, flavor and texture,  
7 that depend on muscle components like fat, proteins and pigments, and on tridimensional  
8 organization of muscle tissue (Robb et al., 2002; Lefevre and Bugeon, 2008; Listrat et al.,  
9 2016; Hatae et al., 1990). While technological quality is assessed by measuring yields such as  
10 carcass and fillet yields, organoleptic quality is assessed by describing the sensorial  
11 characteristics of the product i.e. color, texture, and taste during a sensory analysis or by  
12 quantifying these characteristics using instrumental measurements (Dunajski, 1979; Hyldig  
13 and Nielsen, 2001; Lefevre and Bugeon, 2008; Skrede and Storebakken, 1986). The control of  
14 fish flesh quality is necessary to ensure public acceptance of farmed fish products and to fit  
15 the sustainability of aquaculture. Intrinsic factors such as genetics, sexual maturation and age,  
16 as well as extrinsic factors such as diet, environment and handling procedures before and after  
17 slaughter, are known to influence fish quality (Fauconneau et al., 1995; Haard, 1992; Lefevre  
18 and Bugeon, 2008; Rasmussen, 2001).

19        Sexual maturation deeply compromises technological and organoleptic qualities of edible  
20 fish (Aussanasuwannakul et al., 2011; Manor et al., 2012). Specifically in female salmonids,  
21 somatic tissues provide nutrients, carotenoid pigments and energy necessary for the formation  
22 of the egg yolk, which constitutes the reserves of the future embryo (Steven, 1949; Tyler et  
23 al., 1990; Cerdà et al., 2008). The large mobilization of carcass, and visceral reserves during  
24 egg formation leads to the deterioration of the fish technological properties (Aksnes et al.,  
25 1986; Nassour and Léger, 1989; Tyler et al., 1990; Shearer, 1994; Cleveland et al., 2012;

1 Salem et al., 2006; Janhunen et al., 2019). In addition, fillet mechanical resistance and fillet  
2 color, which are both among the most important traits determining flesh quality for producers,  
3 processors, and consumers, are strongly altered during sexual maturation (Torrissen and  
4 Torrissen, 1984; Bilinski et al., 1984; Aksnes et al., 1986; Hyldig and Nielsen, 2001;  
5 Aussanasuwannakul et al., 2011; Reid and Durance, 1992; Reid, 1991).

6 To meet the increasing demand for large trout, especially for smoked fillets, triploid  
7 female are mostly reared because they are sexually sterile and as such do not exhibit flesh  
8 quality deterioration. Nevertheless, diploid female fish are reared for reproduction but also to  
9 produce “trout caviar” for human consumption. The flesh of these mature female is strongly  
10 deteriorated after spawning, and quite unsuitable for fillet valorization. Empirical practices  
11 suggest that fillet quality can progressively recover during the post-spawning season but this  
12 feature has never been investigated.

13 This study was carried out to describe the evolution of flesh quality in rainbow trout after  
14 spawning. Specifically, we measured fish biometric parameters and assessed the technological  
15 quality as well as some organoleptic traits of raw and smoked fillets through instrumental  
16 measurements. Our study provides new knowledge on the recovery of trout product quality  
17 after spawning and points out the possibility of re-using female after reproduction for  
18 salmonid farm industry.

## 19 **2. Material and methods**

### 20 **2.1. Fish rearing**

21 Diploid female rainbow trout from the same autumnal strain cohort (hatched in 2015)  
22 were reared in the INRAE's experimental facilities (PEIMA, Sizun, France). Prior to  
23 spawning, trout were reared in two 6m diameter circular tanks containing 25m<sup>3</sup> of water from  
24 the “Drennec” Lake (Sizun, France). At 23 months of age, trout were individually tagged and  
25 measured for body weight and length. During spawning season (late October to November

1 2017), 24-month-old female were checked for ovulation once a week by applying a manual  
2 pressure on the abdomen. After ovulation and stripping, females from the same spawning date  
3 were placed into a circular 2m diameter tank containing 2m<sup>3</sup> of water. A total of nine  
4 experimental groups of post-spawning trout (n = 25) were constituted. In parallel, two (n =  
5 25) control groups were randomly formed from immature female trout of the same cohort.  
6 The water temperature was measured daily during the experiment.

7 Mature and immature trout were fed with the same diet throughout the course of the trial.  
8 From early July 2017 to the end of August 2017, all trout reared in the same 6m diameter tank  
9 were fed by an automatic feeder, which delivered a commercial feed (37-39% crude protein,  
10 30-32% fat, 5-7% ash and 1-3.1% crude cellulose; A40 EFICO YS 891, BioMar<sup>®</sup>, France).  
11 Fish growth was estimated using a growth model (Muller-Feuga A., 1990) and every 3 weeks  
12 to 1 month, a 10% representative sample of the whole group is counted and weighed to  
13 readjust the feed rations to the actual growth of the fish. From the end of August 2017,  
14 another standard commercial feed (40% crude protein, 24% fat, 11% ash, 1.4% crude  
15 cellulose, and 25 ppm natural astaxanthin; B-MEGA 20, Le Gouessant, France) was  
16 distributed until mature trout ceased eating. When 10% of trout from the cohort were  
17 ovulated, the feeding of fish in the tank was stopped. Immediately after spawning and  
18 constitution of experimental groups, trout were re-fed with a post-reproduction diet (46%  
19 crude protein, 16% fat, 8.7% ash, 1.8% crude cellulose, and 32 ppm natural astaxanthin; NEO  
20 REPRO II, Le Gouessant, France). Feed was distributed with automatic feeders, and feed  
21 intake was monitored during the first two months to assess trout appetite and thus adjust the  
22 feed ration. The feed conversion rate, during this early post-spawning period, was between 1.5  
23 and 2.0 for all groups. After this early post-spawning period, fish were fed *ad libitum*. Fish  
24 growth curves were similar between the different groups (data not shown).

1                   **2.2. Sampling and slaughter procedure**

2           Sampling was carried out between mid-November 2017 and late June 2018. Specifically,  
3   20 fish from the same tank were sequentially slaughtered at 0, 1, 2, 4, 8, 13, 16, 24, and 33  
4   weeks (PS0, PS1, PS2, PS4, PS8, PS13, PS16, PS24, PS33; Table 1) after spawning. Control  
5   trout (i.e., immature female that did not produce egg) were also sampled at the beginning (C0)  
6   and at the end (C33) of the experimental period. Ploidy of trout from the control groups was  
7   checked on muscle samples using flow cytometry. Some spontaneous triploids were found (6  
8   in total) in C0 and C33 batches and then discarded. Post-spawning and control trout were  
9   fasted for 48 h prior to sampling.

10          Fish care and sampling were in strict accordance with European policies and the  
11   guidelines of the National Legislation on Animal Care and Use Ethical Committee (Decree  
12   N°2013-118, February 1<sup>st</sup>, 2013; European Directive 2010-63, September 22, 2010). The  
13   INRAE PEIMA facilities are authorized for animal experimentation under French regulations  
14   (D29-277-02).

15                   **2.3. Measurements at slaughter**

16          Trout were rapidly caught from the experimental tank, anesthetized with Tricaine  
17   Pharmaq (5g/100L), then killed by a blow to the head and finally bled by gill arch section in  
18   water containing an overdose of anesthetic (5g/50L). Measurements were performed within 1-  
19   2 h after slaughter when fish were in a pre-rigor mortis state. The fish traits measurements  
20   were indexed according to the ontology ATOL (Animal Trait Ontology for Livestock, [https://  
21   www.atol-ontology.com/en/erter-2/](https://www.atol-ontology.com/en/erter-2/) ; Golik et al., 2012).

22          Fish were wiped with tissue, individually weighed (*BW*, ATOL\_0000351) and measured  
23   (standard length *SL*, ATOL\_0001659; maximum body thickness *T*, ATOL\_0005337)  
24   measured at the trunk level). Fish adiposity (ATOL\_0001663) was also assessed using the  
25   Fish Fatmeter<sup>®</sup> (Distell Industries Ltd., Scotland). This instrument was firmly applied on



1 dorsal musculature, parallel to the lateral line (Douirin et al., 1998). Two measurements were  
2 performed at two locations along the dorsal part of the both sides of the fish: the first location  
3 was anterior to the dorsal fin, the second at the dorsal fin level. Fatmeter® value was the mean  
4 of these measurements. Fish were then gutted to collect the carcass, viscera (including  
5 visceral fat) without liver (VW, ATOL\_0002258) and gonads (GW, ATOL\_0001776) which  
6 were weighed. Gutted fish were finally filleted and raw fillet (skinned and trimmed) was  
7 weighed (RFW, ATOL\_0002262). The following parameters were calculated: condition factor  
8  $K = [(BW/SL^3) \times 100000]$  (ATOL\_0001653), shape ratio  $SR = [(T/SL) \times 100]$ , gonadosomatic  
9 index  $GSI = [(GW/BW) \times 100]$  (ATOL\_0001799), viscerosomatic index  $VSI = [(VW/BW) \times$   
10  $100]$  (ATOL\_0002259), raw fillet yield =  $[(RFW/BW) \times 100]$  (ATOL\_0002263).

11 The initial muscle pH (ATOL\_0001684) was measured in the front part of fillet (Figure  
12 1), within 30 min to 1 h *post-mortem*, using a pH meter (Metrohm 826 pH mobile,  
13 Switzerland) equipped with a penetration electrode.

14 The fillet color (ATOL\_0001017) was instrumentally assessed using a portable Minolta  
15 Chromameter CR-400 (France) equipped with a light source C and a 2° observer angle,  
16 calibrated to a white standard. For each fillet, three measurements were performed at three  
17 locations along the dorsal part of the fillet: the first was anterior to the dorsal fin, the second at  
18 the dorsal fin level and the third was anterior to the anal fin (Figure 1). The mean value was  
19 considered for data expression that referred to the L\*, a\*, b\* system, representing lightness,  
20 redness, and yellowness, respectively, as recommended by the CIELAB color space (CIE,  
21 1976).

22 Fillets were then separately vacuum-packed in plastic bags and stored for 48 h at 4°C.

#### 23 **2.4. Raw fillet quality measurements at 48 h *post-mortem***

24 After 48 h of storage, quality parameters analysis was carried out on one fillet in our  
25 laboratory (Rennes, France). Fillet pH (ultimate pH, ATOL\_0001684) was performed using 5

1 g of muscle, removed from the front part of the fillet (Figure 1) and homogenized in three  
2 volumes of distilled water. Dry matter content (ATOL\_0000101) was determined in duplicate  
3 by drying approximately 9 g of minced raw fillet (Figure 1) for 72 h in an oven (Memmert  
4 854 Schwabach, Germany) at 105°C. A sample of minced raw fillet was kept and stored at -  
5 20°C in a domestic freezer for further chemical composition analysis (Figure 1). The fillet  
6 color was measured as described above at slaughter. The post-rigor fillet (64 mm length from  
7 the middle part of fillet; Figure 1) mechanical resistance (ATOL\_0001649) was performed  
8 using a Kramer shear cell mounted on a static load cell of 2 kN (Instron 5544, INSTRON  
9 Ltd., England). The maximum shear force was recorded with a constant speed of 1 mm/s and  
10 divided by the sample weight (specific resistance).

## 11 **2.5. Smoking procedure and smoked fillet quality measurements**

12 At 48 h *post-mortem*, the other fillet was smoked at PEIMA fish processing facility. Fillet  
13 was weighed and hand-salted proportionally to the fillet weight (7%) for 4 h on grids using  
14 pure dried vacuum salt (INEOS). Fillet was thereafter rinsed with tap water to remove excess  
15 salt, drained, and then cold-smoked for 5 h at 23°C with green beech wood in an air-  
16 conditioned and horizontally-ventilated smoking cabinet equipped with a GF 200 automatic  
17 smoke generator (Arcos® CTF 100 SH). Fillet was weighed before and after the salting and  
18 smoking procedure to estimate the smoking yield of fillet (by dividing the weight of the  
19 smoked fillet by the weight of the raw fillet before salting and smoking). Smoked fillets were  
20 vacuum-packed and cold-stored (0-4°C) until quality measurements at 7 days *post-mortem*.  
21 Quality parameters measurements were performed on the smoked fillet as described above for  
22 the raw fillet.

## 23 **2.6. Fillet chemical composition**

24 Chemical composition analysis was carried out by Eurofins Analytics (Nantes, France)  
25 on subsamples (n=10) of raw fillets (Figure 1) from four groups: C0; PS0, PS33 and C33.

1 Total fat content, protein and collagen content were determined using Eurofins Analytics  
2 internal methods: microwave extraction (AMG0-1), adapted-Kjeldahl Nitrogen method  
3 (C0090) and determination of collagen-hydroxyproline by spectrophotometer (AAS03),  
4 respectively.

## 5 **2.7. Statistical analyses**

6 A one-way ANOVA analysis was used to test the effect of time after spawning on quality  
7 parameters in all post-spawning groups (PS0, PS1, PS2, PS4, PS8, PS13, PS16, PS24, and  
8 PS33). A one-way ANOVA analysis was also used to compare the quality parameters of post-  
9 spawning and control fish measured at the same time (PS0 vs. C0 and PS33 vs. C33).  
10 Significant differences revealed in ANOVAs were followed by a Student-Newman-Keuls  
11 (SNK) multiple comparison test to determine differences among post-spawning groups. In  
12 addition, the Pearson correlation coefficient was calculated to analyze the significance of the  
13 linear relationships between variables in all post-spawning fish analyzed over the entire  
14 recovery period (Supplemental data: Tables S1 and S2). All of these analyses were performed  
15 using *Statistica* for Windows (version 5.1). The number of fish measured for each parameter  
16 is specified below figures or tables.

## 17 **3. Results**

### 18 **3.1. Fish biometric parameters at slaughter**

19 Immediately after spawning, trout showed a significantly lower body weight, condition  
20 factor, shape ratio and Fatmeter<sup>®</sup> value than C0 trout (Table 2). At 13 weeks, post-spawning  
21 trout body weight, condition factor, shape ratio (Table 3) and Fatmeter<sup>®</sup> value (Figure 2) were  
22 significantly higher than at 1, 2, 4 and 8 weeks after spawning and continued to increase till  
23 the end of the experiment. At the end of the experiment, post-spawning trout exhibited similar  
24 morphology parameters and Fatmeter<sup>®</sup> value to those found in immature C33 trout (Table 2).

1 Evolutions of viscerosomatic (VSI) and gonadosomatic (GSI) indexes are presented in  
2 Figure 3. PS0 trout exhibited a significantly lower VSI at spawning than C0 trout (Table 2). In  
3 contrast, the GSI was higher in post-spawning trout than in immature C0 trout. At 13 weeks  
4 post-spawning, VSI was found to be higher than at 1, 2, 4 and 8 weeks following spawning,  
5 and remained constant until the 33<sup>th</sup> week. However, one week after spawning, GSI dropped  
6 and remained low until the 33<sup>th</sup> week. At the 33<sup>th</sup> week after spawning, VSI was still lower in  
7 post-spawning trout compared to C33 trout while their GSI did not differ (Table 2).

### 8 **3.2. Fillet yields and smoking yield**

9 Immediately after spawning, PS0 trout showed a significantly lower skinned and trimmed  
10 raw and smoked fillets yields than C0 trout (Table 2). Raw and smoked fillets yields were  
11 found to slightly increase after spawning with significantly higher values after the 16<sup>th</sup> week  
12 (Figure 4). At the end of the experiment, there were no significant differences in the raw and  
13 smoked fillets yields between PS33 and C33 trout (Table 2).

14 Regarding the salting and smoking procedure, the smoking yield of PS0 trout was  
15 significantly lower than that of C0 trout, and showed a significantly higher value only at the  
16 24<sup>th</sup> week compared to the previous weeks following spawning (Figure 4). At 33 weeks after  
17 spawning, the PS33 smoking yield was similar to that of C33 trout (Table 2).

### 18 **3.3. Flesh quality**

19 No significant difference in lipid, protein, or collagen content was measured between  
20 post-spawning and control fish, whether at spawning time (Time 0) or at the end of the  
21 experiment (33 weeks after spawning) (Table 4).

22 Dry matter content of raw and smoked fillets was lower in PS0 trout compared to C0  
23 trout (Table 5). From 13 weeks after spawning, raw fillet dry matter content was found to  
24 increase till the 24<sup>th</sup> week, and then remained constant until the 33<sup>th</sup> week. In smoked fillet,  
25 dry matter content increased only after 16 weeks post-spawning and did not change

1 afterwards (Figure 2). At 33 weeks after spawning, no significant difference was observed in  
2 raw and smoked fillet dry matter content between control C33 and PS33 trout (Table 5).

3 Change in muscle pH was observed over the experiment (Tables 5 and 6). At spawning, a  
4 lower value was measured in post-spawning fillet compared to control fillet for initial pH  
5 ( $\text{pH}_i$ ) and ultimate pH ( $\text{pH}_u$ ).  $\text{pH}_i$  value was higher one week after spawning, remained fairly  
6 constant from the 1<sup>st</sup> week to the 4<sup>th</sup> week, and then exhibited the highest value at the 8<sup>th</sup>  
7 week. The values of  $\text{pH}_i$  progressively decreased from the 8<sup>th</sup> week until the end of the  
8 experiment. At the end of experiment muscle  $\text{pH}_i$  did not differ between post-spawning trout  
9 and immature C33 trout. A decrease in muscle pH was observed at 48 h *post-mortem* and this  
10 variation ( $\Delta\text{pH}$ ) was globally the same at each measurement point. Muscle  $\text{pH}_u$  was found to  
11 be globally similar over the experiment, except at 33 weeks where lower value was measured  
12 in PS33 compared to those of the preceding post-spawning trout and also compared to that of  
13 C33 trout. Smoked fillet pH of post-spawning trout was significantly lower than that of  
14 control at the beginning and at the end of the experiment and only slightly changed over time.

15 Figure 5 shows changes in color parameters of raw fillet measured at slaughter and of  
16 smoked fillet in trout after spawning. At the beginning of the experiment, raw fillet from PS0  
17 trout was less colored (lower redness  $a^*$ ) and presented higher lightness  $L^*$  value than that  
18 from C0 trout (Table 5). Lightness of fillet steadily decreased from the 4<sup>th</sup> week to the 24<sup>th</sup>  
19 week and did not change afterwards, whereas fillet redness increased from the 8<sup>th</sup> week to the  
20 24<sup>th</sup> week after spawning. At the end of the experiment, raw fillet color was similar between  
21 PS33 and C33 trout except the fillet lightness, which was higher in post-spawning fillet (Table  
22 5). Changes in smoked fillet color after spawning were similar to those observed in raw fillet.  
23 However, the fillet lightness ( $L^*$ ) remained constant after a slight rise at the 4<sup>th</sup> week. At the  
24 end of the experiment, smoked fillet redness ( $a^*$ ) was similar between PS33 and C33 trout  
25 while lightness and yellowness ( $b^*$ ) of PS33 fillet were higher.

1 Raw fillet mechanical resistance was similar between trout PS0 and C0 trout (Table 5).  
2 Afterwards, post-spawning fillet mechanical resistance clearly decreased from the 13<sup>th</sup> week  
3 onwards (Figure 6). Concerning smoked fillet, mechanical resistance globally followed the  
4 evolution observed in raw fillet, but with a progressive decrease from two weeks after  
5 spawning until the end of the experiment. At 33 weeks, raw and smoked fillets mechanical  
6 resistance did not differ between PS33 and C33 (Table 5).

#### 7 **4. Discussion**

8 The deleterious effect of sexual maturation and spawning on flesh quality in female fish  
9 is well described in literature. In this study we show that the technological and organoleptic  
10 properties of fillet are recovered in female trout 24 weeks after spawning.

##### 11 **4.1. Fish and raw fillet qualities at spawning**

12 In accordance with previous studies on female fish, especially salmonids (Aksnes et al.,  
13 1986; Kawai et al., 1990), our results show that sexual maturation and spawning affect fish  
14 biometrics, such as body weight and condition factor. Additionally, we showed that post-  
15 spawning trout were slimmer than immature trout as shown by their lower shape ratio.  
16 Concurrently, we observed that immediately after spawning, trout had less fat stores than  
17 immature trout as previously reported (Aksnes et al., 1986; Jonsson et al., 1997; Kawai et al.,  
18 1990; Nassour and Léger, 1989). The fact that trout used fat from their somatic tissues,  
19 largely muscle and viscera to produce eggs, likely explains their lower VSI in contrast with  
20 their higher GSI. Changes in fat stores and shape following egg production contributed  
21 furthermore to lower raw fillet yield showing therefore that fish technological quality was  
22 affected upon spawning. About organoleptic traits, fillet color was greatly altered around  
23 spawning as already observed in salmonids (Aksnes et al., 1986; Janhunen et al., 2019; Reid  
24 et al., 1993; Steven, 1949; Torrissen and Torrissen, 1984) and this alteration results from the  
25 mobilization of carotenoid pigments from muscle towards ovaries during egg production

1 (Crozier, 1970; Storebakken and No, 1992). Fillet color alteration could also be due to the  
2 lower voluntary feed consumption around spawning, which reduces pigments intake during  
3 the period preceding spawning, as previously reported (Storebakken and No, 1992; Torrissen  
4 and Torrissen, 1984). Concerning textural properties, we found no detectable effect of  
5 spawning on raw fillet immediately after spawning as shown by the same mechanical  
6 resistance between post-spawning and immature trout. Divergent data have been reported  
7 regarding the effect of sexual maturation and spawning on the texture of fish flesh. In  
8 salmonids, comparing diploid maturing female versus triploid sterile one, some authors have  
9 reported fillet toughening (Aussanasuwannakul et al., 2011, 2012; Salem et al., 2013) while  
10 others observed fillet softening (Salem et al., 2006) in diploid female. However, it should be  
11 kept in mind that diploid and triploid are two distinct genetic models that, beyond spawning,  
12 have intrinsically different textural properties (Bjørnevik et al., 2004; Lefevre et al., 2015;  
13 Lerfall et al., 2017a, 2017b; Segato et al., 2007), and the effect measured may be in part due  
14 to ploidy level and not to sexual maturation. There are only few studies comparing immature  
15 and mature salmonid diploid female upon spawning that also reported opposite effects of  
16 spawning on flesh texture. Mature female fillet were indeed found to be either tougher  
17 (Aksnes et al., 1986) or softer (Reid and Durance, 1992). In these latter studies, texture was  
18 assessed through sensory analysis, but the products considered were quite different as Aksnes  
19 et al. (1986) analyzed steamed pieces of fillet from farmed Atlantic salmon, whereas Reid and  
20 Durance (1992) measured canned fillet from commercial migratory wild chum salmon.  
21 Moreover, Aksnes et al. (1986), who used fish model close with ours, reported that fillet  
22 toughening in mature fish was associated with a significant decrease of muscle protein  
23 content, a feature that we did not observed on our side, and that could explain an absence of  
24 texture deterioration in our study. Finally, in contrast with the above mentioned reports on

1 immature and mature salmonids, but in agreement with our results, sexual maturation has not  
2 been shown to affect fillet texture in Atlantic halibut (Roth et al., 2007).

3 Given all these observations, our post-spawning trout represented a suitable model for  
4 describing the evolution of quality after spawning.

#### 5 **4.2. Evolution of fish and fillet qualities after spawning**

6 Immediately after spawning, trout were fed to satiation to allow the full expression of  
7 their growth potential. However, the post-spawning re-establishment of each quality  
8 parameter was not synchronous. The recovery period following spawning can be divided into  
9 three phases: **early**, **transitional** and **late** phase.

10 **During the earliest phase** that covers the period from 0 to 8 weeks after spawning,  
11 almost all measured parameters remained unchanged. This period corresponded to last  
12 autumn, with decreasing photoperiod and water temperature, which did not favor fish  
13 recovering after spawning. For example, no change in fillet color was noticed up to 8 weeks  
14 after spawning. Recovery of flesh color after spawning could have been delayed by a low  
15 water temperature, as mentioned above, that generally leads to a reduction of voluntary feed  
16 intake in trout (Kestemont and Baras, 2001). Consistently, the only parameter that varied in  
17 that early period was the GSI. After spawning, the involution of the ovaries could explain this  
18 evolution. The GSI remained thereafter low corresponding to female sexual resting period as  
19 previously mentioned for rainbow trout (Bobe et al., 2010). Nevertheless, it can be noted that  
20 the GSI values remained higher than those of the immature fish at the beginning of the  
21 experiment.

22 **The second transitional phase**, which covers the period from 8 to 16 weeks after  
23 spawning, is mainly related to changes in biometrics. It was only at 13 weeks after spawning  
24 that the body weight of the measured fish was higher, as were condition factor and body shape  
25 ratio. This observation suggests a resumption of overall growth, associated with a resumption



1 of muscle growth, which would explain the higher values of the body shape ratio. In addition,  
2 post-spawning trout re-accumulated reserves, which were mainly fat as indicated by increase  
3 in muscular and perivisceral adiposity. Such observations are in accordance with a recent  
4 study by Jenkins et al. (2019) that reported an increase in lipid energy reserves rapidly after  
5 spawning in “consecutive spawners” (trout that spawn twice in two consecutive years) like  
6 our post-spawning trout in contrast to “skip spawners” (trout that skip at least one year  
7 between two successive spawnings). More generally, our data show that rainbow trout, like  
8 Atlantic salmon (Rørvik et al., 2018), are able to rapidly replenish lipid stores following a  
9 period of unfavourable somatic growth conditions. On the whole, the fat accumulation we  
10 observed in post-spawning trout may have prepared the desirable evolution of fillet yield and  
11 quality parameters even though the complete recovery occurred later.

12 **The late phase**, that covers the period beyond 16 weeks, was marked by the recovery of  
13 technological and organoleptic qualities. Regarding the technological quality, fillet yield  
14 increased 16 weeks after spawning, while trout became thicker and heavier and had more  
15 muscle mass. However, we cannot rule out the possibility, in line with Haffray et al. (2013)  
16 who showed that fillet yield also depends on fish morphology, that the important increase in  
17 fillet yield we observed after spawning could result from changes in trout body shape. This  
18 argument that the shape affects fillet yield was also strengthened by our observation, mentioned  
19 above, of such a relationship comparing C0 and PS0. Moreover, a positive correlation  
20 between shape ratio and raw fillet yield ( $r = 0.36$ ,  $p < 0.001$ ) also confirms a link between  
21 these two parameters. Nevertheless, the body conformation change of post-spawning trout is  
22 thus worth further investigation to determine whether the evolution of fillet yield is related to  
23 that of fish shape. Furthermore, the increase in fillet yield could be also explained by the  
24 relative reduction of losses during filleting according to Bugeon et al. (2010). The increase in  
25 muscle percentage compared to head and bones percentages of the post-spawning trout

1 carcass (data not shown) is a sought-after factor considering production purpose whereby the  
2 offal percentage must be reduced to maximize the profit. Concerning the organoleptic traits,  
3 progressive restoration of flesh coloration was found to occur in post-spawning trout,  
4 beginning with the transitional recovery phase and continuing afterwards. This observation is  
5 in line with previous report from Choubert (1992) showing that pigment concentration tends  
6 to increase in fish muscle after spawning. The restoration of fillet color may relate to the  
7 increase in pigment amount ingested by trout and fixed within the muscle after feeding  
8 resumption. Moreover, the recovery of color might be related to the favorable growth stage of  
9 fish. Indeed, larger trout take-up carotenoids more efficiently than smaller ones as already  
10 noticed (Storebakken and No, 1992; Torrissen, 1989). Trout growth, as that observed after  
11 spawning, is also generally associated with an increase in flesh coloration as previously  
12 mentioned (Olsen and Mortensen, 1997; Torrissen, 1995). Fillet coloration increased till the  
13 24<sup>th</sup> week beyond which muscle was probably no longer able to fix more astaxanthin.  
14 Choubert (1992) similarly reported that the red color of trout muscle tends towards a  
15 maximum, which cannot be exceeded despite the continuous ingestion of pigments. In terms  
16 of texture properties, the significant decline in mechanical resistance might be caused by the  
17 progressive increase in muscle fat content we observed during the transitional recovery  
18 period. Moreover we can note that we have measured strong negative correlations between  
19 mechanical resistance and fish adiposity (for example,  $r = -0.75$ ,  $p < 0.001$  between Fat-meter  
20 value and specific resistance). Likewise, several studies also reported that high fat content in  
21 farmed fish leads to flesh softening (Aussanasuwannakul et al., 2011, 2012; Fauconneau et  
22 al., 1993; Johansson et al., 2000; Green-Petersen and Hyldig, 2010; Thakur et al., 2003;  
23 Lefevre et al., 2015). However, we cannot rule out the possibility that the decrease in  
24 mechanical resistance may also result from an increase in muscle fiber size, a feature that has  
25 been reported to be an important determinant of flesh texture (Johnston, 1999). In keeping

1 with this, it would be also of interest to examine the evolution of muscle cellularity during the  
2 post-spawning period.

3 At the end of the experiment, post-spawning trout exhibited globally the same values of  
4 quality parameters as immature trout. For example, the two groups of immature and post-  
5 spawning trout had similar body weight, which validates, in comparison to the control, the  
6 growth resumption in post-spawning trout. In addition, GSI became similar between post-  
7 spawning and control groups. This feature can be explained by the fact that control trout that  
8 were initially immature by the time of spawning, started their first oogenesis while post-  
9 spawning trout restarted a second one. At last, we found that post-spawning trout after the late  
10 phase of restoration, displayed a fillet yield similar to that of immature and close to that  
11 typically reported in large farmed rainbow trout of the same age (Davidson et al., 2014).  
12 Concerning redness ( $a^*$ ), values obtained for post-spawning fish at the end of the experiment,  
13 was similar to those of the control. Nevertheless, as the controls were much redder at the  
14 beginning, it is interesting to note that the increase in pigmentation during the 33 weeks of the  
15 experiment was much more pronounced for post-spawning fish than for control ones.  
16 However, lightness ( $L^*$ ) of post-spawning fish fillet remained higher than that of control. This  
17 difference in lightness cannot be explained by the increase in muscle fat content as previously  
18 reported (Christiansen et al., 1995; Marty-Mahé et al., 2004; Mørkøre et al., 2001) given that  
19 fat content was similar between immature and post-spawning trout. Higher fillet lightness  
20 may result from the difference in muscle structure between mature and immature trout that  
21 could have affected the optical properties of the muscle as previously reported (Einen and  
22 Thomassen, 1998; Johnston et al., 2000; Lefevre and Bugeon, 2008). The reason of the partial  
23 recovery of fillet lightness in post-spawning fish therefore remains to be lightened.

### **4.3. Quality of smoked fillet after spawning: relationship with raw fillet**

1                   **4.3. Quality of smoked fillet after spawning: relationship with raw fillet**  
2           The technological and organoleptic qualities of the smoked trout fillet did also change  
3 after spawning. Concerning technological quality, we considered two important parameters  
4 for processors, namely the smoking yield and smoked fillet yield. The smoking yield which is  
5 an indicator of the weight gain after the processing was lower at spawning in mature trout  
6 fillet, and this may result from the lower raw fillet dry matter content in mature trout  
7 compared to that of immature. Low dry matter content indicates low fat content and high  
8 water content which may be lost during salting and smoking, as previously reported (Cardinal  
9 et al., 2001; Lerfall et al., 2017b; Mørkøre et al., 2001). After spawning and specifically  
10 during the late recovery phase, the increase in the smoking yield could be attributed to the  
11 significant increase in muscle fat content, which is generally associated with a reduction in  
12 water loss in the fillet of large fish (Shearer, 1994; Rørå et al., 1998). The smoked fillet yield,  
13 which depends on raw fillet yield and the smoking yield, was logically lower at spawning  
14 time in mature trout compared to immature, given that fillet and smoking yields were also  
15 lower in mature trout. After spawning, the smoked fillet yield likewise increased as it  
16 benefited from both improvement of raw fillet yield and the smoking yield, and thus become a  
17 key point to achieve economic profit. Regarding organoleptic traits, the evolution of smoked  
18 fillet color and mechanical resistance was globally similar to that of raw fillet. However, the  
19 higher smoked fillet mechanical resistance in trout that have just spawned compared to  
20 immature, may be due to their lower fat content as has been already observed (Mørkøre and  
21 Rørvik, 2001). Another explanation to this higher mechanical resistance could be related to  
22 the difference in muscle structure due to fillet processing. In this regard, we propose that, as  
23 with the cooking process previously reported to affect muscle structure and texture (Hatae et  
24 al., 1990), the smoking process in our study may also have led to a greater shrinkage of

1 muscle fibers in mature fillet following their greater water loss than immature fillet and  
2 contributed subsequently to higher muscle mechanical resistance.

3 Smoked fillet quality depends on salting and smoking conditions (Rørå et al., 1998;  
4 Cardinal et al., 2001). The quality of raw material is also known to be an important factor to  
5 produce a high quality smoked product (Lerfall et al., 2012, 2017b). For that reason, quality  
6 controls should be applied for raw fillet from fish that have spawned, and that are intended to  
7 the smoking process. In the present study, evolution of smoked post-spawning fillet quality  
8 could be due to the raw fillet characteristics from which they derive, as the salting and  
9 smoking conditions were the same over the experiment. Here, since both raw and smoked  
10 fillets were measured on the same fish, we can correlate raw fillets color and texture  
11 parameters with those of smoked fillets. Concerning post-spawning fillet color, smoking  
12 procedure resulted in a decrease of fillet lightness ( $L^*$ ) in line with previous studies (Choubert  
13 et al., 1992; Rørå et al., 1998), and to a lesser extent, a decrease of redness (Cardinal et al.,  
14 2001; Mørkøre et al., 2001; Skrede and Storebakken, 1986). Interestingly, our study showed  
15 that fillet lightness ( $L^*$ ) defect after spawning was concealed by smoking. On the other hand,  
16 the low redness ( $a^*$ ) values measured in the weeks following spawning on raw fillets were  
17 also measurable on smoked fillet, which constitutes a quality defect of the smoked product  
18 since redness is the parameter most correlated with human color visual perception  
19 (Christiansen et al., 1995). To avoid unmarketable products, our data suggest that processors  
20 could predict smoked fillet color from that of raw material as the redness of all post-spawning  
21 smoked fillet was strongly correlated with that of raw fillet ( $r = 0.93$ ,  $p < 0.001$ ). This latter  
22 result is in accordance with that of Choubert et al. (1992) who report a strong correlation  
23 between raw fillet color parameters (lightness, chroma and hue) and those of smoked fillets.  
24 About textural properties, trout smoked fillet exhibited higher mechanical resistance than that  
25 of raw fillet throughout the experiment, probably due to water loss as it has been shown in

1 Atlantic salmon following salting and smoking (Sigurgisladottir et al., 2000). Another  
2 explanation to the difference between raw and smoked fillet texture might be the change of  
3 muscle structure and properties during the salting and smoking processes as previously  
4 mentioned (Sigurgisladottir et al., 2001). Interestingly, in contrast with previous studies  
5 (Birkeland et al., 2004), post-spawning smoked fillet texture could also be predicted from that  
6 of raw fillet, suggesting that smoked fillet mechanical resistance may have the same  
7 determinism as raw fillet. Indeed, mechanical resistance of smoked fillet was positively  
8 correlated to that of raw fillet ( $r = 0.89$ ,  $p < 0.001$  for the shear force and  $r = 0.91$ ,  $p < 0.001$   
9 for specific resistance). Overall, these results may contribute to extend, on post-spawning  
10 fillet, knowledge about the effect of raw material characteristics on smoked product quality.

## 11 **5. Conclusions**

12 The present study described the evolution of trout flesh quality after spawning. We found  
13 that the major changes in flesh quality significantly began 8 weeks after spawning and that  
14 restorations of fillet technological and organoleptic properties were effective only 24 weeks  
15 after spawning ( $\approx 1400^\circ\text{C}\cdot\text{day}$ ). In addition, we have shown that post-spawning fillets are  
16 suitable for smoking especially for market purposes, and that the evolution of smoked flesh  
17 quality was similar to that of raw fillet. Consequently, this study provides a useful timetable to  
18 obtain eating quality in fish after spawning that fits the sustainability of fish farming. Further  
19 muscle histologic and transcriptomic analyses should provide insights into the biological  
20 processes involved in the recovery of quality following spawning. The effect of zootechnical  
21 factors around the spawning period should also be investigated to achieve maximum  
22 efficiency of the recovery process.

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*Flesh quality recovery in trout after spawning*

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**Figures**

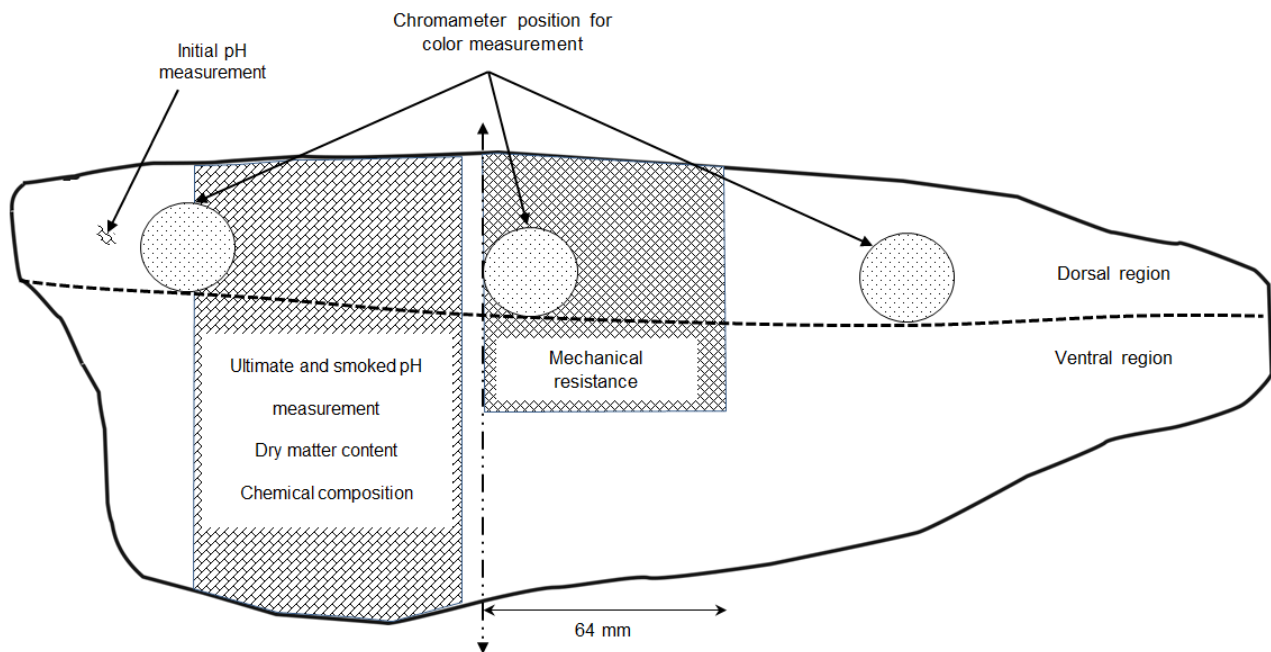


Figure 1 : Schematic representation of measurements and sampling locations for quality analyses of rainbow trout raw and smoked fillets; for details see text.

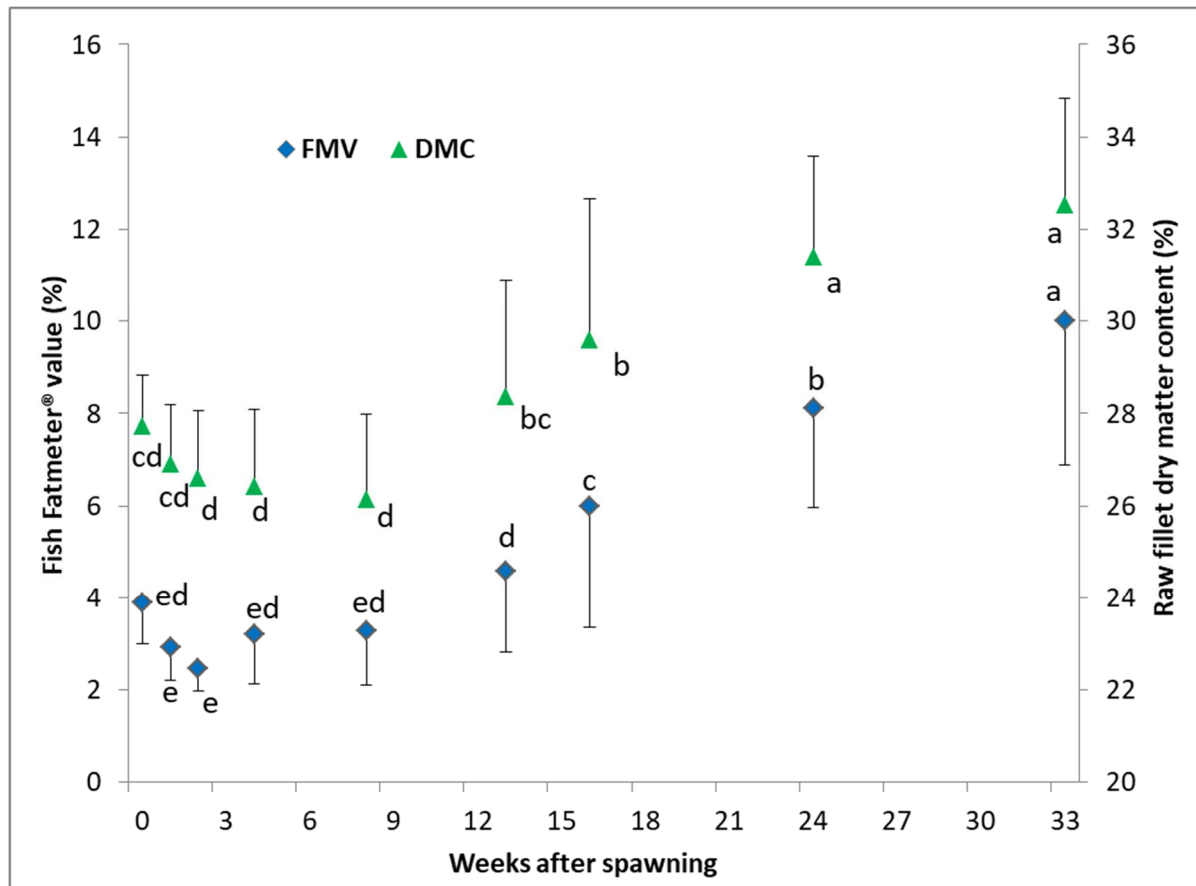


Figure 2 : Evolutions of adiposity parameters, fish Fatmeter® value (FMV) and raw fillet dry matter content (DMC), in rainbow trout after spawning:. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between groups are denoted with different letters (p < 0.05).

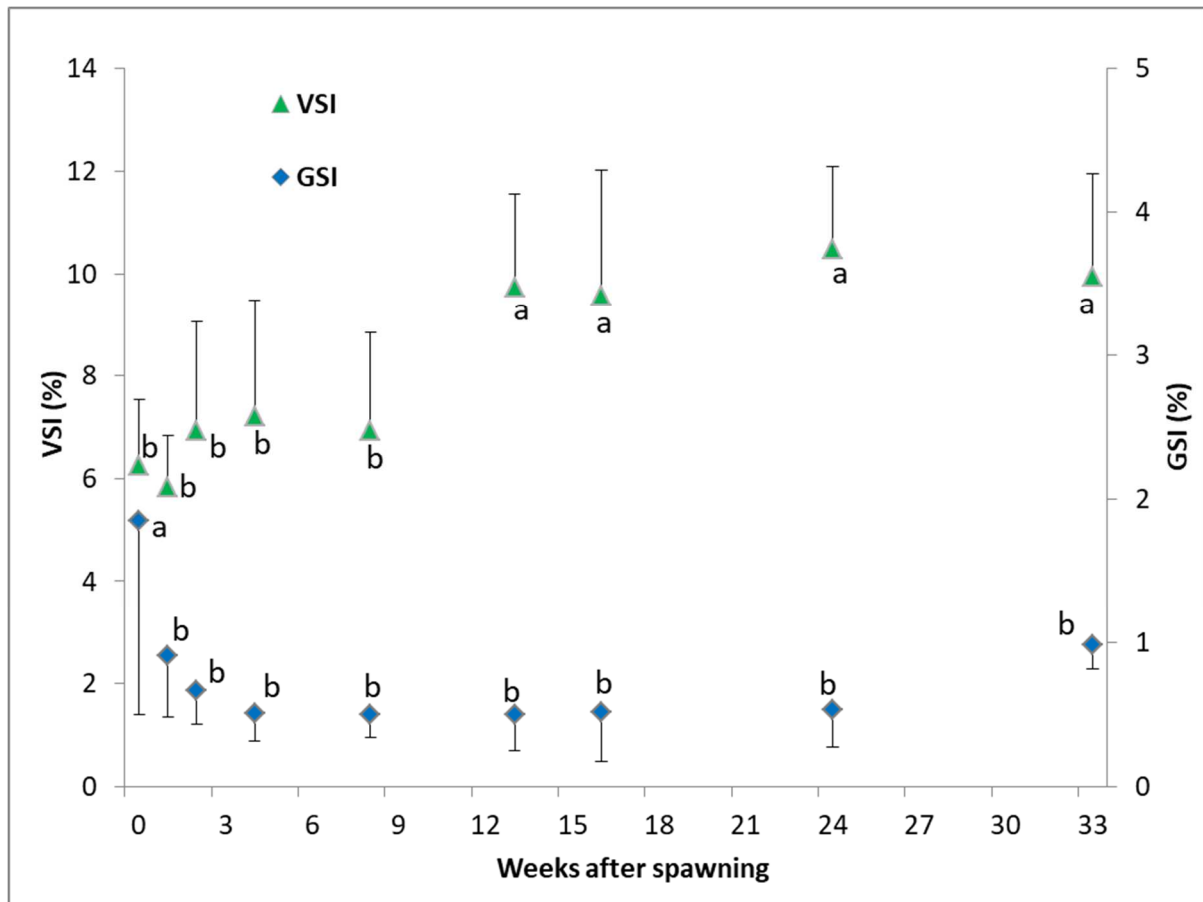


Figure 3 : Evolutions of viscerosomatic index (VSI) and gonadosomatic index (GSI) in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning are denoted with different letters (p < 0.05).

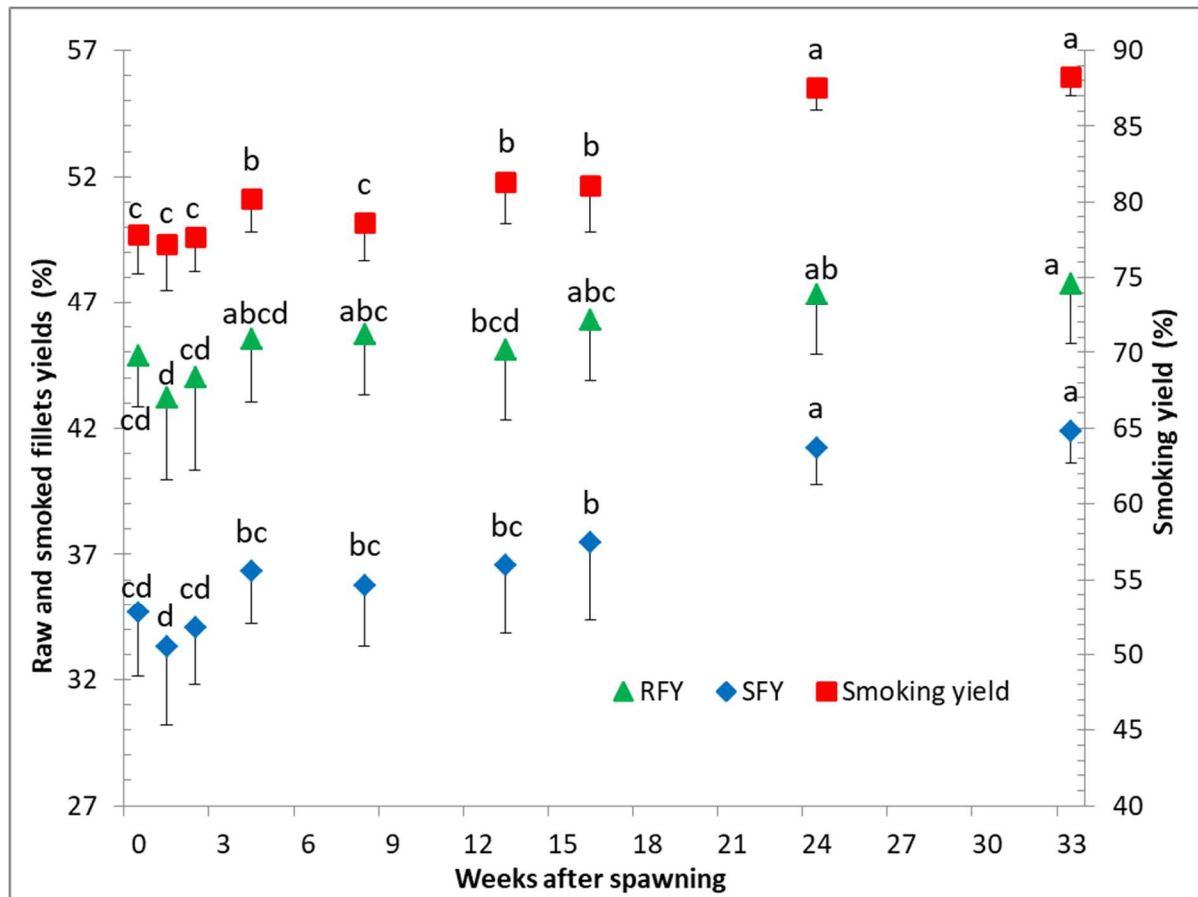


Figure 4 : Evolutions of raw (RFY) and smoked fillets (SFY) yields and smoking yield in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning are denoted with different letters (p < 0.05).

*Flesh quality recovery in trout after spawning*

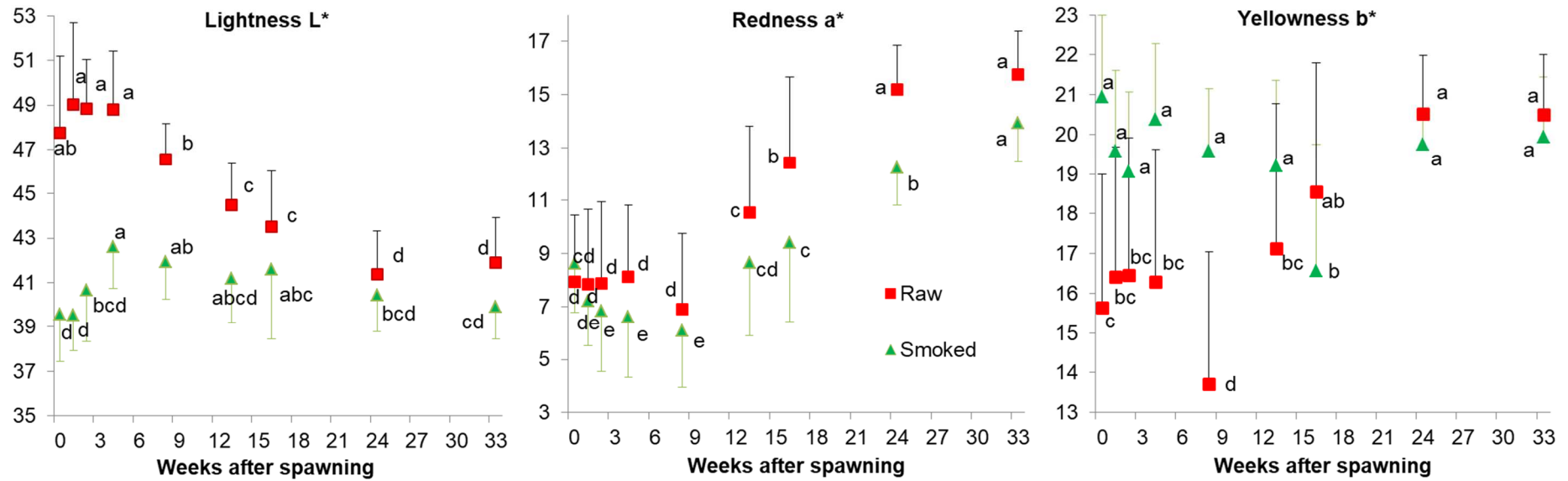


Figure 5 : Changes in lightness (L\*), redness (a\*) and yellowness (b\*) of raw and smoked fillets in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning are denoted with different letters (p < 0.05).

*Flesh quality recovery in trout after spawning*

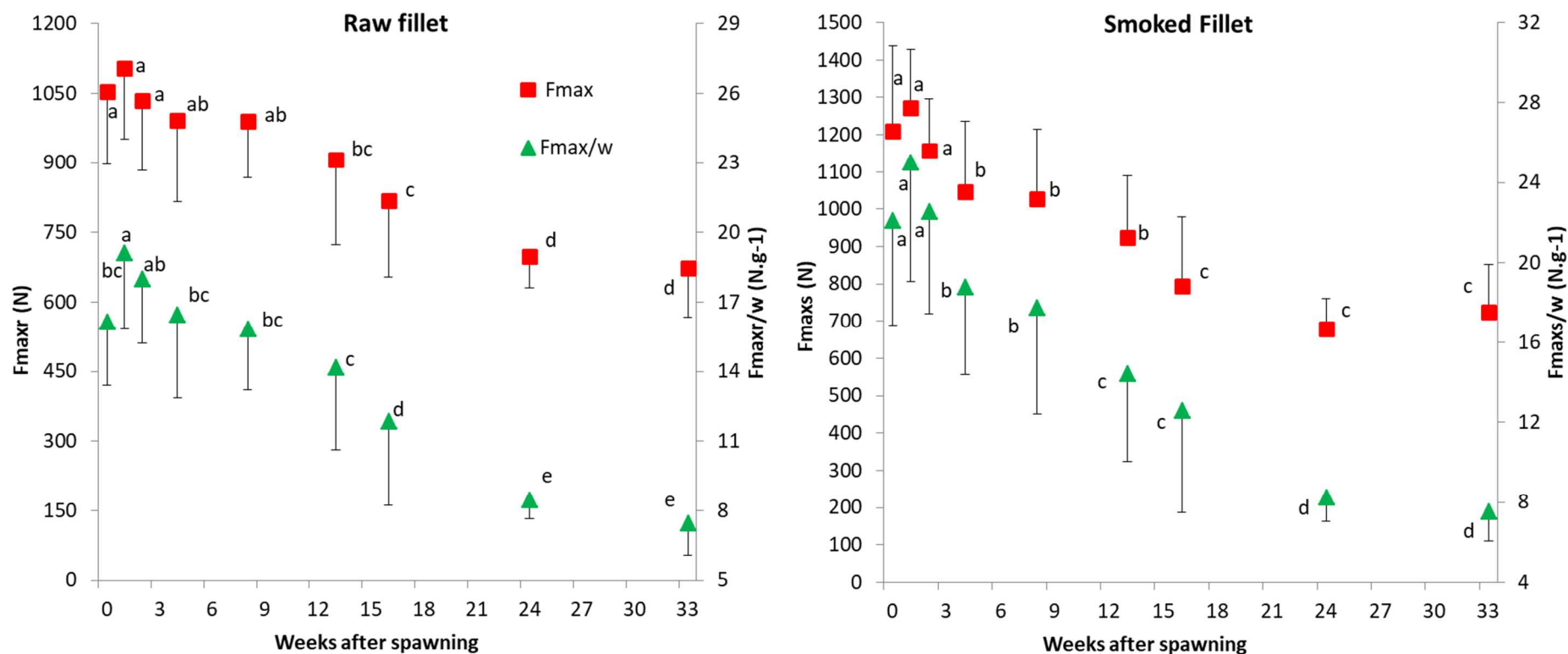


Figure 6 : Evolution of maximum shear force (Fmax) and specific resistance (Fmax/w) of raw and smoked fillets in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning are denoted with different letters (p < 0.05).

**Tables**

Table 1 : Timetable of mean daily water temperature and post-spawning time expressed in degree per day for each sampling groups (n=20).

<b>Time post-spawning (weeks)</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>4</b>	<b>8</b>	<b>13</b>	<b>16</b>	<b>24</b>	<b>33</b>
Sampling groups	PS0	PS1	PS2	PS4	PS8	PS13	PS16	PS24	PS33
Mean water temperature (°C)	11	11	11	8	8	7	7	9	12
Post-spawning duration (°C.day)	0	130	220	350	520	800	1030	1400	2100



*Flesh quality recovery in trout after spawning*

Table 2 : Comparison of fish traits between control (C) and post-spawning (PS) fish at spawning time

(time 0) and at the end of the experiment (33 weeks after).

Parameters	Spawning Time – 0 week			33 weeks post-spawning		
	C0	PS0	Anova :	C33	PS33	Anova :
Body weight (g)	1456 ± 238	1254 ± 164	**	3238 ± 675	3321 ± 447	ns
Maximum body thickness (mm)	61.7 ± 4.6	57.7 ± 3.9	**	85.2 ± 8.2	86.1 ± 4.7	ns
Standard length (mm)	428 ± 19	417 ± 20	ns	515 ± 37	519 ± 24	ns
Condition factor <sup>1</sup>	1.8 ± 0.1	1.7 ± 0.1	*	2.3 ± 0.2	2.4 ± 0.2	ns
Shape ratio <sup>2</sup>	14.4 ± 0.6	13.8 ± 0.7	*	16.5 ± 0.9	16.6 ± 0.7	ns
Fat-meter value (%)	5.1 ± 1.1	3.9 ± 0.9	***	9.6 ± 2.6	10.0 ± 3.1	ns
VSI <sup>3</sup> (%)	9.6 ± 1.3	6.2 ± 1.3	***	11.5 ± 2.2	10.0 ± 2.0	*
GSI <sup>4</sup> (%)	0.12 ± 0.08	1.85 ± 1.35	***	0.89 ± 0.33	0.98 ± 0.17	ns
Raw fillet yield <sup>5</sup> (%)	47.8 ± 2.0	44.9 ± 2.1	***	47.6 ± 2.6	47.8 ± 2.4	ns
Smoked fillet yield <sup>6</sup> (%)	38.4 ± 2.4	34.7 ± 2.3	***	41.9 ± 2.9	41.9 ± 2.3	ns

Mean ± standard deviation, n = 20, 18 and 14, respectively in post-spawning, C0 and C33 groups.

\* and \*\* indicate significant differences between post-spawning and control trout (p < 0.05 and p < 0.01 respectively).

ns means no significant differences found between post spawning and control trout measured at the same time.

<sup>1</sup> Condition factor = (Body weight/Standard length<sup>3</sup>) x 100000.

<sup>2</sup> Shape ratio = (Maximum body thickness/Standard length) x 100.

<sup>3</sup> VSI = viscero-somatic index = (viscera weight/body weight) x 100

<sup>4</sup> GSI = gonado-somatic index = (gonad weight/body weight) x 100

<sup>5</sup> Raw fillet yield = (raw fillet weight/body weight) x 100

<sup>6</sup> Smoked fillet yield = (smoked fillet weight/body weight) x 100

*Flesh quality recovery in trout after spawning*

Table 3 : Biometric parameters of female slaughtered at different times following spawning (Mean  $\pm$  standard deviation, n = 20).

Parameters	Groups								
	PS0	PS1	PS2	PS4	PS8	PS13	PS16	PS24	PS33
Body weight (g)	1254 $\pm$ 164 <sup>d</sup>	1373 $\pm$ 184 <sup>d</sup>	1246 $\pm$ 213 <sup>d</sup>	1366 $\pm$ 224 <sup>d</sup>	1482 $\pm$ 199 <sup>d</sup>	1728 $\pm$ 385 <sup>c</sup>	1781 $\pm$ 347 <sup>c</sup>	2355 $\pm$ 326 <sup>b</sup>	3321 $\pm$ 447 <sup>a</sup>
Maximum body thickness (mm)	57.7 $\pm$ 3.9 <sup>de</sup>	56.8 $\pm$ 3.2 <sup>de</sup>	55.3 $\pm$ 3.4 <sup>e</sup>	57.4 $\pm$ 3.0 <sup>de</sup>	59.7 $\pm$ 3.2 <sup>d</sup>	62.8 $\pm$ 5.1 <sup>c</sup>	63.6 $\pm$ 4.8 <sup>c</sup>	70.0 $\pm$ 3.8 <sup>b</sup>	86.1 $\pm$ 4.7 <sup>a</sup>
Standard length (mm)	417 $\pm$ 20 <sup>e</sup>	436 $\pm$ 19 <sup>cd</sup>	415 $\pm$ 23 <sup>e</sup>	426 $\pm$ 21 <sup>de</sup>	433 $\pm$ 17 <sup>cde</sup>	445 $\pm$ 27 <sup>c</sup>	440 $\pm$ 18 <sup>cd</sup>	470 $\pm$ 23 <sup>b</sup>	519 $\pm$ 24 <sup>a</sup>
Condition factor <sup>1</sup>	1.7 $\pm$ 0.1 <sup>de</sup>	1.6 $\pm$ 0.1 <sup>e</sup>	1.7 $\pm$ 0.1 <sup>de</sup>	1.8 $\pm$ 0.1 <sup>de</sup>	1.8 $\pm$ 0.1 <sup>cd</sup>	1.9 $\pm$ 0.2 <sup>c</sup>	2.1 $\pm$ 0.3 <sup>b</sup>	2.3 $\pm$ 0.2 <sup>a</sup>	2.4 $\pm$ 0.2 <sup>a</sup>
Shape ratio <sup>2</sup>	13.8 $\pm$ 0.7 <sup>de</sup>	13.0 $\pm$ 0.4 <sup>f</sup>	13.3 $\pm$ 0.7 <sup>ef</sup>	13.5 $\pm$ 0.6 <sup>ef</sup>	13.8 $\pm$ 0.4 <sup>de</sup>	14.1 $\pm$ 0.7 <sup>cd</sup>	14.4 $\pm$ 0.8 <sup>c</sup>	14.9 $\pm$ 0.7 <sup>b</sup>	16.6 $\pm$ 0.7 <sup>a</sup>

Values in the same row with different letters are significantly different (p < 0.05).

<sup>1</sup> Condition factor = (Body weight/Standard length<sup>3</sup>) x 100000.

<sup>2</sup> Shape ratio = (Maximum body thickness/Standard length) x 100.

*Flesh quality recovery in trout after spawning*

Table 4 : Chemical composition for raw fillet of control and post-spawning trout measured at spawning time

(time 0) and at the end of the experiment (33 weeks after).

Parameters	Spawning Time – 0 week			33 weeks post-spawning		
	C0	PS0	Anova :	C33	PS33	Anova :
Total fat (%)	8.76 ± 1.27	7.45 ± 1.52	ns	8.61 ± 2.39	10.26 ± 2.29	ns
Protein (%)	21.39 ± 1.27	21.83 ± 1.38	ns	22.19 ± 1.54	21.61 ± 1.50	ns
Collagen (%)	0.46 ± 0.07	0.40 ± 0.07	ns	0.45 ± 0.13	0.40 ± 0.06	ns

Mean ± standard deviation, n = 10, 9, 10 and 7, respectively in PS0, C0, PS33 and C33 groups.

“ns” means no significant difference. -

Table 5 : Comparison of fillet quality traits between control and post-spawning fish at spawning time

(time 0) and at the end of the experiment (33 weeks after).

Parameters	Spawning Time – 0 week			33 weeks post-spawning		
	C0	PS0	Anova :	C33	PS33	Anova :
<i>Raw fillet</i>						
Raw DMC (%)	29.4 ± 1.4	27.7 ± 1.1	***	33.6 ± 3.7	32.5 ± 2.3	ns
Initial pH (pH <sub>i</sub> )	7.09 ± 0.13	6.89 ± 0.22	**	7.06 ± 0.13	7.08 ± 0.11	ns
Ultimate pH (pH <sub>u</sub> )	6.48 ± 0.08	6.39 ± 0.13	*	6.36 ± 0.05	6.29 ± 0.04	***
ΔpH (=pH <sub>u</sub> –pH <sub>i</sub> )	-0.61 ± 0.14	-0.49 ± 0.22	ns	-0.70 ± 0.13	-0.79 ± 0.12	ns
Raw L*	42.4 ± 1.5	47.7 ± 3.5	***	38.2 ± 2.2	41.9 ± 2.0	***
Raw a*	11.3 ± 1.8	7.9 ± 2.5	***	15.5 ± 1.7	15.8 ± 1.6	ns
Raw b*	17.2 ± 2.0	15.6 ± 3.6	ns	19.3 ± 1.9	20.5 ± 1.5	ns
Raw Fmax (N)	1068 ± 106	1055 ± 158	ns	723 ± 93	673 ± 106	ns
Raw Fmax/w (N/g)	15.4 ± 2.1	16.2 ± 2.8	ns	8.0 ± 1.5	7.5 ± 1.4	ns
<i>Smoked fillet</i>						
Smoking yield	80.9 ± 2.1	77.8 ± 2.6	***	88.5 ± 1.7	88.3 ± 1.3	ns
Smoked DMC (%)	35.75 ± 1.05	34.33 ± 1.47	**	37.51 ± 2.55	37.00 ± 2.21	ns
Smoked fillet pH	6.30 ± 0.08	6.10 ± 0.10	***	6.23 ± 0.06	6.17 ± 0.05	**
Smoked L*	36.9 ± 0.9	39.6 ± 2.2	***	38.2 ± 2.0	39.9 ± 1.4	**
Smoked a*	9.4 ± 1.4	8.6 ± 1.9	ns	13.6 ± 1.3	13.9 ± 1.5	ns
Smoked b*	16.7 ± 1.0	20.9 ± 2.0	***	18.3 ± 1.2	19.9 ± 1.5	**
Smoked Fmax (N)	1069 ± 87	1210 ± 228	*	690 ± 95	724 ± 128	ns
Smoked Fmax/w (N/g)	18.0 ± 3.1	22.1 ± 5.2	**	7.5 ± 1.5	7.5 ± 1.5	ns

Mean ± standard deviation, n = 20, 18 and 14, respectively in post-spawning, C0 and C33 groups.

DMC = Dry Matter Content

\*, \*\* and \*\*\* indicate significant differences between post-spawning and control trout measured at the same time (p < 0.05, p < 0.01 and p < 0.001 respectively).

ns means no significant differences found between post spawning and control trout measured at the same time.

*Flesh quality recovery in trout after spawning*

Table 6 : Raw and smoked fillet pH and smoked fillet dry matter content of rainbow trout after spawning (Mean  $\pm$  standard deviation, n = 20).

Parameters	Groups								
	PS0	PS1	PS2	PS4	PS8	PS13	PS16	PS24	PS33
	<i>Raw fillet</i>								
Initial pH (pH <sub>i</sub> )	6.89 $\pm$ 0.22 <sup>d</sup>	7.16 $\pm$ 0.18 <sup>bc</sup>	7.17 $\pm$ 0.11 <sup>bc</sup>	7.17 $\pm$ 0.12 <sup>bc</sup>	7.31 $\pm$ 0.16 <sup>a</sup>	7.25 $\pm$ 0.12 <sup>ab</sup>	7.21 $\pm$ 0.12 <sup>abc</sup>	7.20 $\pm$ 0.08 <sup>bc</sup>	7.08 $\pm$ 0.11 <sup>c</sup>
Ultimate pH (pH <sub>u</sub> )	6.39 $\pm$ 0.13 <sup>ab</sup>	6.43 $\pm$ 0.08 <sup>a</sup>	6.46 $\pm$ 0.09 <sup>a</sup>	6.45 $\pm$ 0.07 <sup>a</sup>	6.40 $\pm$ 0.07 <sup>ab</sup>	6.41 $\pm$ 0.05 <sup>a</sup>	6.41 $\pm$ 0.06 <sup>a</sup>	6.34 $\pm$ 0.04 <sup>b</sup>	6.29 $\pm$ 0.04 <sup>c</sup>
$\Delta$ pH (=pH <sub>u</sub> -pH <sub>i</sub> )	-0.49 $\pm$ 0.22 <sup>a</sup>	-0.72 $\pm$ 0.21 <sup>b</sup>	-0.71 $\pm$ 0.13 <sup>b</sup>	-0.72 $\pm$ 0.16 <sup>b</sup>	-0.92 $\pm$ 0.16 <sup>c</sup>	-0.84 $\pm$ 0.12 <sup>bc</sup>	-0.80 $\pm$ 0.12 <sup>bc</sup>	-0.85 $\pm$ 0.08 <sup>bc</sup>	-0.79 $\pm$ 0.12 <sup>bc</sup>
	<i>Smoked fillet</i>								
Smoked fillet pH	6.10 $\pm$ 0.10 <sup>e</sup>	6.20 $\pm$ 0.10 <sup>cd</sup>	6.37 $\pm$ 0.14 <sup>a</sup>	6.26 $\pm$ 0.10 <sup>bc</sup>	6.16 $\pm$ 0.08 <sup>d</sup>	6.18 $\pm$ 0.04 <sup>d</sup>	6.20 $\pm$ 0.04 <sup>cd</sup>	6.28 $\pm$ 0.04 <sup>b</sup>	6.17 $\pm$ 0.05 <sup>d</sup>
Smoked Dry matter content (%)	34.33 $\pm$ 1.47 <sup>b</sup>	33.86 $\pm$ 1.43 <sup>b</sup>	33.64 $\pm$ 1.79 <sup>b</sup>	32.86 $\pm$ 1.91 <sup>b</sup>	33.05 $\pm$ 1.52 <sup>b</sup>	34.08 $\pm$ 1.64 <sup>b</sup>	36.75 $\pm$ 3.08 <sup>a</sup>	35.84 $\pm$ 1.97 <sup>a</sup>	37.00 $\pm$ 2.21 <sup>a</sup>

Values in the same row with different letters are significantly different between post-spawning groups (p < 0.05).

Flesh quality recovery in trout after spawning

Supplemental data

**Table S1** : Pearson correlations between measured parameters for raw fillet in all post-spawning groups (9 groups : PS0, PS1, ..., PS33) n≥175.

	BW	Thick.	SL	K	Shape	Fat	VSI	GSI	FilY	L*r	a*r	b*r	pHi	pHu	ΔpH	DMCr	Fmaxr
<b>Thick.</b>	0.98 ***	-															
<b>SL</b>	0.93 ***	0.90 ***	-														
<b>K</b>	0.81 ***	0.81 ***	0.57 ***	-													
<b>Shape</b>	0.82 ***	0.90 ***	0.61 ***	0.89 ***	-												
<b>Fat</b>	0.77 ***	0.77 ***	0.64 ***	0.79 ***	0.74 ***	-											
<b>VSI</b>	0.52 ***	0.52 ***	0.35 ***	0.70 ***	0.59 ***	0.56 ***	-										
<b>GSI</b>	-0.04 NS	0.01 NS	-0.05 NS	-0.09 NS	0.06 NS	-0.00 NS	-0.23 **	-									
<b>FilY</b>	0.42 ***	0.44 ***	0.44 ***	0.30 ***	0.36 ***	0.35 ***	0.05 NS	-0.15 NS	-								
<b>L*r</b>	-0.62 ***	-0.61 ***	-0.53 ***	-0.67 ***	-0.60 ***	-0.59 ***	-0.54 ***	0.17 *	-0.35 ***	-							
<b>a*r</b>	0.73 ***	0.72 ***	0.62 ***	0.76 ***	0.69 ***	0.75 ***	0.62 ***	-0.12 NS	0.42 ***	-0.67 ***	-						
<b>b*r</b>	0.53 ***	0.53 ***	0.46 ***	0.56 ***	0.50 ***	0.56 ***	0.49 ***	-0.09 NS	0.33 ***	-0.43 ***	0.92 ***	-					
<b>pHi</b>	-0.06 NS	-0.08 NS	-0.04 NS	0.00 NS	-0.09 NS	-0.06 NS	0.09 NS	-0.30 ***	0.04 NS	-0.03 NS	-0.05 NS	-0.08 NS	-				
<b>pHu</b>	-0.53 ***	-0.56 ***	-0.47 ***	-0.50 ***	-0.54 ***	-0.46 ***	-0.38 ***	-0.01 NS	-0.33 ***	0.40 ***	-0.48 ***	-0.39 ***	0.15 *	-			
<b>ΔpH</b>	-0.19 *	-0.18 *	-0.18 *	-0.23 **	-0.16 *	-0.16 *	-0.27 ***	0.29 ***	-0.19 *	0.22 **	-0.18 *	-0.10 NS	-0.89 ***	0.32 ***	-		
<b>DMCr</b>	0.72 ***	0.71 ***	0.59 ***	0.76 ***	0.69 ***	0.83 ***	0.53 ***	-0.00 NS	0.36 ***	-0.56 ***	0.76 ***	0.63 ***	-0.12 NS	-0.46 ***	-0.10 NS	-	
<b>Fmaxr</b>	-0.62 ***	-0.64 ***	-0.47 ***	-0.73 ***	-0.70 ***	-0.66 ***	-0.66 ***	0.20 **	-0.42 ***	0.56 ***	-0.72 ***	-0.59 ***	-0.01 NS	0.55 ***	0.27 ***	-0.63 ***	-
<b>FM/wr</b>	-0.77 ***	-0.79 ***	-0.64 ***	-0.82 ***	-0.80 ***	-0.75 ***	-0.64 ***	0.10 NS	-0.51 ***	0.65 ***	-0.79 ***	-0.62 ***	0.05 NS	0.58 ***	0.22 **	-0.72 ***	0.92 ***

BW: Body Weight; Thick: body Thickness; SL: Standard Length; K: condition factor; Shape: Shape ratio; Fat: Fat-meter value; VSI: Viscero-Somatic Index; GSI: Gonado-Somatic Index; FilY: raw Fillet Yield; L\*r, a\*r, b\*r: raw fillet lightness, redness, yellowness; pHi: initial pH; pHu: ultimate pH; ΔpH: Delta pH; DMCr: raw fillet dry matter content; Fmaxr: raw Max Force; MF/wr: raw Max Force/sample weight. NS: not significant, \*: p<0.05, \*\*: p<0.01, \*\*\*: p<0.001

*Flesh quality recovery in trout after spawning*

**Table S2** : Pearson correlations between measured parameters for smoked fillet in all post-spawning groups (9 groups : PS0, PS1, ..., PS33) n≥175.

	BW	Thick.	SL	K	Shape	Fat	VSI	GSI	FilY	L*r	a*r	b*r	pHi	pHu	ΔpH	DMr	Fmaxr	FM/wr	SmokY	SFilY	L*s	a*s	b*s	pHs	DMCs	Fmaxs
<b>SmokY</b>	0.86 ***	0.84 ***	0.79 ***	0.80 ***	0.73 ***	0.79 ***	0.53 ***	-0.09 NS	0.59 ***	-0.66 ***	0.80 ***	0.64 ***	0.01 NS	-0.53 ***	-0.26 ***	0.77 ***	-0.70 ***	-0.84 ***	-							
<b>SFilY</b>	0.71 ***	0.71 ***	0.68 ***	0.59 ***	0.60 ***	0.62 ***	0.31 ***	-0.14 NS	0.91 ***	-0.55 ***	0.67 ***	0.53 ***	0.04 NS	-0.47 ***	-0.25 ***	0.62 ***	-0.62 ***	-0.74 ***	0.88 ***	-						
<b>L*s</b>	-0.10 NS	-0.10 NS	-0.10 NS	-0.02 NS	-0.08 NS	-0.16 *	0.07 NS	-0.19 *	0.13 NS	0.28 ***	-0.10 NS	-0.04 NS	0.15 *	-0.02 NS	-0.16 *	-0.12 NS	-0.16 *	-0.08 NS	0.04 NS	0.09 NS	-					
<b>a*s</b>	0.74 ***	0.75 ***	0.63 ***	0.74 ***	0.73 ***	0.76 ***	0.59 ***	0.04 NS	0.34 ***	-0.58 ***	0.93 ***	0.85 ***	-0.19 **	-0.55 ***	-0.07 NS	0.77 ***	-0.68 ***	-0.76 ***	0.74 ***	0.59 ***	-0.22 **	-				
<b>b*s</b>	0.05 NS	0.08 NS	0.05 NS	0.02 NS	0.09 NS	0.07 NS	0.02 NS	0.19 *	-0.00 NS	0.36 ***	0.07 NS	0.20 **	-0.24 **	-0.32 ***	0.08 NS	0.09 NS	-0.08 NS	-0.08 NS	0.08 NS	0.04 NS	0.10 NS	0.30 ***	-			
<b>pHs</b>	-0.06 NS	-0.10 NS	-0.07 NS	0.01 NS	-0.11 NS	-0.05 NS	-0.04 NS	-0.15 NS	-0.01 NS	0.06 NS	0.01 NS	0.07 NS	0.26 ***	0.47 ***	-0.03 NS	-0.02 NS	0.08 NS	0.07 NS	0.08 NS	0.05 NS	-0.03 NS	-0.11 NS	-0.25 **	-		
<b>DMCs</b>	0.46 ***	0.46 ***	0.35 ***	0.56 ***	0.48 ***	0.70 ***	0.40 ***	0.02 NS	0.17 *	-0.38 ***	0.54 ***	0.43 ***	-0.08 NS	-0.33 ***	-0.08 NS	0.70 ***	-0.45 ***	-0.49 ***	0.46 ***	0.35 ***	-0.16 *	0.58 ***	0.04 NS	-0.07 NS	-	
<b>Fmaxs</b>	-0.63 ***	-0.65 ***	-0.50 ***	-0.76 ***	-0.70 ***	-0.70 ***	-0.68 ***	0.22 **	-0.48 ***	0.60 ***	-0.71 ***	-0.56 ***	-0.14 NS	0.59 ***	0.41 ***	-0.65 ***	0.89 ***	0.89 ***	-0.78 ***	-0.69 ***	-0.21 **	-0.64 ***	-0.05 NS	0.03 NS	-0.50 ***	-
<b>MF/ws</b>	-0.75 ***	-0.77 ***	-0.67 ***	-0.79 ***	-0.74 ***	-0.73 ***	-0.63 ***	0.16 *	-0.60 ***	0.66 ***	-0.76 ***	-0.59 ***	-0.08 NS	0.61 ***	0.37 ***	-0.69 ***	0.81 ***	0.91 ***	-0.89 ***	-0.82 ***	-0.15 *	-0.69 ***	-0.06 NS	0.05 NS	-0.45 ***	0.91 ***

BW: Body Weight; Thick: body Thickness; SL: Standard Length; K: condition factor; Shape: Shape ratio; Fat: Fat-meter value; VSI: Viscero-Somatic Index; GSI: Gonado-Somatic Index; FilY: raw Fillet Yield; L\*r, a\*r, b\*r: raw fillet lightness, redness, yellowness; pHi: initial pH; pHu: ultimate pH; ΔpH: Delta pH; DMCr: raw fillet dry matter content; Fmaxr: raw Max Force; MF/wr: raw Max Force/sample weight; SmokY: Smoking yield; SFilY: Smoked Fillet Yield; L\*s, a\*s, b\*s: smoked fillet lightness, redness, yellowness; pHs: smoked pH; DMCs: smoked fillet dry matter content; Fmaxs: smoked Max Force; MF/ws: smoked Max Force/sample weight. NS: not significant, \*: p<0.05, \*\*: p<0.01, \*\*\*: p<0.001