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

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Highlights

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

Abstract

In fish rearing industry, sexual maturation results in loss of profit or at least in a delay to valorize spawning fish. Indeed, many edible fish display poor fillet quality after sexual maturation and as such cannot be processed immediately after spawning. So, a post-spawning rearing period may allow the recovering of an acceptable fillet quality. So far, flesh quality restoration after spawning has received little attention. In the present study, the evolution of technological and organoleptic qualities was investigated in diploid autumnal strain female rainbow trout (24 months of age) after spawning. Immediately after spawning, nine groups of trout (n = 25) from the same cohort were placed separately into circular tanks and fed *ad libitum*. Fish were then sampled at 0, 1, 2, 4, 8, 13, 16, 24, and 33 weeks after spawning (PS0, PS1, PS2, PS4, PS8, PS13, PS16, PS24, and PS33). Immature (no egg produced) female trout from the same cohort were also sampled as controls at the beginning (C0) and at the end (C33) of the experiment. Immediately after spawning, PS0 trout showed a significantly lower raw fillet yield than control (C0). Furthermore, raw fillet from these trout was less colored (lower redness a*) and presented higher lightness L* value than raw fillet from C0 trout while their fillet mechanical resistance was similar. Raw fillet yield increased after the 16th week post-spawning. The fillet lightness steadily decreased from the 4th week to the 24th week post-spawning and did not change afterwards, whereas fillet redness increased from the 8th week to the 24th week after spawning. Fillet mechanical resistance declined progressively after spawning with a significant change from the 13th week. Concerning the smoked fillet, the smoking yield of PS0 trout was significantly lower than that of C0 trout. Thereafter the smoking yield of post-spawning trout slowly increased until reaching a significantly higher value at the 24th week. The evolution of smoked fillet color and mechanical resistance after spawning was similar to that of raw fillet. At the end of the experiment, most quality parameters of PS33 trout fillet were similar to those of C33 trout. We discuss the post-spawning quality parameters recovery in three sequential phases. On the whole, our study reports that the technological and organoleptic properties of the flesh were recovered in female trout 24 weeks after spawning (≈1400°C.day).

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

1. Introduction

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

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

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

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

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

2. Material and methods

2.1. Fish rearing

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

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

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

2.2. Sampling and slaughter procedure

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

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

2.3. Measurements at slaughter

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

Fish were wiped with tissue, individually weighed (*BW*, ATOL_0000351) and measured (standard length *SL*, ATOL_0001659; maximum body thickness *T*, ATOL_0005337) measured at the trunk level). Fish adiposity (ATOL_0001663) was also assessed using the Fish Fatmeter® (Distell Industries Ltd., Scotland). This instrument was firmly applied on dorsal musculature, parallel to the lateral line (Douirin et al., 1998). Two measurements were performed at two locations along the dorsal part of the both sides of the fish: the first location was anterior to the dorsal fin, the second at the dorsal fin level. Fatmeter® value was the mean of these measurements. Fish were then gutted to collect the carcass, viscera (including visceral fat) without liver (*VW,* ATOL_0002258) and gonads (*GW*, ATOL_0001776) which were weighed. Gutted fish were finally filleted and raw fillet (skinned and trimmed) was weighed (*RFW*, ATOL_0002262). The following parameters were calculated: condition factor $K = [(BW/SL^3) \times 100000]$ (ATOL_0001653), shape ratio $SR = [(T/SL) \times 100]$, gonadosomatic index $GSI = [(GW/BW) \times 100]$ (ATOL_0001799), viscerosomatic index $VSI = [(VW/BW) \times 100]$ (ATOL_0002259), raw fillet yield = $[(RFW/BW) \times 100]$ (ATOL_0002263).

The initial muscle pH (ATOL_0001684) was measured in the front part of fillet (Figure 1), within 30 min to 1 h *post-mortem*, using a pH meter (Metrohm 826 pH mobile, Switzerland) equipped with a penetration electrode.

The fillet color (ATOL_0001017) was instrumentally assessed using a portable Minolta Chromameter CR-400 (France) equipped with a light source C and a 2° observer angle, calibrated to a white standard. For each fillet, three measurements were performed at three locations along the dorsal part of the fillet: the first was anterior to the dorsal fin, the second at the dorsal fin level and the third was anterior to the anal fin (Figure 1). The mean value was considered for data expression that referred to the L*, a*, b* system, representing lightness, redness, and yellowness, respectively, as recommended by the CIELAB color space (CIE, 1976).

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

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

After 48 h of storage, quality parameters analysis was carried out on one fillet in our laboratory (Rennes, France). Fillet pH (ultimate pH, ATOL_0001684) was performed using 5 g of muscle, removed from the front part of the fillet (Figure 1) and homogenized in three volumes of distilled water. Dry matter content (ATOL_0000101) was determined in duplicate by drying approximately 9 g of minced raw fillet (Figure 1) for 72 h in an oven (Memmert 854 Schwabach, Germany) at 105°C. A sample of minced raw fillet was kept and stored at -20°C in a domestic freezer for further chemical composition analysis (Figure 1). The fillet color was measured as described above at slaughter. The post-rigor fillet (64 mm length from the middle part of fillet; Figure 1) mechanical resistance (ATOL_0001649) was performed using a Kramer shear cell mounted on a static load cell of 2 kN (Instron 5544, INSTRON Ltd., England). The maximum shear force was recorded with a constant speed of 1 mm/s and divided by the sample weight (specific resistance).

2.5. Smoking procedure and smoked fillet quality measurements

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

2.6. Fillet chemical composition

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

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

2.7. Statistical analyses

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

3. Results

3.1. Fish biometric parameters at slaughter

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

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

3.2. Fillet yields and smoking yield

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

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

3.3. Flesh quality

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

Dry matter content of raw and smoked fillets was lower in PS0 trout compared to C0 trout (Table 5). From 13 weeks after spawning, raw fillet dry matter content was found to increase till the 24th week, and then remained constant until the 33th week. In smoked fillet, dry matter content increased only after 16 weeks post-spawning and did not change afterwards (Figure 2). At 33 weeks after spawning, no significant difference was observed in raw and smoked fillet dry matter content between control C33 and PS33 trout (Table 5).

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

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

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

4. Discussion

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

4.1. Fish and raw fillet qualities at spawning

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

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

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

4.2. Evolution of fish and fillet qualities after spawning

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

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

The second transitional phase, which covers the period from 8 to 16 weeks after spawning, is mainly related to changes in biometrics. It was only at 13 weeks after spawning that the body weight of the measured fish was higher, as were condition factor and body shape ratio. This observation suggests a resumption of overall growth, associated with a resumption of muscle growth, which would explain the higher values of the body shape ratio. In addition, post-spawning trout re-accumulated reserves, which were mainly fat as indicated by increase in muscular and perivisceral adiposity. Such observations are in accordance with a recent study by Jenkins et al. (2019) that reported an increase in lipid energy reserves rapidly after spawning in "consecutive spawners" (trout that spawn twice in two consecutive years) like our post-spawning trout in contrast to "skip spawners" (trout that skip at least one year between two successive spawnings). More generally, our data show that rainbow trout, like Atlantic salmon (Rørvik et al., 2018), are able to rapidly replenish lipid stores following a period of unfavourable somatic growth conditions. On the whole, the fat accumulation we observed in post-spawning trout may have prepared the desirable evolution of fillet yield and quality parameters even though the complete recovery occurred later.

The late phase, that covers the period beyond 16 weeks, was marked by the recovery of technological and organoleptic qualities. Regarding the technological quality, fillet yield increased 16 weeks after spawning, while trout became thicker and heavier and had more muscle mass. However, we cannot rule out the possibility, in line with Haffray et al. (2013) who showed that fillet yield also depends on fish morphology, that the important increase in fillet yield we observed after spawning could result from changes in trout body shape. This argument that the shape affects fillet yield was also strengthen by our observation, mentioned above, of such a relationship comparing C0 and PS0. Moreover, a positive correlation between shape ratio and raw fillet yield ($r = 0.36$, $p < 0.001$) also confirms a link between these two parameters. Nevertheless, the body conformation change of post-spawning trout is thus worth further investigation to determine whether the evolution of fillet yield is related to that of fish shape. Furthermore, the increase in fillet yield could be also explained by the relative reduction of losses during filleting according to Bugeon et al. (2010). The increase in muscle percentage compared to head and bones percentages of the post-spawning trout carcass (data not shown) is a sought-after factor considering production purpose whereby the offal percentage must be reduced to maximize the profit. Concerning the organoleptic traits, progressive restoration of flesh coloration was found to occur in post-spawning trout, beginning with the transitional recovery phase and continuing afterwards. This observation is in line with previous report from Choubert (1992) showing that pigment concentration tends to increase in fish muscle after spawning. The restoration of fillet color may relate to the increase in pigment amount ingested by trout and fixed within the muscle after feeding resumption. Moreover, the recovery of color might be related to the favorable growth stage of fish. Indeed, larger trout take-up carotenoids more efficiently than smaller ones as already noticed (Storebakken and No, 1992; Torrissen, 1989). Trout growth, as that observed after spawning, is also generally associated with an increase in flesh coloration as previously mentioned (Olsen and Mortensen, 1997; Torrissen, 1995). Fillet coloration increased till the 24th week beyond which muscle was probably no longer able to fix more astaxanthin. Choubert (1992) similarly reported that the red color of trout muscle tends towards a maximum, which cannot be exceeded despite the continuous ingestion of pigments. In terms of texture properties, the significant decline in mechanical resistance might be caused by the progressive increase in muscle fat content we observed during the transitional recovery period. Moreover we can note that we have measured strong negative correlations between mechanical resistance and fish adiposity (for example, $r = -0.75$, $p < 0.001$ between Fat-meter value and specific resistance). Likewise, several studies also reported that high fat content in farmed fish leads to flesh softening (Aussanasuwannakul et al., 2011, 2012; Fauconneau et al., 1993; Johansson et al., 2000; Green-Petersen and Hyldig, 2010; Thakur et al., 2003; Lefevre et al., 2015). However, we cannot rule out the possibility that the decrease in mechanical resistance may also result from an increase in muscle fiber size, a feature that has been reported to be an important determinant of flesh texture (Johnston, 1999). In keeping with this, it would be also of interest to examine the evolution of muscle cellularity during the post-spawning period.

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

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

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

Atlantic salmon following salting and smoking (Sigurgisladottir et al., 2000). Another explanation to the difference between raw and smoked fillet texture might be the change of muscle structure and properties during the salting and smoking processes as previously mentioned (Sigurgisladottir et al., 2001). Interestingly, in contrast with previous studies (Birkeland et al., 2004), post-spawning smoked fillet texture could also be predicted from that of raw fillet, suggesting that smoked fillet mechanical resistance may have the same determinism as raw fillet. Indeed, mechanical resistance of smoked fillet was positively correlated to that of raw fillet ($r = 0.89$, $p < 0.001$ for the shear force and $r = 0. 91$, $p < 0.001$ for specific resistance). Overall, these results may contribute to extend, on post-spawning fillet, knowledge about the effect of raw material characteristics on smoked product quality.

5. Conclusions

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

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References

Aksnes, A., Gjerde, B., Roald, S.O., 1986. Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. Aquaculture 53, 7–20. https://doi.org/10.1016/0044-8486(86)90295-4

Aussanasuwannakul, A., Kenney, P.B., Weber, G.M., Yao, J., Slider, S.D., Manor, M.L., Salem, M., 2011. Effect of sexual maturation on growth, fillet composition, and texture of female rainbow trout (*Oncorhynchus mykiss*) on a high nutritional plane. Aquaculture 317, 79–88. https://doi.org/10.1016/j.aquaculture.2011.04.015

Aussanasuwannakul, A., Weber, G.M., Salem, M., Yao, J., Slider, S., Manor, M.L., Brett Kenney, P., 2012. Effect of Sexual Maturation on Thermal Stability, Viscoelastic Properties, and Texture of Female Rainbow Trout, *Oncorhynchus mykiss*, Fillets. J. Food Sci. 77, S77–S83. https://doi.org/10.1111/j.1750-3841.2011.02512.x

Bilinski, E., Jonas, R.E.E., Peters, M.D., Choromanski, E.M., 1984. Effects of Sexual Maturation on the Quality of Coho Salmon (*Oncorhynchus kisutch*) Flesh. Can. Inst. Food Sci. Technol. J. 17, 271–273. https://doi.org/10.1016/S0315-5463(84)72570-3

Birkeland, S., Rørå, A.M.B., Skåra, T., Bjerkeng, B., 2004. Effects of cold smoking procedures and raw material characteristics on product yield and quality parameters of cold smoked Atlantic salmon (*Salmo salar* L.) fillets. Food Res. Int. 37, 273–286. https://doi.org/10.1016/j.foodres.2003.12.004

Bjørnevik, M., Espe, M., Beattie, C., Nortvedt, R., Kiessling, A., 2004. Temporal variation in muscle fibre area, gaping, texture, colour and collagen in triploid and diploid Atlantic salmon (*Salmo salar* L). J. Sci. Food Agric. 84, 530–540. https://doi.org/10.1002/jsfa.1656

Bobe, J., Guiguen, Y., Jalabert, B., Kah, O., Labbé, C., Lareyre, J.-J., Le Bail, P.-Y., Le Gac, F., Leveroni Calvi, S., Mahé, S., Quillet, E., Vandeputte, M., 2010. Sexualité et reproduction, in: La Truite Arc-En-Ciel: De La Biologie à l'élevage. Paris, pp. 39–79.

Bugeon, J., Lefevre, F., Cardinal, M., Uyanik, A., Davenel, A., Haffray, P., 2010. Flesh quality in large rainbow trout with high or low fillet yield: fillet yield and flesh quality in large rainbow trout. J. Muscle Foods 21, 702–721. https://doi.org/10.1111/j.1745-4573.2010.00214.x

Cardinal, M., Knockaert, C., Torrissen, O., Sigurgisladottir, S., Mørkøre, T., Thomassen, M., Luc Vallet, J., 2001. Relation of smoking parameters to the yield, colour and sensory quality of smoked Atlantic salmon (*Salmo salar*). Food Res. Int. 34, 537–550. https://doi.org/10.1016/S0963-9969(01)00069-2

Cerdà, J., Bobe, J., Babin, P.J., Admon, A., Lubzens, E., 2008. Functional Genomics and Proteomic Approaches for the Study of Gamete Formation and Viability in Farmed Finfish. Rev. Fish. Sci. 16, 56–72. https://doi.org/10.1080/10641260802324685

Choubert, G., 1992. Salmonid pigmentation : Dynamics and factors of variation. A review. INRA Prod. Anim. 5, 235–246.

Choubert, G., Blanc, J.-M., Courvalin, C., 1992. Muscle carotenoid content and colour of farmed rainbow trout fed astaxanthin or canthaxanthin as affected by cooking and smoke-curing procedures. Int. J. Food Sci. Technol. 27, 277–284. https://doi.org/10.1111/j.1365-2621.1992.tb02029.x

Christiansen, R., Struksnæs, G., Estermann, R., Torrissen, O.J., 1995. Assessment of flesh colour in Atlantic salmon, *Salmo salar* L. Aquac. Res. 26, 311–321. https://doi.org/10.1111/j.1365-2109.1995.tb00919.x

CIE, 1976. Colorimetry, Publication, Bureau central de la Commission Internationale de l'Eclairage, Vienna, Austria.

Cleveland, B.M., Kenney, P.B., Manor, M.L., Weber, G.M., 2012. Effects of feeding level and sexual maturation on carcass and fillet characteristics and indices of protein degradation in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 338–341, 228–236. https://doi.org/10.1016/j.aquaculture.2012.01.032

Crozier, G.F., 1970. Tissue Carotenoids in Prespawning and Spawning Sockeye Salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 27, 973–975. https://doi.org/10.1139/f70-110

Davidson, J.W., Kenney, P.B., Manor, M., Good, C.M., Weber, G.M., Aussanasuwannakul, A., Turk, P.J., Welsh, C., Summerfelt, S.T., 2014. Growth Performance, Fillet Quality, and Reproductive Maturity of Rainbow Trout (*Oncorhynchus mykiss*) Cultured to 5 Kilograms within Freshwater Recirculating Systems. J Aquac Res Dev. 5. https://doi.org/10.4172/2155-9546.1000238

Douirin, C., Haffray, P., Vallet, J.L., Fauconneau, B., 1998. Determination of the lipid content of rainbow trout (*Oncorhynchus mykiss*) fillets with the Torry Fish Fat Meter(R). Sci. Ali 18, 527–535.

Dunajski, E., 1979. Texture of Fish Muscle. J. Texture Stud. 10, 301–318. https://doi.org/10.1111/j.1745-4603.1980.tb00862.x

Einen, O., Thomassen, M.S., 1998. Starvation prior to slaughter in Atlantic salmon (*Salmo salar*): II. White muscle composition and evaluation of freshness, texture and colour characteristics in raw and cooked fillets. Aquaculture 169, 37–53. https://doi.org/10.1016/S0044-8486(98)00332-9

Fauconneau, B., Chmaitilly, J., Andre, S., Cardinal, M., Cornet, J., Vallet, J.L., Dumont, J.P., Laroche, M., 1993. Characteristics of rainbow-trout flesh .2. Physical and sensory aspects. Sci. Aliments 13, 189–199.

Fauconneau, B., Alami-Durante, H., Laroche, M., Marcel, J., Vallot, D., 1995. Growth and meat quality relations in carp. Aquaculture, The Carp 129, 265–297. https://doi.org/10.1016/0044-8486(94)00309-C

Golik, W., Dameron, O., Bugeon, J., Fatet, A., Hue, I., Hurtaud, C., Reichstadt, M., Salaün, M.-C., Vernet, J., Joret, L., Papazian, F., Nédellec, C., Le Bail, P.-Y., 2012. ATOL: The Multi-species Livestock Trait Ontology, in: Dodero, J.M., Palomo-Duarte, M., Karampiperis, P. (Eds.), Metadata and Semantics Research, Communications in Computer and Information Science. Springer, Berlin, Heidelberg, pp. 289–300. https://doi.org/10.1007/978-3-642-35233-1_28

Green-Petersen, D.M.B., Hyldig, G., 2010. Variation in Sensory Profile of Individual Rainbow Trout (*Oncorhynchus mykiss*) from the Same Production Batch. J. Food Sci. 75, S499–S505. https://doi.org/10.1111/j.1750-3841.2010.01830.x

Haard, N.F., 1992. Control of chemical composition and food quality attributes of cultured fish. Food Res. Int. 25, 289–307. https://doi.org/10.1016/0963-9969(92)90126-P

Haffray, P., Bugeon, J., Rivard, Q., Quittet, B., Puyo, S., Allamelou, J.M., Vandeputte, M., Dupont-Nivet, M., 2013. Genetic parameters of in-vivo prediction of carcass, head and fillet yields by internal ultrasound and 2D external imagery in large rainbow trout (*Oncorhynchus mykiss*). Aquaculture 410–411, 236–244. https://doi.org/10.1016/j.aquaculture.2013.06.016

Hatae, K., Yoshimatsu, F., Matsumoto, J.J., 1990. Role of Muscle Fibers in Contributing Firmness of Cooked Fish. J. Food Sci. 55, 693–696. https://doi.org/10.1111/j.1365-2621.1990.tb05208.x

Hyldig, G., Nielsen, D., 2001. A review of sensory and instrumental methods used to evaluate the texture of fish muscle. J. Texture Stud. 32, 219–242. https://doi.org/10.1111/j.1745-4603.2001.tb01045.x

Janhunen, M., Vehviläinen, H., Koskela, J., Forsman, A., Kankainen, M., 2019. Added value from an added chromosome: Potential of producing large fillet fish from autumn to spring with triploid rainbow trout, *Oncorhynchus mykiss*. Aquac. Res. 50, 818–825. https://doi.org/10.1111/are.13952

Jenkins, L.E., Pierce, A.L., Graham, N.D., Medeiros, L.R., Hatch, D.R., Nagler, J.J., 2019. Elevated plasma triglycerides and growth rate are early indicators of reproductive status in post-spawning female steelhead trout (*Oncorhynchus mykiss*). Conserv. Physiol. 7. https://doi.org/10.1093/conphys/coz038

Johansson, L., Kiessling, A., Kiessling, K.-H., Berglund, L., 2000. Effects of altered ration levels on sensory characteristics, lipid content and fatty acid composition of rainbow trout (*Oncorhynchus mykiss*). Food Qual. Prefer. 11, 247–254. https://doi.org/10.1016/S0950-3293(99)00073-7

Johnston, I.A., 1999. Muscle development and growth: potential implications for flesh quality in fish. Aquaculture 177, 99–115. https://doi.org/10.1016/S0044-8486(99)00072-1

Johnston, I.A., Alderson, R., Sandham, C., Dingwall, A., Mitchell, D., Selkirk, C., Nickell, D., Baker, R., Robertson, B., Whyte, D., Springate, J., 2000. Muscle fibre density in relation to the colour and texture of smoked Atlantic salmon (*Salmo salar* L.). Aquaculture 189, 335–349. https://doi.org/10.1016/S0044-8486(00)00373-2

Jonsson, N., Jonsson, B., Hansen, L., 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. J. Anim. Ecol. 66, 425–436. https://doi.org/10.2307/5987

Kawai Y., Hirayama H., Hatano M., 1990. Emulsifying ability and physicochemical properties of muscle proteins of fall chum salmon *Oncorhynchus keta* during spawning migration. Nippon Suisan Gakkaishi 56, 625–632. https://doi.org/10.2331/suisan.56.625

Kestemont, P., Baras, E., 2001. Environmental Factors and Feed Intake: Mechanisms and Interactions, in: Food Intake in Fish. John Wiley & Sons, Ltd, pp. 131–156. https://doi.org/10.1002/9780470999516.ch6

Lefevre, F., Bugeon, J., 2008. Biological basis of fish quality. Sci. Aliments 28, 365–377. https://doi.org/10.3166/sda.28.365-377

Lefevre, F., Bugeon, J., 2015. What quality for fish products? INRA Prod. Anim. 28, 119–124.

Lefevre, F., Cardinal, M., Bugeon, J., Labbe, L., Medale, F., Quillet, E., 2015. Selection for muscle fat content and triploidy affect flesh quality in pan-size rainbow trout, *Oncorhynchus mykiss*. Aquaculture 448, 569–577. https://doi.org/10.1016/j.aquaculture.2015.06.029

Lerfall, J., Larsson, T., Birkeland, S., Taksdal, T., Dalgaard, P., Afanasyev, S., Bjerke, M.T., Mørkøre, T., 2012. Effect of pancreas disease (PD) on quality attributes of raw and smoked fillets of Atlantic salmon (*Salmo salar* L.). Aquaculture 324–325, 209–217. https://doi.org/10.1016/j.aquaculture.2011.11.003

Lerfall, J., Hasli, P.R., Skare, E.F., Olsen, R.E., Rotabakk, B.T., Roth, B., Slinde, E., Egelandsdal, B., 2017a. A comparative study of diploid versus triploid Atlantic salmon (*Salmo salar* L.). The effects of rearing temperatures (5, 10 and 15°C) on raw material characteristics and storage quality. Food Chem. 225, 37–44. https://doi.org/10.1016/j.foodchem.2017.01.012

Lerfall, J., Skuland, A.V., Skare, E.F., Hasli, P.R., Rotabakk, B.T., 2017b. Quality characteristics and consumer acceptance of diploid and triploid cold smoked Atlantic salmon reared at 5, 10 and 15 °C. LWT - Food Sci. Technol. 85, 45–51. https://doi.org/10.1016/j.lwt.2017.06.055

Listrat, A., Lebret, B., Louveau, I., Astruc, T., Bonnet, M., Lefaucheur, L., Picard, B., Bugeon, J., 2016. How Muscle Structure and Composition Influence Meat and Flesh Quality. Sci. World J. 2016, 1–14. https://doi.org/10.1155/2016/3182746

Manor, M.L., Weber, G.M., Salem, M., Yao, J., Aussanasuwannakul, A., Kenney, P.B., 2012. Effect of sexual maturation and triploidy on chemical composition and fatty acid content of energy stores in female rainbow trout, *Oncorhynchus mykiss*. Aquaculture 364–365, 312–321. https://doi.org/10.1016/j.aquaculture.2012.08.012

Marty-Mahé, P., Loisel, P., Fauconneau, B., Haffray, P., Brossard, D., Davenel, A., 2004. Quality traits of brown trouts (*Salmo trutta*) cutlets described by automated color image analysis. Aquaculture 232, 225–240. https://doi.org/10.1016/S0044-8486(03)00458-7

Mørkøre, T., Rørvik, K.-A., 2001. Seasonal variations in growth, feed utilisation and product quality of farmed Atlantic salmon (*Salmo salar*) transferred to seawater as 0+smolts or 1+smolts. Aquaculture 199, 145–157. https://doi.org/10.1016/S0044-8486(01)00524-5

Mørkøre, T., Vallet, J.L., Cardinal, M., Gomez-Guillen, M.C., Montero, P., Torrissen, O.J., Nortvedt, R., Sigurgisladottir, S., Thomassen, M.S., 2001. Fat Content and Fillet Shape of Atlantic Salmon: Relevance for Processing Yield and Quality of Raw and Smoked Products. J. Food Sci. 66, 1348–1354. https://doi.org/10.1111/j.1365-2621.2001.tb15213.x

Muller-Feuga, A., 1990. Modélisation de la croissance des poissons en élevage. Rapp. Sci. Tech. Ifremer, 21: 1-58.

Nassour, I., Léger, C.L., 1989. Deposition and mobilisation of body fat during sexual maturation in female trout (*Salmo gairdneri* Richardson). Aquat. Living Resour. 2, 153–159. https://doi.org/10.1051/alr:1989018

Olsen, R.E., Mortensen, A., 1997. The influence of dietary astaxanthin and temperature on flesh colour in Arctic charr *Salvelinus alpinus* L. Aquac. Res. 28, 51–58. https://doi.org/10.1046/j.1365-2109.1997.00828.x

Rasmussen, R.S., 2001. Quality of farmed salmonids with emphasis on proximate composition, yield and sensory characteristics. Aquac. Res. 32, 767–786. https://doi.org/10.1046/j.1365-2109.2001.00617.x

Reid, R.A., 1991. Textural and chemical changes in the muscle of chum salmon (*Oncorhynchus keta*) during spawning migration (PhD Thesis). University of British Columbia, Vancouver, Canada. https://doi.org/10.14288/1.0098641

Reid, R.A., Durance, T.D., 1992. Textural Changes of Canned Chum Salmon Related to Sexual Maturity. J. Food Sci. 57, 1340–1342. https://doi.org/10.1111/j.1365-2621.1992.tb06852.x

Reid, R.A., Durance, T.D., Walker, D.C., Reid, P.E., 1993. Structural and chemical changes in the muscle of chum salmon (*Oncorhynchus keta*) during spawning migration. Food Res. Int. 26, 1–9. https://doi.org/10.1016/0963-9969(93)90099-5

Robb, D.H.F., Kestin, S.C., Warriss, P.D., Nute, G.R., 2002. Muscle lipid content determines the eating quality of smoked and cooked Atlantic salmon (*Salmo salar*). Aquaculture 205, 345–358. https://doi.org/10.1016/S0044-8486(99)00273-2

Rørå, A.M.B., Kvåle, A., Mørkøre, T., Rørvik, K.-A., Hallbjoørn, S., Thomassen, S., Magny, S., 1998. Process yield, colour and sensory quality of smoked Atlantic salmon (*Salmo salar*) in relation to raw material characteristics. Food Res. Int. 31, 601–609. https://doi.org/10.1016/S0963-9969(99)00034-4

Rørvik, K.-A., Dessen, J.-E., Åsli, M., Thomassen, M.S., Hoås, K.G., Mørkøre, T., 2018. Low body fat content prior to declining day length in the autumn significantly increased growth and reduced weight dispersion in farmed Atlantic salmon *Salmo salar* L. Aquac. Res. 49, 1944–1956. https://doi.org/10.1111/are.13650

Roth, B., Jenssen, M.D., Jonassen, T.M., Foss, A., Imsland, A., 2007. Change in flesh quality associated with early maturation of Atlantic halibut (*Hippoglossus hippoglossus*). Aquac. Res. 38, 757–763. https://doi.org/10.1111/j.1365-2109.2007.01729.x

Salem, M., Kenney, P.B., Rexroad, C.E., Yao, J., 2006. Molecular characterization of muscle atrophy and proteolysis associated with spawning in rainbow trout. Comp. Biochem. Physiol. Part D Genomics Proteomics 1, 227–237. https://doi.org/10.1016/j.cbd.2005.12.003

Salem, M., Manor, M.L., Aussanasuwannakul, A., Kenney, P.B., Weber, G.M., Yao, J., 2013. Effect of sexual maturation on muscle gene expression of rainbow trout: RNA-Seq approach. Physiol. Rep. 1, e00120. https://doi.org/10.1002/phy2.120

Segato, S., Fasolato, L., Bertotto, D., Libertini, A., Balzan, S., Corato, A., Novelli, E., 2007. Effect of triploidy on quality traits of shi drum (*Umbrina cirrosa* L.) until the second rearing year. Aquac. Res. 38, 59–65. https://doi.org/10.1111/j.1365-2109.2006.01630.x

Shearer, K.D., 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 119, 63–88. https://doi.org/10.1016/0044-8486(94)90444-8

Sigurgisladottir, S., Sigurdardottir, M.S., Torrissen, O., Vallet, J.L., Hafsteinsson, H., 2000. Effects of different salting and smoking processes on the microstructure, the texture and yield of Atlantic salmon (*Salmo salar*) fillets. Food Res. Int. 33, 847–855. https://doi.org/10.1016/S0963-9969(00)00104-6

Sigurgisladottir, S., Sigurdardottir, M.S., Ingvarsdottir, H., Torrissen, O.J., Hafsteinsson, H., 2001. Microstructure and texture of fresh and smoked Atlantic salmon, *Salmo salar* L., fillets from fish reared and slaughtered under different conditions. Aquac. Res. 32, 1–10. https://doi.org/10.1111/j.1365-2109.2001.00503.x

Skrede, G., Storebakken, T., 1986. Instrumental colour analysis of farmed and wild Atlantic salmon when raw, baked and smoked. Aquaculture 53, 279–286. https://doi.org/10.1016/0044-8486(86)90358-3

Steven, D.M., 1949. Studies on Animal Carotenoids: II. Carotenoids in the Reproductive Cycle of the Brown Trout. J. Exp. Biol. 26, 295–303.

Storebakken, T., No, H.K., 1992. Pigmentation of rainbow trout. Aquaculture 100, 209–229. https://doi.org/10.1016/0044-8486(92)90372-R

Thakur, D.P., Morioka, K., Itoh, Y., Obatake, A., 2003. Lipid composition and deposition of cultured yellowtail *Seriola quinqueradiata* muscle at different anatomical locations in relation to meat texture. Fish. Sci. 69, 487–494. https://doi.org/10.1046/j.1444-2906.2003.00649.x

Torrissen, O.J., 1989. Pigmentation of salmonids: Interactions of astaxanthin and canthaxanthin on pigment deposition in rainbow trout. Aquaculture 79, 363–374. https://doi.org/10.1016/0044-8486(89)90478-X

Torrissen, O.J., 1995. Strategies for salmonid pigmentation. J. Appl. Ichthyol. 11, 276–281. https://doi.org/10.1111/j.1439-0426.1995.tb00027.x

Torrissen, K.R., Torrissen, O.J., 1984. Sexual maturation: effect on protease activities and carotenoid levels in Atlantic salmon (*Salmo salar*). Presented at the International Council for the Exploration of the Sea.

Tyler, C.R., Sumpter, J.P., Witthames, P.R., 1990. The dynamics of oocyte growth during vitellogenesis in the rainbow trout (*Oncorhynchus mykiss*). Biol. Reprod. 43, 202–209. https://doi.org/10.1095/biolreprod43.2.202

Figures

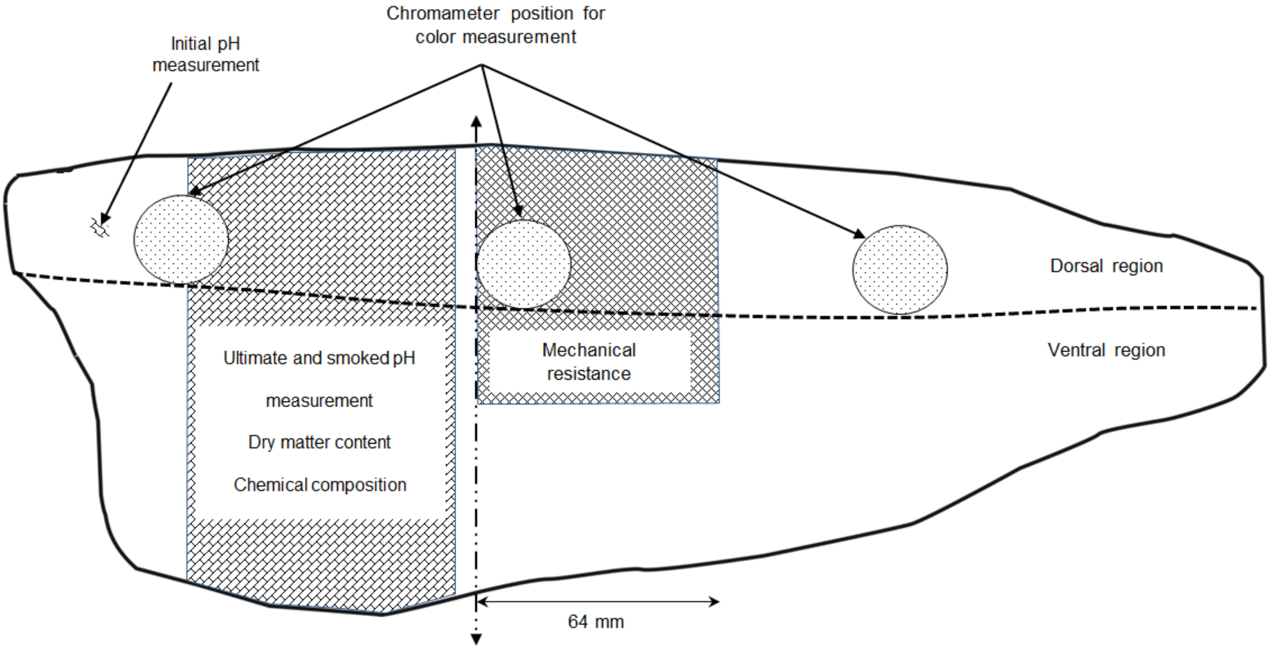

Figure 1 : Schematic representation of measurements and sampling locations for quality analyses of rainbow trout raw and smoked fillets; for details see text.

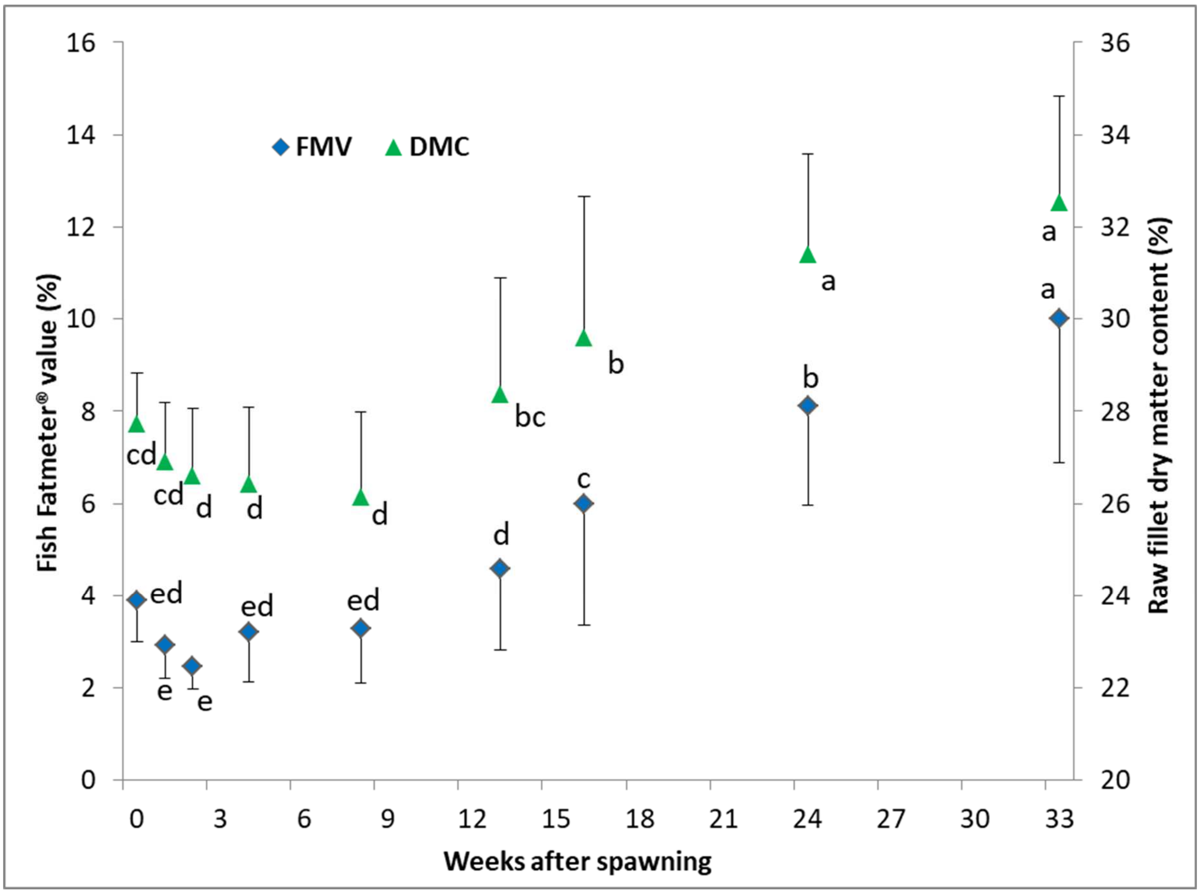

Figure 2 : Evolutions of adiposity parameters, fish Fatmeter® value (FMV) and raw fillet dry matter content (DMC), in rainbow trout after spawning:. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between groups are denoted with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

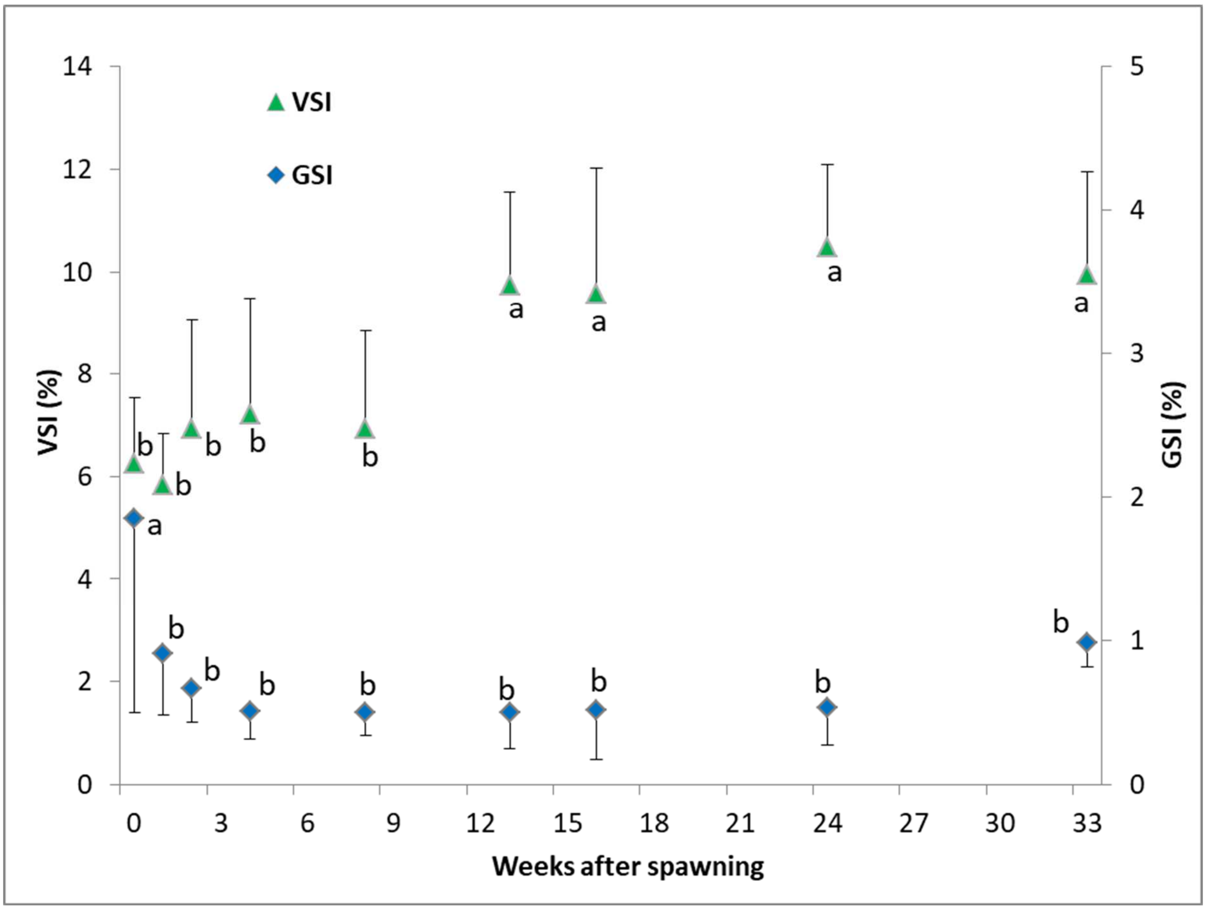

Figure 3 : Evolutions of viscero-somatic index (VSI) and gonado-somatic index (GSI) in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning are denoted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

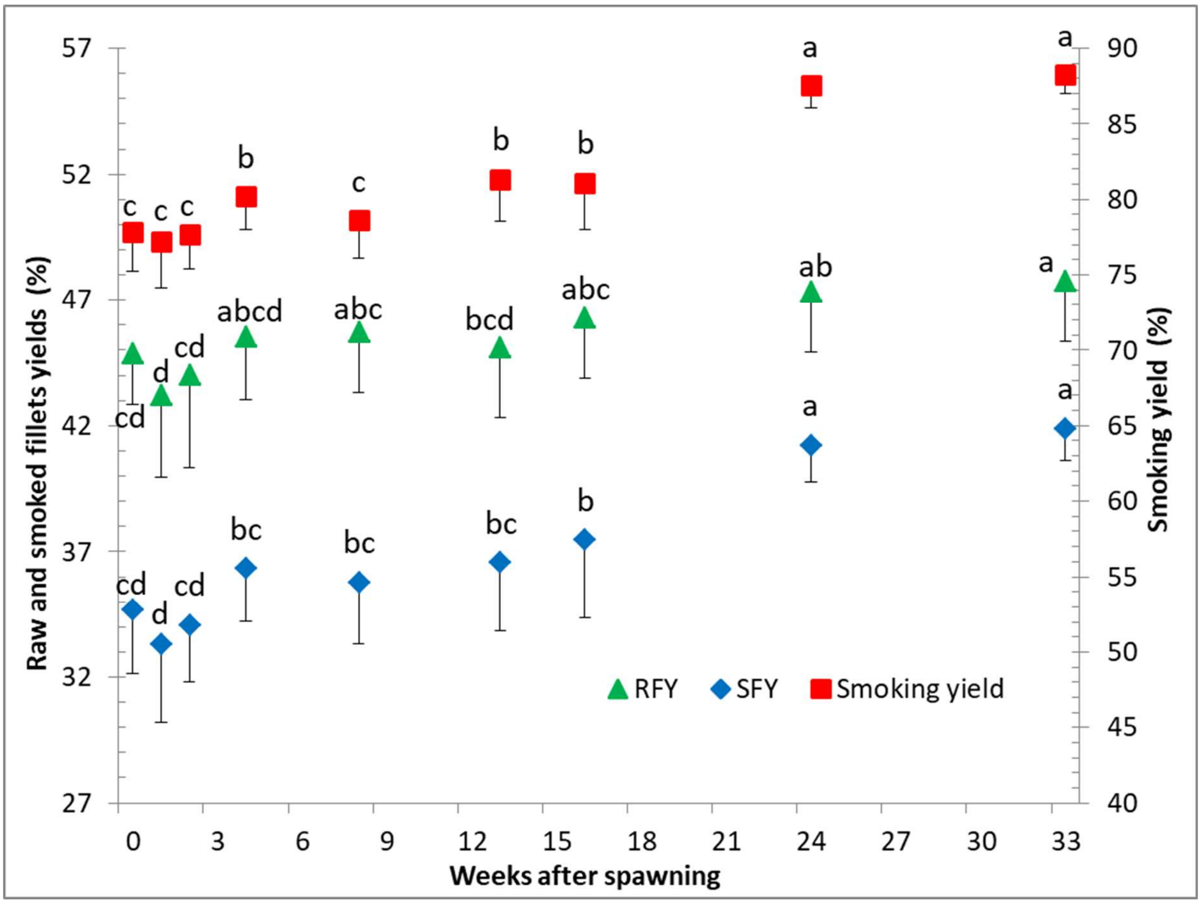

Figure 4 : Evolutions of raw (RFY) and smoked fillets (SFY) yields and smoking yield in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning are denoted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

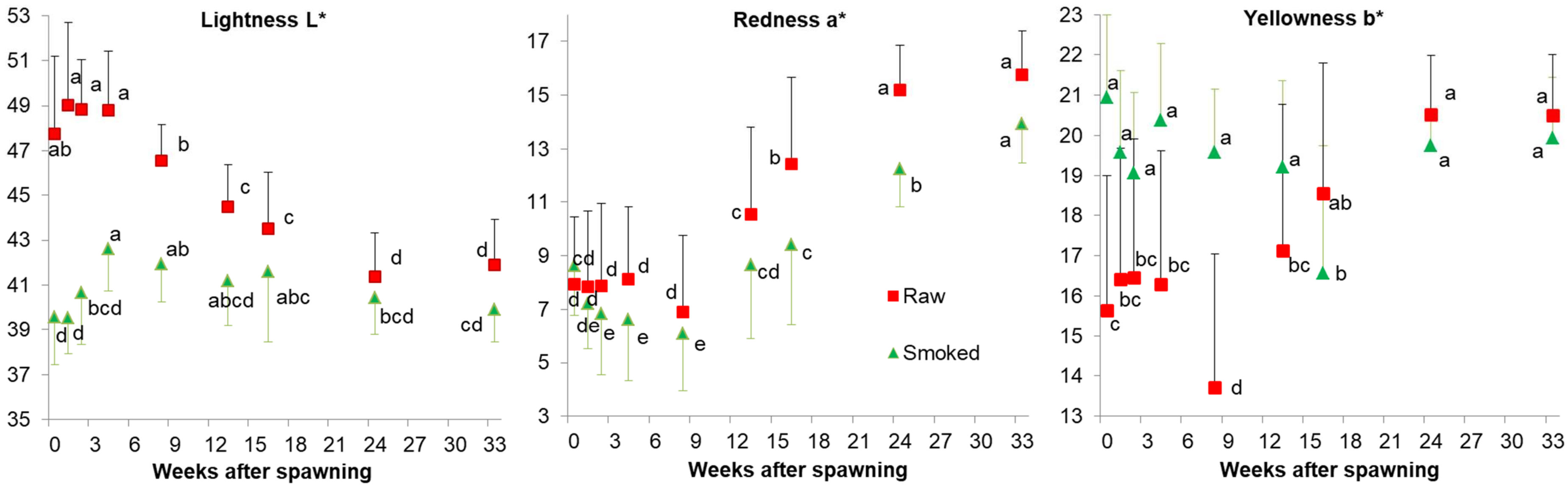

Figure 5 : Changes in lightness (L*), redness (a*) and yellowness (b*) of raw and smoked fillets in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks after spawning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

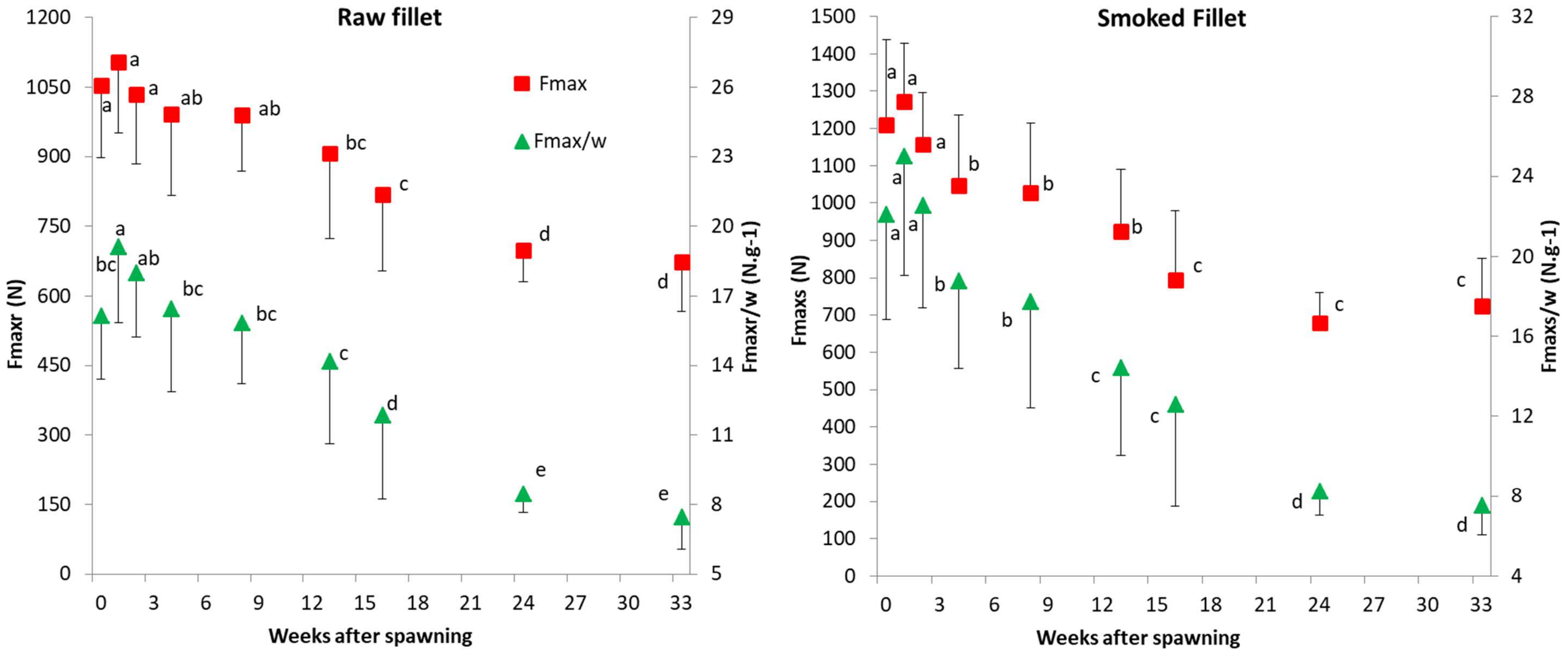

Figure 6 : Evolution of maximum shear force (Fmax) and specific resistance (Fmax/w) of raw and smoked fillets in rainbow trout after spawning. Data represent means and unidirectional vertical bar represents the standard deviation (n = 20). Significant differences between post-spawning groups among weeks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

Time post-spawning (weeks)	**0**	**1**	**2**	**4**	**8**	**13**	**16**	**24**	**33**
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

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[1]	1.8 ± 0.1	1.7 ± 0.1	*	2.3 ± 0.2	2.4 ± 0.2	ns
Shape ratio[2]	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[3] (%)	9.6 ± 1.3	6.2 ± 1.3	***	11.5 ± 2.2	10.0 ± 2.0	*
GSI[4] (%)	0.12 ± 0.08	1.85 ± 1.35	***	0.89 ± 0.33	0.98 ± 0.17	ns
Raw fillet yield[5] (%)	47.8 ± 2.0	44.9 ± 2.1	***	47.6 ± 2.6	47.8 ± 2.4	ns
Smoked fillet yield[6] (%)	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.
[1] Condition factor = (Body weight/Standard length^3) x 100000.
[2] Shape ratio = (Maximum body thickness/Standard length) x 100.
[3] VSI = viscero-somatic index = (viscera weight/body weight) x 100
[4] GSI = gonado-somatic index = (gonad weight/body weight) x 100
[5] Raw fillet yield = (raw fillet weight/body weight) x 100
[6] Smoked fillet yield = (smoked fillet weight/body weight) x 100

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

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

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

[1] Condition factor = (Body weight/Standard length^{3}) x 100000.

[2] Shape ratio = (Maximum body thickness/Standard length) x 100.

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 :**
			Raw fillet			
Raw DMC (%)	29.4 ± 1.4	27.7 ± 1.1	***	33.6 ± 3.7	32.5 ± 2.3	ns
Initial pH (pH_i)	7.09 ± 0.13	6.89 ± 0.22	**	7.06 ± 0.13	7.08 ± 0.11	ns
Ultimate pH (pH_u)	6.48 ± 0.08	6.39 ± 0.13	*	6.36 ± 0.05	6.29 ± 0.04	***
ΔpH ($=pH_u-pH_i$)	-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
			Smoked fillet			
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.

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

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

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

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**
Thick.	0.98 ***	-															
SL	0.93 ***	0.90 ***	-														
K	0.81 ***	0.81 ***	0.57 ***	-													
Shape	0.82 ***	0.90 ***	0.61 ***	0.89 ***	-												
Fat	0.77 ***	0.77 ***	0.64 ***	0.79 ***	0.74 ***	-											
VSI	0.52 ***	0.52 ***	0.35 ***	0.70 ***	0.59 ***	0.56 ***	-										
GSI	-0.04 NS	0.01 NS	-0.05 NS	-0.09 NS	0.06 NS	-0.00 NS	-0.23 **	-									
FilY	0.42 ***	0.44 ***	0.44 ***	0.30 ***	0.36 ***	0.35 ***	0.05 NS	-0.15 NS	-								
L*r	-0.62 ***	-0.61 ***	-0.53 ***	-0.67 ***	-0.60 ***	-0.59 ***	-0.54 ***	0.17 *	-0.35 ***	-							
a*r	0.73 ***	0.72 ***	0.62 ***	0.76 ***	0.69 ***	0.75 ***	0.62 ***	-0.12 NS	0.42 ***	-0.67 ***	-						
b*r	0.53 ***	0.53 ***	0.46 ***	0.56 ***	0.50 ***	0.56 ***	0.49 ***	-0.09 NS	0.33 ***	-0.43 ***	0.92 ***	-					
pHi	-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	-				
pHu	-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 *	-			
ΔpH	-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 ***	-		
DMCr	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	-	
Fmaxr	-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 ***	-
FM/wr	-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

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
SmokY	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 ***	-							
SFilY	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 ***	-						
L*s	-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	-					
a*s	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*s	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 ***	-			
pHs	-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 **	-		
DMCs	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	-	
Fmaxs	-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 ***	-
MF/ws	-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, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$