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Muscle fibre density in relation to the colour and texture of smoked Atlantic salmon (*Salmo salar* L.)

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Abstract

Muscle fibre cellularity was quantified during seawater growth in populations of predominantly early (strain X) and late maturing (strain Y) Atlantic salmon (*Salmo salar* L.). The fibre density (number mm^{-2} white muscle cross-sectional area) in the fresh fillet was related to pigment concentration, colour as determined with the Roche *Salmo*Fan™, and lipid content. The relationship between fibre density and the textural characteristics of the smoked fillet, as assessed by trained taste panels, was also determined. There was no significant correlation between astaxanthin concentration and muscle fibre density. However, significant positive relationships were obtained between Roche *Salmo*Fan™ score and fibre density, explaining 33% and 44% of the total variation in colour visualisation in strains X and Y, respectively. Significant positive correlations were observed between muscle fibre density and all four measures of texture assessed by the taste panels, ''chewiness'', ''firmness'', ''mouth-feel'' and ''dryness''. A firm texture was therefore associated with a high muscle fibre density. At harvest, the lipid content of the fillet was significantly higher in strain X (11.2%) than strain Y (7.0%). There was, however, no significant

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correlation found between sensoric ''oiliness'' score and the percentage lipid content of the fillet. The results indicate that muscle fibre cellularity is an important factor in several key flesh quality traits. The potential for manipulating muscle cellularity to produce desirable flesh quality characteristics is briefly discussed.

Keywords: Atlantic salmon; Muscle fibres; Growth; Flesh quality; Astaxanthin

1. Introduction

One of the advantages of aquaculture over wild fisheries is the ability to achieve some control over the quality of the flesh as food. For salmonids, increasing worldwide production and pricing pressures have focused attention on flesh quality issues to satisfy market preferences. Although there is no simple definition of flesh quality factors, of particular importance are the nutritional value, safety, flavour, colour, preservation and processing characteristics of the fillets (Haard, 1992).

The texture (firmness) of fish meat is both a valued sensory characteristic for consumers and an important attribute for the mechanical processing of fillets by the food industry (Dunajski, 1979; Haard, 1992). It is influenced by both the intrinsic structural properties of the fillet and post-mortem changes associated with slaughter and storage (Fauconneau et al., 1995, 1997). Studies with numerous species have shown that cultured fish tend to have softer flesh than wild fish (see the work of Haard, 1992). It is known from research on mammalian species that both the connective tissue matrix and the muscle fibres themselves contribute to the intrinsic textural properties of meat (Offer et al., 1989).

The trunk musculature of fish is divided into a series of myomeres and muscle fibres insert via short tendons into collagenous sheets called myosepta. Networks of collagen fibres surround both individual and groups of muscle fibres. The geometrical arrangement of the fibres is complex with individual fibres being arranged in helical trajectories between successive myomeres (Alexander, 1969). White muscle fibres are tightly packed with myofibrils (~ 1 μm diameter) containing actin and myosin filaments. Fish muscle contains lower amounts of collagen that is significantly less cross-linked than in the flesh of birds and mammals (Hallett and Bremner, 1988; Bracho and Haard, 1990).

The range of muscle fibre diameters influences both the amount of connective tissue matrix and the passive mechanical properties of the actomyosin component of the muscle in mammals (Offer et al., 1989). Although collagen fibres contribute to the texture of raw fish flesh, they are thought to be relatively unimportant after cooking (Hatae et al., 1986). Following cooking the muscle fibres themselves probably provide the main resistance to mastication (Dunajski, 1979). Several inter-specific comparisons have shown significant correlations between average muscle fibre diameter and the ''firmness'' of the flesh (Hatae et al., 1990; Hurling et al., 1996). For example, in a study of seven species of marine fish, a trained taste panel found a negative correlation between sensory firmness and average muscle fibre diameter in cooked flesh. The dab (*Limanda limanda* L.) had the smallest average diameter fibres and the highest sensory firmness, whilst flying fish (*Exocoetidae* sp.) contained the largest average diameter fibres and scored the lowest firmness (Hurling et al., 1996).

Colour is a particularly important quality characteristic in salmonids, with a uniform red colour being preferred by the consumer. The pigmentation of wild salmon is derived from the absorption and deposition of oxygenated carotenoids from the diet. The main pigment, astaxanthin, occurs at a concentration of 3–11 mg kg^{-1} in wild salmon (Skrede and Storebakken, 1986) and 4–10 mg kg^{-1} in farmed salmon (Torrissen et al., 1989). Astaxanthin is thought to bind non-specifically to hydrophobic sites on the actomyosin (Hennmi et al., 1990). The deposition of astaxanthin is partly genetically determined but also varies with age, growth rate and maturation (Torrissen and Nævdal, 1984, 1988; Choubert et al., 1997). Nickell and Bromage (1998) suggested that variations in the number and size distribution of muscle fibres could influence the number of astaxanthin binding sites and, thus, account for the observed variations in pigment concentration in different parts of the fillet. In farmed salmon, synthetic astaxanthin and canthaxanthin account for 10–15% of feed costs (Torrissen et al., 1995; Prendergast et al., 1994). There would be a significant economic benefit from achieving good colouration of the fillet with a lower input of dietary pigment.

Significant but non-linear relationships have been established between astaxanthin concentrations and Roche Colour Card Score (Christiansen et al., 1995), as well as various instrumental colour measurements (Skrede and Storebakken, 1986; Christiansen et al., 1995; Choubert et al., 1997; Nickell and Bromage, 1998). The light scattering and absorption properties of the muscle are likely to be important factors in colour perception (Offer et al., 1989).

In the preceding paper, we reported major differences in the patterns of muscle growth between early and late maturing strains of Atlantic salmon (Johnston et al., 2000). The aim of the present study was to investigate potential relationships between the density of muscle fibres and the colour and/or textural characteristics of the fillet. Colour was determined on the fresh flesh under standardised conditions using the Roche *Salmo*Fan™, and textural characteristics were assessed on smoked fillets using a trained taste panel.

2. Materials and methods

2.1. Fish stocking and culture

Two populations of Atlantic salmon (*Salmo salar* L.) were studied corresponding to a high grilsing stock of West Coast Scottish origin (strain X derived from the ''Lochy'' stock), and a low grilsing stock of Norwegian origin (strain Y derived from the ''Namsen'' stock). Individually, passive integrated transponder-tagged (PIT; supplied by Fish Eagle, Gloucestershire, England) and freeze-branded S1 smolts were transferred from Loch Arkaig (freshwater) to Loch Duich (seawater) on the 14th of April 1997. Fish were stocked into two adjacent steel-construction cages ($5 \times 5 \times 5$ m) with 12 mm mesh cube nets (Pens A and B). Pen A was stocked with 585 smolts with an average mass of 55 g, representing six families of strain X and six families of strain Y. Pen B was stocked with 579 smolts with an average mass of 40 g, representing the same six families of strain X, together with some additional fish from separate families of the same strain. Fish were fed by hand to satiation between 1 and 3 times per day depending

on season. The diet used was a standard commercial ration of the Ecolife® series from BioMar. Composition ranged from 23/49 (oil/protein) in the smaller pellet size to 28/46 in the larger. The diet was supplemented with 250 mg/kg Vitamin E and synthetic astaxanthin (CAROPHYLL® Pink from Roche Products) was added to give a final concentration at delivery of 70 mg kg^{-1}. Daylength was extended in cage B from the 5th of November 1997 to the 25th of May 1998. Illumination was provided by a single 400 W submersible light suspended at a depth of 1 m in the centre of the cage. The lights were switched-on 2 h before dusk and switched-off 2 h after dawn each day. Further details of fish husbandry are given in Johnston et al. (2000).

2.2. Carcass processing

Fish were batch-netted into a sample weigh bin, anaesthetized with benzocaine in acetone, identified by PIT tag, and mass, fork length and maturity status were recorded. Salmon were killed by percussion stunning, gill-tagged and placed on ice. Following evisceration, gonads and liver were weighed, and fish gutted mass were recorded. Fish from strain X were sampled from cage A in May 1998 and cages A and B in June 1998. A final sample of strain Y was taken from cage A in September 1998 when the fish had reached a similar mean body mass to the May sample of strain X. These fish were used for the full range of muscle and flesh quality measurements. The harvest samples contained a representative selection of families from the two populations.

Fish were starved for 7 days, harvested, bled and eviscerated, and sent on ice to Pinneys of Scotland (Annan, Scotland). At Pinneys, one fillet was removed for processing to provide the smoked product for the organoleptic investigation. The second fillet was left on the skeleton and the section anterior to a cut immediately behind the dorsal fin was sent to St. Andrews on ice for the analysis of muscle cellularity. The posterior portion of the fillet was sent to Marine Harvest McConnell (Fort William, Scotland) where a 5-cm wide section was removed and homogenised from the front part of this portion of the fillet. This was used for the chemical determination of pigment and flesh lipid.

2.3. Colour and pigment measurements

The visual colour of the fresh salmon fillet was assessed by comparison with the Roche *Salmo*Fan™ (Hoffmann La-Roche, Basel, Switzerland), under standardised conditions employing a light cabinet fitted with a cool, blue fluorescent discharge light ($Ra > 90$, colour temperature 6500 K). Two scorers independently measured the colour of sample fillets at a position adjacent to the first dorsal fin ray and level with the lateral line.

The total pigment concentration was determined in 5 g samples of raw flesh from one side of the fish at the same position as measurements of colour and muscle fibre density using a spectrophotometric method. The flesh samples were homogenised in four volumes of acetone, and allowed to stand for 15 min to allow dissociation of the pigment. Homogenates were centrifuged for 15 min at $1600 \times g$, the supernatant removed, and the pellet re-extracted with 20 ml acetone. The supernatants were pooled, made up to 50 ml and clarified by centrifugation. Optical densities of the clear solvent

abstracts were measured at 475 nm against an acetone blank, and the concentration of total pigment estimated using an $E_{1\%,\ 1\ cm}$ of 2000 for astaxanthin in acetone.

2.4. Flesh lipid

Flesh lipid levels were estimated gravimetrically by an indirect method relying on the antithetic relationship between carcass moisture and lipid (Shearer, 1989). The raw flesh was homogenised and 5 g aliquots weighed into aluminium foil trays and heated to 105°C for 24 h in an oven. The moisture content was calculated by mass loss. Assuming a constant protein fraction by dry mass, both protein and moisture were subtracted from the total components to obtain an estimate of flesh lipid levels. No account was taken of the relatively small contribution of carbohydrates to the carcass mass.

2.5. Determination of muscle fibre density

A 5-mm thick transverse steak was prepared at the level of the first dorsal fin ray and either photographed with a digital camera or traced on an acetate sheet. The total cross-sectional area of the white muscle was digitised using an Image Analysis System (Tema2, ScanBeam, Denmark). The steak from one half of the body was divided up into 12 labelled blocks so as to obtain a representative sample of the entire cross-section. Blocks were mounted on cork strips and frozen in 2-methyl butane cooled to near its freezing point (-159°C) in liquid nitrogen. Samples were wrapped in tin foil to avoid desiccation and stored in a liquid nitrogen refrigerator. Frozen sections, 8-μm thick, were cut, air dried, and stained with Mayer's haematoxylin. The outlines of 150–200 muscle fibres were digitized from each block using the Image Analysis System and fibre diameters were computed. 1000–1500 muscle fibres were digitised per fish, distributed approximately equally between the different blocks. The fibre density was calculated as the number of fibres per mm^2 of muscle cross-sectional area.

2.6. Production of the smoked product

The first fillet that had been removed at Pinneys was taken through a standard smoking procedure. The fillet was robotically salted using dry salt adjusted in proportion to the fillet weight. Salted fillets were transferred to a horizontal flow kiln and smoked for 14 h using hardwood oak. Kiln temperature and humidity levels were pre-programmed and consistent for each batch. Following smoking, the fillets were chilled to 5°C and held in maturation for 3 days to allow smoke and salt equilibrium. The fillet was trimmed in the normal way by removal of the dorsal and ventral fat deposits and the surface pellicle. It was then machine-sliced in D slice format and packs of four replicates per fish were prepared and transported under chill conditions at 0–5°C to Queen Margaret College, Edinburgh for taste panel evaluation.

2.7. Taste panel assessment

The samples were tasted by a panel of specialised assessors (ISO 8586-1, 1993). Assessments for all attributes were scored on a nine-point scale. Because of the number

of samples assessed, tasting sessions were held over several days and not all of the panellists were able to taste all of the samples. The data from replicate samples was used to assess panellist performance. Out of 17 panellists that were involved in the tasting, seven were excluded either because they had sampled very few fish or because they demonstrated poor discriminatory ability (BSI, 1993). To arrive at mean scores for each fish, all the individual results for that fish for each attribute were used to calculate the average score.

2.8. Statistics

The data from the two populations was compared using a Student's *t*-test or in cases were conditions of normality and equal variance were not satisfied, by a Mann–Whitney Rank Sum test. Since it has been suggested that lipid may mask colour visualisation (Nickell and Bromage, 1998), an ANCOVA was carried out with colour score as the dependent variable, population as a fixed factor, and with lipid content as a covariate. The relationships between fibre density and pigment concentration, colour and texture measurements were investigated using regression analysis and ANOVA (SigmaStat Statistical Software, Spss, USA).

3. Results

The average body mass of the fish studied was 2863 ± 116 g ($n = 16$) for the early maturing population (strain X) and 2556 ± 83 g ($n = 11$) for the late maturing population (strain Y). The average density of muscle fibres (mm^{-2}) was not significantly different for strain X (110.4 ± 4.2, $n = 18$, including six fish from the B pen) and strain

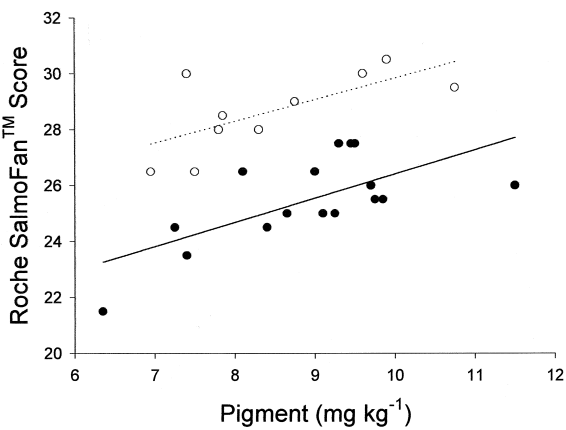

Fig. 1. The relationship between the concentration of carotenoid pigments (mg kg^{-1}) and Roche *Salmo*Fan™ score in Atlantic salmon from strain X (closed circles) and strain Y (open circles). The lines were fitted by least-squares linear regression (Roche *Salmo*Fan™ score = $a + b *$ pigment concentration: strain X: $a = 17.77 \pm 2.19$, $t = 8.11$, $P < 0.0001$; $b = 0.87 \pm 0.24$, $t = 3.58$, $P < 0.01$, $n = 16$; strain Y: $a = 22.13 \pm 2.60$, $t = 8.51$, $P < 0.001$; $b = 0.77 \pm 0.30$, $t = 2.56$, $P < 0.05$, $n = 11$).

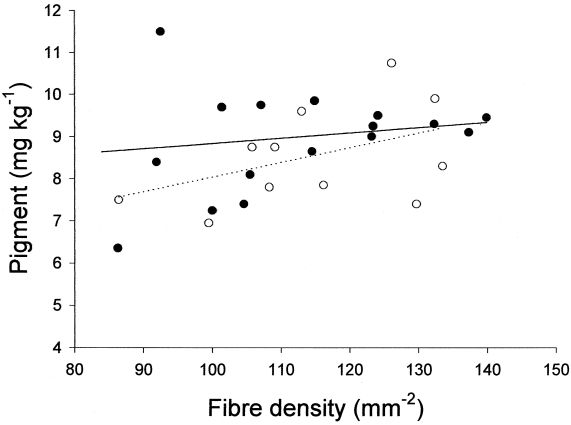

Fig. 2. The relationship between the concentration of carotenoid pigments (mg kg^{-1}) and muscle fibre density (fibres mm^{-2} muscle cross-sectional area) in Atlantic salmon from strain X (closed circles) and strain Y (open circles). The lines were fitted by least-squares linear regression. There was no significant correlation between variables (strain X: R^2 adjusted = 0.026, $P = 0.26$, $n = 15$; strain Y: R^2 adjusted = 0.12, $P = 0.16$).

Y (115.2 ± 4.9, $n = 10$) (mean $\pm$ SE). There was also no significant difference in fibre density between fish from strain X sampled from cage A (107.8 ± 4.4; $n = 10$) and cage B (120.1 ± 7.6; $n = 6$).

3.1. Muscle cellularity, pigment concentration and colour

The pigment concentration had a similar range in the two strains, with most values falling between 7 and 11 mg kg^{-1}. (Fig. 1). The mean pigment concentration was

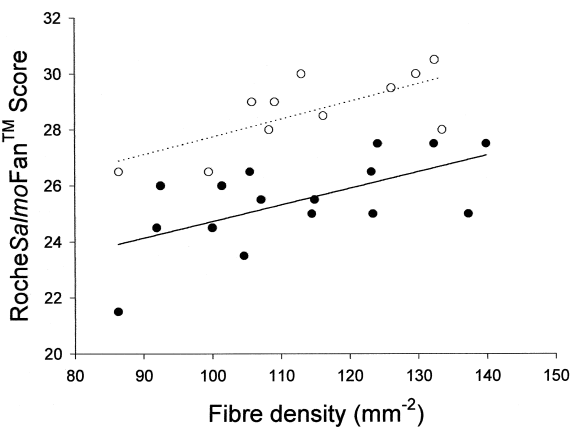

Fig. 3. The relationship between muscle fibre density (fibres mm^{-2} muscle cross-sectional area) and Roche *Salmo*Fan™ score in Atlantic salmon from strain X (closed circles) and strain Y (open circles). The lines were fitted by least-squares linear regression (Roche *Salmo*Fan™ score = $a + b *$ fibre density: strain X: $a = 18.81 \pm 2.29$, $t = 8.24$, $P < 0.0001$; $b = 0.059 \pm 0.020$, $t = 2.94$, $P < 0.05$, $n = 16$; strain Y: $a = 21.39 \pm 2.48$, $t = 8.62$, $P < 0.0001$; $b = 0.064 \pm 0.022$, $t = 2.96$, $P < 0.05$, $n = 11$).

9.0 ± 0.3 for strain X ($n = 16$) and 8.6 ± 0.4 ($n = 11$) for strain Y. There was a significant correlation between pigment and Roche *Salmo*Fan™ score for fish from strain X (R^2 adjusted = 0.44; ANOVA: $F_{1,\ 15} = 12.78$; $P < 0.01$) and strain Y (R^2 adjusted = 0.38; ANOVA: $F_{1,\ 10} = 7.95$; $P < 0.05$) (mean ± SE) (Fig. 1). The average value for Roche *Salmo*Fan™ scores from the mid-line regions of the myotome was 25.5 ± 0.4 for strain X ($n = 16$) and 28.8 ± 0.4 for strain Y ($n = 11$) ($P < 0.01$; Mann–Whitney Rank Sum test). An ANCOVA with colour score as the dependent

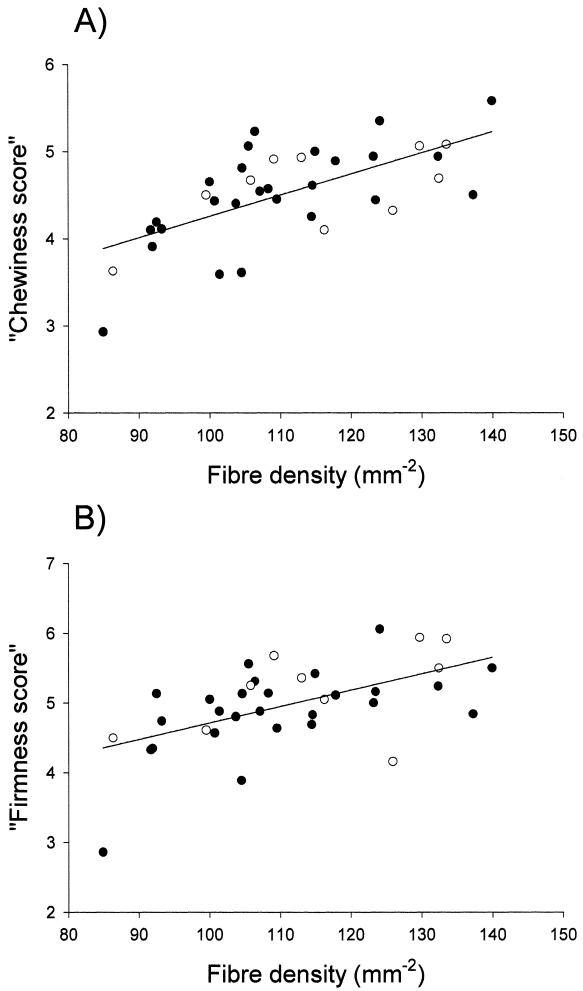

Fig. 4. The relationship between muscle fibre density (fibres mm^{-2} muscle cross-sectional area) in Atlantic salmon and textural characteristics measured by taste panels. (A) ''chewiness'', and (B) ''firmness''. Fish from strain X are represented by closed circles and from strain Y, by open circles. The data was fitted using a first order linear regression (A) ''chewiness'' = 1.82 (±0.55) + 0.024 (±0.0049) * fibre density, R^2 adjusted = 0.40, $df = 34$, $P < 0.001$, (B) ''firmness'' = 2.36 (±0.67) + 0.024 (±0.0059) * fibre density, $R^2 = 0.30$, $df = 34$, $P < 0.001$. Mean ± SE.

variable, strain as a fixed factor and lipid content as a covariate revealed a significant main effect of strain on colour ($P < 0.001$), whereas the covariate was not significant.

There was no significant correlation between pigment concentration and muscle fibre density in either strain (Fig. 2). However, in both populations, there was a significant correlation between muscle fibre density and Roche *Salmo*Fan™ score explaining 27% ($F_{1, 17} = 6.61$; $P < 0.05$) and 44% ($F_{1, 96} = 7.50$; $P < 0.05$) of the variation in strains X and Y, respectively (Fig. 3).

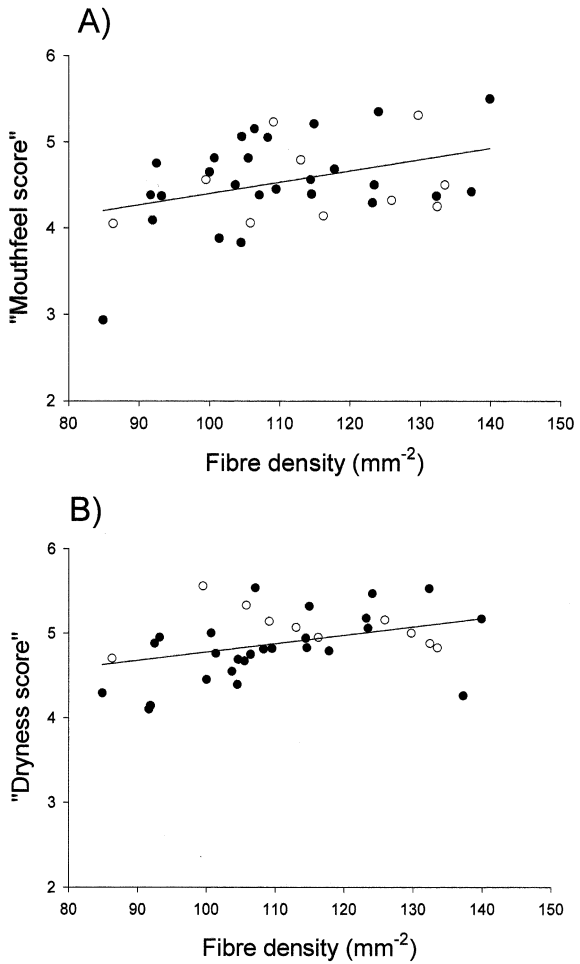

Fig. 5. The relationship between muscle fibre density (fibres mm^{-2} muscle cross-sectional area) in Atlantic salmon and textural characteristics measured by taste panels (A) ''mouth-feel'' and (B) ''dryness''. Fish from strain X are represented by closed circles and from strain Y by open circles. The data was fitted using a first-order linear regression (A) ''mouth-feel'' = 3.08 ($\pm$0.61) + 0.013 ($\pm$0.0055) $*$ fibre density, R^2 adjusted = 0.12, $df = 34$, $P < 0.05$, (B) ''dryness'' = 3.78 ($\pm$0.46) + 0.010 ($\pm$0.0041) $*$ fibre density, $R^2 = 0.12$, $df = 34$, $P < 0.05$. Mean $\pm$ SE.

3.2. Muscle cellularity and texture characteristics

In order to investigate the relationship between the textural characteristics of the smoked fillet and the fibre density of the raw starting material, the data for the two populations were combined. The data set for strain X includes an additional eight fish for which pigment analysis was not available. Four textural characteristics assessed by taste panels were ''firmness'', ''chewiness'', ''mouth-feel'' and ''dryness''. A signifi-

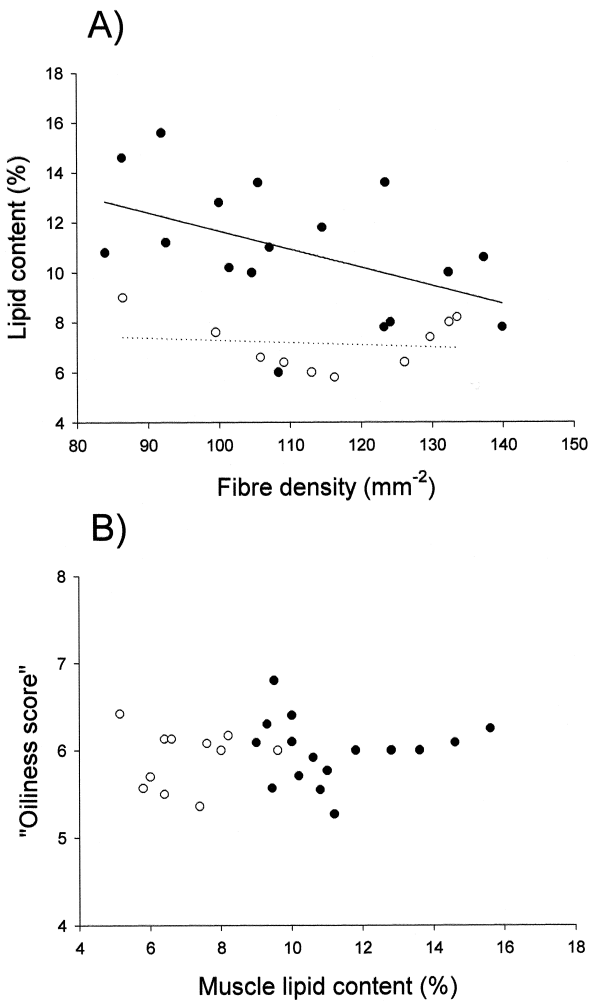

Fig. 6. The relationship between (A) muscle lipid content (%) and fibre density (fibres mm^{-2} muscle cross-sectional area) and (B) ''oiliness flavour'' score and muscle lipid content (%). Fish from strain X are represented by closed circles and from strain Y, by open circles. The lines that were fitted in (A) were fitted by least-squares linear regression (lipid content $= a + b *$ fibre density: strain X: $a = 18.92 \pm 3.79$, $t = 4.99$, $P < 0.001$; $b = -0.073 \pm 0.034$, $t = -2.14$, $P < 0.05$, $n = 16$; strain Y: $a = 8.21 \pm 2.77$, $t = 2.96$, $P < 0.05$; $b = -0.0093 \pm 0.024$, $t = -0.39$, $P = 71$, $n = 11$).

cant correlation was observed between the density of muscle fibres and all the four measures of texture. The best correlation was obtained for ''chewiness'' (Fig. 4A) (R^2 adjusted = 0.40; ANOVA: $F_{1, 34} = 24.5$; $P < 0.0001$) followed by ''firmness'' (Fig. 4B) (R^2 adjusted = 0.30; ANOVA: $F_{1, 34} = 15.7$; $P = 0.0004$). Weaker but still significant correlations were observed between ''mouth-feel'' (Fig. 5A) (R^2 adjusted = 0.12; ANOVA: $F_{1, 34} = 5.71$; $P = 0.02$) and ''dryness'' (Fig. 5B) (R^2 adjusted = 0.12; ANOVA: $F_{1, 34} = 5.86$; $P = 0.02$).

3.3. Flesh lipid content and ''oiliness'' score

At harvest, the gravimetric estimate of lipid content (%) in the fillet was significantly higher in strain X ($11.2 \pm 0.5\%$) ($n = 16$) than in strain Y ($7.0 \pm 0.4\%$) ($n = 11$) (mean $\pm$ SE) ($P < 0.001$; *t*-test). There was a weak negative correlation between muscle fibre density and lipid content for strain X (R^2 adjusted = 0.19; $F_{1, 15} = 4.58$; $P < 0.05$), but not for strain Y (Fig. 6A). There was also no significant correlation between the sensoric assessment of ''oiliness flavour'' and the percentage lipid content of the fillet (Fig. 6B).

4. Discussion

Previous research has demonstrated negative correlations between average muscle fibre diameter and the ''firmness'' of the flesh in different fish species using both instrumental methods (Hatae et al., 1990) and sensory assessment (Hurling et al., 1996). The present study is the first to demonstrate that intra-specific variation in texture is correlated with muscle cellularity. Muscle growth in fish involves the continuous recruitment and hypertrophy of muscle fibres resulting in a spectrum of fibre diameters. The two populations of salmon in the present study had very different muscle growth patterns (Johnston et al., 2000). Fish from the late maturing population recruited more muscle fibres per mm^2 muscle growth in the late summer than in the early maturing population, but few new fibres were added after January. In contrast, the early maturing population added fibres throughout the winter at a reduced level before increasing recruitment again in the spring and summer (Johnston et al., 2000). The smoothed distributions of muscle fibre diameter were bimodal and showed significant differences between the two populations in the final harvest sample. The smallest size class of fibres was absent in strain Y because of the cessation of recruitment, whereas, the right-hand peak of maturing fibres was at higher diameters in strain X than in strain Y due to the greater rate of fibre hypertrophy (Johnston et al., 2000).

In the present study, we used measurements of fibre density averaged over the whole fillet as a more robust estimate of muscle cellularity than the average fibre diameter. Fish from both populations and two adjacent cages subjected to different light regimes were combined to give a range of fibre densities (85–140 fibres mm^{-2}). Of the four organoleptic characteristics related to texture examined, the strongest correlations were obtained for ''chewiness'' and ''firmness'' scores (Fig. 4A,B). The fish with the lowest and highest scores for ''chewiness'' had the lowest and highest fibre densities, respec-

tively, of the fish examined. The fish with the lowest ''chewiness'' score also had the lowest ''firmness'' and ''mouth-feel'' scores but not the lowest ''dryness'' score. Fish with the greatest relative contribution of fibre recruitment to hypertrophy would be expected to have the highest fibre density, and this was correlated with a firmer texture. Hurling et al., (1996) found an inverse correlation between the average fibre cross-sectional area in different species and the sensory assessment of ''firmness'' in cooked fish. In cooked fish, the contribution of connective tissue to the texture is likely to be negligible (Hatae et al., 1986). Since textural characteristics were assessed on smoked fillets in the present study, it is likely that both collagen fibres and the passive mechanical properties of the muscle fibres contributed to the scores obtained (Hatae et al., 1986). A reduction in average fibre size would result in an increase in fibre density and a higher surface-to-volume ratio of the muscle fibres. The connective tissue sheath surrounding each fibre would therefore be relatively more abundant in a muscle with a high than a low fibre density, and this would be expected to contribute to a firmer texture (Dunajski, 1979). A variety of other factors are known to affect the texture of fish muscle. For example, sexual maturation may increase proteolytic enzyme activity and tenderise the flesh (Ando et al., 1986). However, there was no evidence for this in the present study since the sensory evaluation of ''firmness'' was no higher in the maturing than in the immature population of fish (Fig. 4).

The visualisation of the pigment as measured by the Roche *Salmo*Fan™ was significantly correlated with the average muscle fibre density for the whole myotomal cross-section accounting for between 27% and 44% of the variation in the average score for the dorsal and mid-belly portion of the fillet (Fig. 3A,B). The colour of salmon flesh is likely to be a function of both light scattering and absorption by the muscle. In samples with a high light scattering ability, light would not penetrate so deeply in the fillet before being scattered, resulting in relatively little absorption by astaxanthin and, therefore, a pale colour. In contrast, samples with a low scattering ability would allow greater penetration of the light, which would be more strongly absorbed by the astaxanthin, producing a deeper red colour. It has been suggested that the light scattering properties of beef and pork reside in the myofibrils (Offer and Trinick, 1983), or the gaps between myofibrils (Offer et al., 1989). The present results suggest that light scattering also varies with the density of muscle fibres in salmon, with the fillets containing fewer larger diameter fibres scattering more light. Muscle fibre density is around one third higher in diploid than in triploid Atlantic salmon (Johnston et al., 1999). Interestingly, Choubert et al. (1997) found that muscle in diploid salmon had a higher chroma, measured using the CIELCH colour space chromameter, than in triploid fish. In both cases, fish with a higher muscle fibre density show a tendency for better colour visualisation for a given pigment concentration. Our results did not support the suggestion by Nickell and Bromage (1998) that variation in the number and size distribution of fibres could influence pigment concentration by altering the availability of astaxanthin binding sites.

The early maturing population had significantly higher flesh lipid levels than the late maturing population (Fig. 6A), however, this was not associated with differences in the texture of the smoked product (Figs. 4 and 5) or ''oiliness'' flavour as assessed by the taste panel (Fig. 6B). Sheehan et al., (1996) fed salmon different levels of dietary fat

sufficient to alter muscle lipid levels. They only found significant differences in the texture and ''oiliness'' flavour of the smoked product after prolonged storage that was towards the limit of the retail shelf life. In contrast, using an Instron compression test, rainbow trout fed a high fat diet were found to be softer on storage than fish fed a low fat diet, and this was correlated with a higher autolytic protease activity (Andersen et al., 1997).

The nuclei for muscle fibre recruitment and hypertrophy are supplied by the division of a population of undifferentiated myoblasts called satellite cells (Koumans et al. 1991; Johnston, 1999). A number of molecular markers of the muscle stem cell population have recently been identified. Dividing satellite cells committed to terminal differentiation express both proliferating cell nuclear antigen (and one or more of the myogenic regulatory factors belonging to the MyoD family of muscle transcription factors MyoD, myogenin, myf-5 and myf-6) (Cornelison and Wold, 1997; Johnston et al., 1999; Yablonka-Reuveni et al., 1999). The c-met tyrosine kinase factor (Cornelison and Wold, 1997) and the winged-helix protein, MNF-β, (Yang et al., 1997) are molecular markers of all classes of muscle satellite cell in mammals. C-met has also been used as a marker of satellite cells in Atlantic salmon (Johnston et al., 1999). Triploid Atlantic salmon had 24% more satellite cells per mm^2 muscle cross-sectional area than diploid fish and had one third fewer fibres (Johnston et al., 1999). A promising strategy for selecting high fibre density and, hence, favourable ''firmness'' and colour visualisation traits of the fillet would be to identify broodstock with both a high fibre number and high density of satellite cells. Using molecular markers, the latter could probably be accomplished using biopsies of the white muscle.

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