Livestock Science ▮ (▮▮▮▮) ▮▮▮–▮▮▮

Contents lists available at ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci

Muscle lipid composition in bulls from 15 European breeds

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ARTICLE INFO

Article history:
Received 30 July 2013
Received in revised form
31 October 2013
Accepted 1 November 2013

Keywords:
Fatty acid profile
Beef cattle
PUFA
Omega-3

ABSTRACT

Cattle meat provides essential nutrients necessary for a balanced diet and health preservation. Besides nutritional quality, consumers' preferences are related to specific attributes such as tenderness, taste and flavour. The present study characterizes the fatty acid composition of beef, which is an important factor in both nutritional and quality values, in 15 European cattle breeds fed a similar diet and reared in five countries (United Kingdom, Denmark, France, Italy and Spain). The effect of possible slight differences on diet composition which might have occurred between countries were included in the breed effect which confounds country, diet, slaughter house and slaughter day as all individuals of a same breed were managed simultaneously. The wide range of breeds studied and the significant differences on lipid profile described here provide a broad characterization of beef meat, which allows giving a better response to the variety of consumers' preferences. Regarding meat health benefits, the groups that stand out are: the double-muscled animals, which displayed lower total fat, lower proportion of saturated (SFA) and monounsaturated (MUFA) fatty acids, and a higher proportion of polyunsaturated (PUFA) fatty acids; and Limousin and Charolais breeds with a significantly higher conversion of 18:3n-3 PUFA to the long chain 22:6n-3 PUFA.

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http://dx.doi.org/10.1016/j.livsci.2013.11.001

1. Introduction

In the last years, a number of epidemiological studies have associated red and processed meat consumption with the development of vascular diseases and colon cancer (Cross et al., 2007; Kontogianni et al., 2008; World Cancer Research Fund/American Institute for Cancer Research, 2007), despite the fact that over many years of evolution, human kind has become adapted to consume large amounts of lean red meat (Mann, 2000). However, associations between red meat consumption and increased disease risks are still unclear given that in many studies it is impossible to isolate the effects of red meat alone (see McAfee et al. (2010) for revision) and other authors have failed to find these negative effects of unprocessed red meat consumption (Alexander et al., 2009; Hodgson et al., 2006; Hodgson et al., 2007; Micha et al., 2010). Instead, several studies point out the possible health benefits in relation to unprocessed red meat intake (McAfee et al., 2010), although isolation of the effects of red meat alone is difficult to accomplish. Its moderate consumption was found to lower total cholesterol, LDL cholesterol and triglycerides (TG) (lean beef diet vs. poultry vs. lean fish diet, Beauchesne-Rondeau et al., 2003), as well as blood pressure (~215 g/d lean meat diet vs. control, Hodgson et al., 2006). Moreover, red meat contributes key nutrients to the diet, notably conjugated linoleic acid (CLA), haem iron, B vitamins, zinc, selenium and retinol, and also can have an important role as a dietary source of n-3 fatty acids (n-3 FAs) (Davey et al., 2003; Givens and Gibbs, 2008; Givens, 2010; McAfee et al., 2010). Therefore, it is unlikely that reducing red meat consumption alone would be sufficient to diminish health risks (McAfee et al., 2010).

Apart from health issues, the fatty acid (FA) composition also influences the technological and sensory quality of meat (Wood et al., 2004) and depends on several factors, mainly on breed effect and systemic location of individual depots in ruminants (Webb et al., 1998; Zembayashi et al., 1995).

The aim of this study is to determine the variation in lipid profile and sensory parameters of *Longissimus thoracis* muscle within and among 15 European cattle breeds, reared under comparable management conditions, and to represent the diversity in fatty acid content among the 15 cattle populations.

2. Material and methods

2.1. Animals and feed system

A total of 436 unrelated pure bred bulls belonging to 15 European breeds were used (EC QLK5 – CT2000-0147). The breeds included beef breeds, either local or worldwide used, and dairy breeds. The whole sample included 31 Jersey, 27 South Devon, 30 Aberdeen Angus, and 29 Highland from United Kingdom; 29 Holstein, 29 Danish Red, and 20 Simmental, from Denmark; 30 Asturiana de los Valles, 31 Asturiana de la Montaña, 30 Avileña-Negra Ibérica, and 31 Pirenaica from Spain; 30 Piedmontese, and 28 Marchigiana from Italy; and 31 Limousin, and 30 Charolais from France.

Bulls were reared in each country in a unique location and under a uniform beef management system representative of those used in the European Union (EU) countries. Animals were reared under intensive conditions with *ad libitum* access to concentrate. Feed composition and management details are described in Albertí et al. (2008). Briefly, animals were fed a total mixed ration containing barley and soy bean with appropriate minerals and vitamins. All ingredients were mixed into a form that prevented selection using molasses up to 3–5% as a binding agent. Metabolizable energy of the ration was 12.5-kJ/kg and straw was available *ad libitum* to provide fibre. Bi-carbonate was added to the ration to prevent acidosis. This diet was designed to achieve the slaughter weight of 75% of mature weight for each breed within a window of 13–17 months. Animals from each breed were slaughtered the same day in either commercial or experimental abattoirs, depending on the experimental facilities of each country. All animals were fasted before slaughter for less than 24 h and had free access to water. Stunning of animals was performed using captive bolt pistol and no electrical stimulation of carcasses was performed.

2.2. Sampling and determination of total lipid content

Carcass processing after slaughter was described by Albertí et al. (2008) and Christensen et al. (2011). For lipid measurements, *Longissimus thoracis* muscle was excised at 24 h postmortem from the left side of the carcass between the 6th and the 13th rib and a sample was taken immediately and frozen for chemical analysis including lipid profile. The remainder was stored at $+2 \pm 1$ °C until 48 h postmortem. Also, samples were taken from the 48 h postmortem section to determine total lipid content. Samples for individual FA analysis were taken from the same position on *Longissimus thoracis* from all animals. Samples were vacuum packed, frozen and transported on dry ice to University of Bristol (United Kingdom) to determine total lipid content.

2.3. Phenotypes measured

Fatness score corresponding to the visual fatness cover was estimated by UE standard (R.(CEE) n° 1208/81, 2930/81, 1026/91 and 1026/91) classification, with a 15-point scale (1, very low fat to 15, very high fat). Fat percentage was also measured as the proportion of subcutaneous and intermuscular fat in the rib dissection (Piedrafita et al., 2003). Fat was extracted by the method of Folch et al. (1957), separated into neutral lipid (NL) and phospholipid (PL), methylated, separated by gas–liquid chromatography (GLC) and the individual peaks of each FA were identified and quantified as described in detail by Scollan et al. (2001). Total lipid content was taken as the sum of the NL and PL fractions. Some additional phenotypes were set as are saturated FA (SFA), monounsaturated FA (MUFA), polyunsaturated FA (PUFA), n-3 PUFA, n-6 PUFA, n-6/n-3 ratio, 18:2/18:3 ratio, P:S1 [(18:2n-6+18:3n-3) / (12:0+14:0+16:0+18:0)] and P:S2 [(18:2n-6+18:3n-3+20:3n-6+20:4n-6+20:5n-3+22:4n-6+22:5n-3+22:6n-3)/(12:0+14:0+16:0+18:0)] ratios, and the antithrombotic potential (ATT), which is the ratio between the sum of the

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antithrombogenic FAs eicosatrienoic acid (20:3n-6) and eicosapentaenoic acid (20:5n-3), and the thrombogenic FA arachidonic acid (20:4n-6) [(20:3+20:5)/20:4] (Ulbricht and Southgate, 1991). Two sensory panels in UK and in Spain assessed meat using an eight-point scale as described in Wood et al. (1995). Adjustments between both panel results were made to ensure comparable results. The criteria assessed were flavour, texture and juiciness – the higher scores corresponding to the characteristic flavour of beef, and very tender and juicy meat, respectively.

2.4. Statistical analysis

Differences between breeds were determined by variance analysis, using the GLM procedure, considering breed as a unique effect, and the Scheffe's multiple-comparison procedure at $\alpha=0.005$ used to test differences among breeds. The effects of country, time of feed, slaughter house and slaughter day are confounded with the breed effect. A principal components analysis (PCA) using the PRINCOMP procedure was performed to determine the main traits that explained most of the variation among the 15 cattle populations. This technique reduces the whole set of n correlated variables to n uncorrelated linear functions of the original measurements. The first principal component is the linear combination of all of the variables showing the maximum variation among the samples. The second, third and further components are similarly linear combinations representing the next largest variations, irrespective of those represented by previous components. The criterion used to determine the number of meaningful components to retain was that the cumulative per cent of variance accounted for at least 70%. All the statistical analyses were carried out using the SAS statistical package v. 9.1.3 (SAS, 2009).

3. Results

3.1. Lipid profiles

Values in mg/100 g of total FAs for total lipid, NL, PL, and the major FA classes of muscle are given in Table 1, as well as the FA ratios important for human nutrition (P:S and n-6/n-3 in total lipid). Fig. 1 graphically represents these traits by grouping breeds according to their lipid content: (A) fat – Danish Red∼Holstein > Jersey∼Aberdeen Angus∼Highland; (B) lean – Pirenaica > Simmental∼Marchigiana > Limousin∼Asturiana de los Valles > Piedmontese; and (C) intermediate – Asturiana de la Montaña > Avileña-Negra Ibérica > South Devon∼-Charolais. Individual total FA, NL and PL are detailed in Table S1. Muscle NL was dominated by 9c18:1, 16:0 and 18:0, which accounted for 33%, 25% and 15% of NL FAs, respectively. PL 18:2 n-6 had an overall proportion of 24% of total PL compared with 2% of NL. The rest of dominant FAs in the PL fraction mirrored those in NL, 9c18:1, 16:0 and 18:0 accounting for 14%, 12% and 10% of total PL, respectively. Longer chain (C20–22) n-6 and n-3 PUFA constituted about 65 mg/100 g muscle in PL whereas they only added up 5 mg/100 g muscle in NL.

All traits measured showed a large amount of variation within and between breeds (Tables 1 and 2, Fig. 1 and Table S1). These variations are speciallciof these studies assessed indios Valles, South Devon, Charolais and Pirenaica breeds, mainly explained by the inclusion of animals with different genotypes for the myostatin gene (*GDF8*) associated with increased muscularity (Grobet et al., 1998) (Table 2). Among hypertrophic breeds, South Devon showed the highest phenotypic variation between the different genotypes for the nt821-del11 mutation (Table 2). Overall, the double-muscled animals included in this study displayed lower total fat, lower proportion of SFA and MUFA, and a higher proportion of PUFA, reflected by high P:S1 and P:S2 ratios (Table 1, Fig. 1).

Comparing all breeds, Aberdeen Angus samples displayed the highest fatness score (11 ± 0.42 s.e.) and n-3 PUFA (61.3 ± 2.2 s.e.) muscle content, whereas Holstein and Danish Red showed the highest total SFA (2126 ± 162 s.e. and 2169 ± 166 s.e., respectively), MUFA (2097 ± 171 s.e., 2296 ± 177 s.e.) and n-6 PUFA (327 ± 16.7 s.e., 311 ± 9.04 s.e.) content (Fig. 1B). Some breeds such as Piedmontese, Asturiana de los Valles, or Limousin had a significant ($P<0.005$) lower fat content. When percentages of lipid profiles are compared, and although Holstein, Aberdeen Angus, Danish Red, and Jersey displayed higher total PUFA contents, Piedmontese and Asturiana de los Valles breeds show the highest proportion of PUFA (31.2 ± 1.54 s.e., 20.47 ± 1.57 s.e.) and n-6 PUFA (29.11 ± 1.45 s.e., 19.04 ± 1.49 s.e.), and South Devon, Limousin, and Piedmontese showed the highest proportion of n-3 PUFA (2.86 ± 0.23 s.e., 2.17 ± 0.15 s.e., 2.09 ± 0.11 s.e.) (Table 1).

Piedmontese and Asturiana de los Valles had the highest P:S ratios, whereas breeds with a low P:S ratio were Holstein and Danish Red. The proportion of n-6 to n-3 was lower in South Devon, Aberdeen Angus and Highland, and significantly higher in Piedmontese, Pirenaica and Asturiana de los Valles. The antithrombotic potential (ATT) (C20:3n-6+C20:5n-3/C20:4n-6) was highest in South Devon and Aberdeen Angus, and lowest in Piedmontese, and Holstein. The phospholipid 22:6 n-3/18:3 n-3 ratio was significantly different between breeds: Charolais and Limousin showed the highest values whereas Jersey and Highland displayed the lowest ones (Table 1).

Regarding organoleptic characteristics, it is worth highlighting that Pirenaica, Asturiana de la Montaña, Charolais, and South Devon breeds obtained the best scores regarding juiciness, Pirenaica had also the highest texture score, and Aberdeen Angus and Highland had the highest flavour marks (Table 1 and Fig. 1).

3.2. Relationships among lipid traits and breeds

The first two dimensions of the PCA analysis explained 79% of the variation among breeds (Fig. 2). When considering the different lipid traits, the first dimension (Factor 1 with 60% of total variance) was mainly explained by total muscle fat content (total lipids, NL, fat percentage, MUFA, SFA, PL, PUFA, n-6, and n-3), fatness score, fat percentage and flavour score, all positively correlated, whereas on the opposite side % n-6, % PUFA 18:2/18:3,

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Table 1
Variations in lipid traits among 15 European cattle breeds reared under comparable management conditions. Values are expressed as means (mg/100 g of total fatty acids) ± standard error.

Breed	JER[1] (*n*=30)	SD[1] (*n*=27)	AA[1] (*n*=30)	HIG[1] (*n*=29)	HOL[1] (*n*=29)	DR[1] (*n*=29)	SM[1] (*n*=20)
Fatness score (FS)[2]	4.23 ± 0.28^{fg}	5.42 ± 0.6^{ef}	11 ± 0.42^{a}	4.3 ± 0.68^{fg}	8.12 ± 0.12^{bc}	9.14 ± 0.31^{b}	7.06 ± 0.38^{cd}
Fat percentage[3]	12.9 ± 0.64^{bc}	14.3 ± 1.14^{b}	21.6 ± 0.71^{a}	19.8 ± 0.88^{a}	19 ± 0.83^{a}	19.5 ± 0.68^{a}	11.2 ± 0.83^{cd}
Flavour	$3.73 \pm 0.1a^{bc}$	3.83 ± 0.1^{ab}	4.07 ± 0.09^{a}	4.06 ± 0.11^{a}	3.61 ± 0.1^{bcd}	3.61 ± 0.1^{bcd}	3.37 ± 0.11^{cd}
Juiciness	$4.76 \pm 0.1a^{bc}$	4.97 ± 0.07^{a}	4.97 ± 0.08^{a}	4.82 ± 0.12^{abc}	4.36 ± 0.12^{c}	4.59 ± 0.1^{abc}	4.31 ± 0.16^{c}
Texture	5.24 ± 0.3^{abc}	5.19 ± 0.14^{abc}	4.91 ± 0.16^{abcd}	4.49 ± 0.17^{c}	5.01 ± 0.14^{abcd}	5.1 ± 0.15^{abc}	4.34 ± 0.2^{cd}
Total lipid (TL)	3529 ± 215^{bc}	2068 ± 202^{def}	3802 ± 213^{b}	3605 ± 230^{bc}	5262 ± 400^{a}	5493 ± 385^{a}	1656 ± 143^{efg}
TL/FS[4]	773 ± 60.7^{a}	415 ± 52.6^{cd}	356 ± 20.5^{cde}	370 ± 61.5^{cde}	652 ± 50^{ab}	611 ± 43.7^{b}	246 ± 26.1^{ef}
PL[5]	622 ± 13.2^{a}	508 ± 14.2^{defg}	597 ± 17.8^{ab}	582 ± 12.8^{abc}	593 ± 14.3^{ab}	625 ± 13.4^{a}	528 ± 18.4^{cdef}
NL[6]	2907 ± 211^{b}	1560 ± 195^{cde}	3204 ± 207^{b}	3024 ± 223^{b}	4667 ± 394^{a}	4868 ± 384^{a}	1128 ± 133^{def}
CLA	12.2 ± 1.14^{ab}	8.07 ± 1.26^{cde}	10.3 ± 0.81^{bcd}	15.3 ± 1.55^{a}	11.4 ± 1.1^{bc}	11.3 ± 1.08^{bc}	3.68 ± 0.49^{fg}
18:3 n-3	29.5 ± 1.57^{b}	24.1 ± 1.75^{c}	36.7 ± 1.85^{a}	30.4 ± 1.98^{b}	16.7 ± 1.65^{d}	15 ± 0.77^{d}	7.66 ± 0.46^{e}
22:5 n-3	10.8 ± 0.43^{c}	13.9 ± 0.56^{ab}	15.1 ± 0.53^{a}	13 ± 0.45^{b}	8.01 ± 0.27^{de}	7.33 ± 0.22^{e}	10.1 ± 0.5^{c}
22:6 n-3	0.81 ± 0.14^{def}	1.36 ± 0.15^{ab}	1.55 ± 0.21^{a}	0.76 ± 0.04^{ef}	0.59 ± 0.07^{ef}	0.5 ± 0.05^{f}	0.85 ± 0.06^{cdef}
P 22:6/18:3	0.07 ± 0.01^{i}	0.1 ± 0.01^{hi}	0.09 ± 0.01^{hi}	0.07 ± 0^{i}	0.13 ± 0.01^{fgh}	0.12 ± 0.01^{ghi}	0.19 ± 0.01^{def}
SFA	1421 ± 96.8^{b}	820 ± 92^{cde}	1477 ± 88.1^{b}	1488 ± 94.6^{b}	2126 ± 162^{a}	2169 ± 166^{a}	571 ± 56.1^{def}
% SFA	42.71 ± 0.48^{ab}	41.21 ± 0.85^{bc}	41.94 ± 0.36^{ab}	44.09 ± 0.28^{a}	42.83 ± 0.46^{ab}	41.52 ± 0.46^{abc}	36.4 ± 0.86^{e}
MUFA	1268 ± 96.3^{b}	683 ± 81.2^{de}	1351 ± 84.1^{b}	1288 ± 94.7^{b}	2097 ± 171^{a}	2296 ± 177^{a}	566 ± 61.9^{def}
% MUFA	37.62 ± 0.69^{cde}	33.9 ± 0.84^{fgh}	38.14 ± 0.43^{cde}	37.69 ± 0.46^{cde}	41.83 ± 0.5^{ab}	43.79 ± 0.56^{a}	35.5 ± 0.99^{efg}
PUFA	327 ± 9.2^{ab}	239 ± 8.98^{c}	339 ± 10.1^{ab}	302 ± 10.8^{b}	355 ± 18.4^{a}	336 ± 9.76^{ab}	247 ± 10.7^{c}
% PUFA	10.98 ± 0.67^{efg}	14.86 ± 1.3^{cde}	10.17 ± 0.4^{fg}	9.46 ± 0.39^{fg}	7.74 ± 0.42^{fg}	7.17 ± 0.44^{g}	17.52 ± 1.29^{bc}
n-3 PUFA	45.7 ± 1.93^{b}	47.6 ± 2.46^{b}	61.3 ± 2.2^{a}	49.6 ± 2.43^{b}	27.6 ± 1.77^{c}	24.9 ± 0.78^{c}	22.2 ± 0.88^{cd}
% n-3 PUFA	1.48 ± 0.06^{cd}	2.86 ± 0.23^{a}	1.83 ± 0.08^{bc}	1.52 ± 0.05^{cd}	0.59 ± 0.03^{g}	0.53 ± 0.03^{g}	1.58 ± 0.12^{cd}
n-6 PUFA	282 ± 7.75^{bc}	192 ± 6.88^{f}	278 ± 8.13^{bc}	253 ± 8.69^{cd}	327 ± 16.7^{a}	311 ± 9.04^{ab}	225 ± 10.1^{def}
% n-6 PUFA	9.5 ± 0.62^{fghi}	11.99 ± 1.09^{efg}	8.34 ± 0.33^{ghi}	7.94 ± 0.35^{hi}	7.15 ± 0.4^{hi}	6.64 ± 0.41^{i}	15.93 ± 1.18^{bcd}
P:S1[7]	0.21 ± 0.01^{defg}	0.28 ± 0.03^{cde}	0.19 ± 0.01^{defg}	0.17 ± 0.01^{efg}	0.14 ± 0.01^{g}	0.13 ± 0.01^{g}	0.34 ± 0.03^{bc}
P:S2[8]	0.26 ± 0.02^{defg}	0.38 ± 0.04^{cdef}	0.24 ± 0.01^{efg}	0.22 ± 0.01^{fg}	0.18 ± 0.01^{g}	0.17 ± 0.01^{g}	0.5 ± 0.05^{bc}
n-6/n:3	6.32 ± 0.2^{de}	4.13 ± 0.14^{f}	4.58 ± 0.09^{f}	5.23 ± 0.15^{ef}	12.1 ± 0.17^{b}	12.6 ± 0.16^{ab}	10.2 ± 0.33^{c}
18:2/18:3	8.1 ± 0.3^{g}	6.84 ± 0.32^{g}	6.41 ± 0.16^{g}	7.15 ± 0.28^{g}	16.4 ± 0.54^{f}	16.6 ± 0.41^{f}	21.7 ± 0.84^{de}
ATT[9]	0.34 ± 0.01^{e}	0.6 ± 0.02^{a}	0.52 ± 0.01^{b}	0.44 ± 0.01^{c}	0.3 ± 0.01^{fg}	0.29 ± 0.01^{fg}	0.31 ± 0.01^{efg}

Breed	LIM[1] (*n*=31)	CHA[1] (*n*=31)	PIE[1] (*n*=30)	MAR[1] (*n*=28)	AST[1] (*n*=30)	CAS[1] (*n*=31)	AVI[1] (*n*=30)	PI[1] (*n*=31)
Fatness score (FS)[2]	8.35 ± 0.1^{b}	9.03 ± 0.15^{b}	3.6 ± 0.11^{g}	4.96 ± 0.18^{ef}	4.07 ± 0.28^{fg}	5.9 ± 0.21^{de}	5.77 ± 0.21^{e}	4.94 ± 0.1^{efg}
Fat percentage[3]	13.2 ± 0.41^{bc}	15.4 ± 0.49^{b}	3.23 ± 0.2^{f}	8.94 ± 0.36^{de}	7.77 ± 0.83^{e}	14.7 ± 0.66^{b}	12.6 ± 0.44^{bc}	9.67 ± 0.51^{de}
Flavour	3.38 ± 0.06^{cd}	3.39 ± 0.07^{cd}	3.35 ± 0.07^{d}	3.4 ± 0.07^{cd}	3.63 ± 0.07^{bcd}	3.57 ± 0.1^{bcd}	3.51 ± 0.09^{bcd}	3.64 ± 0.06^{bcd}
Juiciness	4.95 ± 0.15^{ab}	5.01 ± 0.12^{a}	4.73 ± 0.1^{abc}	4.37 ± 0.15^{bc}	5.02 ± 0.14^{a}	4.51 ± 0.14^{abc}	4.86 ± 0.17^{abc}	5.06 ± 0.16^{a}
Texture	5.2 ± 0.13^{abc}	5.19 ± 0.14^{abc}	5.3 ± 0.17^{ab}	4.17 ± 0.21^{d}	5.22 ± 0.21^{abc}	4.39 ± 0.29^{cd}	5.34 ± 0.2^{ab}	5.62 ± 0.16^{a}
Total lipid (TL)	1326 ± 88.7^{fg}	2045 ± 131^{def}	819 ± 46.2^{g}	1522 ± 120^{efg}	1367 ± 127^{fg}	2910 ± 151^{cd}	2389 ± 148^{de}	1869 ± 157^{ef}
TL/FS[4]	157 ± 9.38^{f}	225 ± 13.2^{ef}	231 ± 13.8^{ef}	309 ± 22.5^{def}	338 ± 18.6^{de}	505 ± 27.7^{bc}	436 ± 36.8^{cd}	375 ± 29.5^{cde}
PL[5]	435 ± 6.1^{h}	433 ± 6.78^{h}	468 ± 10.4^{gh}	469 ± 13.4^{gh}	472 ± 11.9^{fgh}	553 ± 16.5^{bcd}	531 ± 15.2^{cde}	479 ± 12^{efgh}
NL[6]	891 ± 87.3^{ef}	1613 ± 127^{cde}	351 ± 42^{f}	1053 ± 111^{def}	895 ± 125^{ef}	2358 ± 142^{bc}	1858 ± 141^{cd}	1390 ± 153^{de}
CLA	3.87 ± 0.29^{fg}	5.66 ± 0.48^{ef}	1.69 ± 0.17^{g}	4.37 ± 0.43^{fg}	3.5 ± 0.44^{fg}	7.89 ± 0.55^{de}	5.51 ± 0.45^{ef}	4.77 ± 0.53^{efg}
18:3 n-3	6.79 ± 0.29^{e}	7.44 ± 0.62^{e}	5.12 ± 0.23^{e}	6.87 ± 0.51^{e}	4.97 ± 0.29^{e}	8.31 ± 0.41^{e}	6.52 ± 0.32^{e}	5.65 ± 0.33^{e}
22:5 n-3	10.1 ± 0.31^{c}	9.48 ± 0.34^{cd}	6.88 ± 0.25^{e}	7.69 ± 0.31^{e}	6.89 ± 0.26^{e}	9.6 ± 0.27^{c}	8.03 ± 0.38^{de}	6.7 ± 0.3^{e}
22:6 n-3	1.24 ± 0.06^{abc}	1.17 ± 0.08^{abcd}	0.61 ± 0.03^{ef}	0.9 ± 0.05^{cdef}	0.65 ± 0.04^{ef}	0.98 ± 0.06^{bcde}	0.83 ± 0.06^{def}	0.61 ± 0.04^{ef}
P 22:6/18:3	0.27 ± 0.01^{a}	0.3 ± 0.02^{a}	0.16 ± 0.01^{efg}	0.25 ± 0.01^{abc}	0.22 ± 0.01^{bcd}	0.26 ± 0.01^{abc}	0.27 ± 0.02^{ab}	0.21 ± 0.01^{cde}
SFA	481 ± 36.9^{ef}	820 ± 57.8^{cde}	246 ± 17.9^{f}	546 ± 48.1^{ef}	486 ± 55.2^{ef}	1154 ± 65.2^{bc}	935 ± 60.3^{cd}	709 ± 66.8^{de}
% SFA	38.06 ± 0.42^{de}	42.19 ± 0.52^{ab}	31.46 ± 0.68^{f}	37.79 ± 0.63^{de}	36.15 ± 0.92^{e}	41.8 ± 3.02^{ab}	41.41 ± 0.46^{bc}	39.27 ± 0.62^{cd}

MUFA	472 ± 39.4^{def}	766 ± 54.9^{cde}	201 ± 19.6^{f}	486 ± 43.1^{def}	444 ± 55.2^{ef}	1118 ± 65^{bc}	866 ± 62^{cd}	669 ± 70.6^{de}
% MUFA	36.84 ± 0.76^{def}	39.33 ± 0.46^{bcd}	24.86 ± 1.07^{i}	33.54 ± 0.65^{gh}	32.2 ± 1.14^{h}	40.45 ± 0.51^{bc}	37.91 ± 0.61^{cde}	35.94 ± 0.99^{efg}
PUFA	166 ± 3.54^{d}	171 ± 5.58^{d}	222 ± 5.76^{c}	230 ± 8.12^{c}	215 ± 5.4^{c}	248 ± 8.12^{c}	248 ± 9.47^{c}	229 ± 6.24^{c}
% PUFA	14.92 ± 0.92^{cde}	9.74 ± 0.52^{fg}	31.2 ± 1.54^{a}	18.16 ± 1.13^{bc}	20.47 ± 1.57^{b}	9.62 ± 0.51^{fg}	12 ± 0.69^{def}	15.67 ± 1.21^{cd}
n-3 PUFA	23.9 ± 0.8^{cd}	22.8 ± 1.17^{cd}	15.1 ± 0.57^{e}	18.1 ± 0.84^{de}	15.5 ± 0.57^{e}	23.2 ± 0.77^{cd}	18.6 ± 0.74^{de}	15.9 ± 0.69^{e}
% n-3 PUFA	2.17 ± 0.15^{b}	1.28 ± 0.08^{def}	2.09 ± 0.11^{b}	1.41 ± 0.09^{de}	1.43 ± 0.1^{cde}	0.89 ± 0.04^{fg}	0.92 ± 0.07^{fg}	1.05 ± 0.07^{ef}
n-6 PUFA	142 ± 3.43^{g}	148 ± 4.77^{g}	207 ± 5.38^{ef}	212 ± 7.57^{ef}	200 ± 5.08^{ef}	224 ± 7.8^{def}	230 ± 9.11^{de}	214 ± 5.86^{ef}
% n-6 PUFA	12.75 ± 0.8^{def}	8.45 ± 0.46^{ghi}	29.11 ± 1.45^{a}	16.75 ± 1.05^{bc}	19.04 ± 1.49^{b}	8.73 ± 0.48^{ghi}	11.08 ± 0.6^{efgh}	14.62 ± 1.15^{cde}
P:S1[7]	0.27 ± 0.02^{cdef}	0.16 ± 0.01^{fg}	0.77 ± 0.06^{a}	0.35 ± 0.03^{bc}	0.43 ± 0.05^{b}	0.17 ± 0.01^{efg}	0.21 ± 0.01^{defg}	0.3 ± 0.03^{cd}
P:S2[8]	0.4 ± 0.03^{cde}	0.23 ± 0.01^{fg}	1.04 ± 0.08^{a}	0.5 ± 0.04^{bc}	0.61 ± 0.07^{b}	0.23 ± 0.01^{fg}	0.29 ± 0.02^{defg}	0.41 ± 0.04^{cd}
n-6/n:3	6.13 ± 0.27^{de}	6.75 ± 0.27^{d}	14.1 ± 0.41^{a}	12.1 ± 0.56^{b}	13.2 ± 0.41^{ab}	9.88 ± 0.39^{c}	12.7 ± 0.55^{ab}	13.9 ± 0.44^{a}
18:2/18:3	15.9 ± 0.53^{f}	15.8 ± 0.58^{f}	32.1 ± 1.17^{a}	24.8 ± 1.29^{cd}	31.9 ± 1.55^{a}	20.8 ± 0.81^{e}	27 ± 0.94^{bc}	30.1 ± 1.28^{ab}
ATI[9]	0.45 ± 0.01^{c}	0.39 ± 0.01^{d}	0.27 ± 0.01^{g}	0.28 ± 0.01^{fg}	0.29 ± 0.01^{fg}	0.32 ± 0.01^{ef}	0.28 ± 0.01^{fg}	0.28 ± 0.01^{fg}

[a–i]Within row, values with the same letter are not significantly different ($P > 0.005$).

[1] Complete breed names: Jersey (JER), South Devon (SD), Aberdeen Angus (AA), Highland (HIG), Holstein (HOL), Danish Red (DR), Simmental (SM), Limousin (LIM), Charolais (CHA), Piedmontese (PIE), Marchigiana (MAR), Asturiana de los Valles (AST), Asturiana de la Montaña (CAS), Avileña-Negra Ibérica (AVI), Pirenaica (PI).

[2] Visual fatness cover estimated by UE standard. 1: very low–15: very high.

[3] Proportion of subcutaneous and intermuscular fat in the rib dissection.

[4] Total lipid (TL)/Fatness score (FS).

[5] Total phospholipids.

[6] Total neutral lipids.

[7] (18:2n-6 + 18:3n-3)/(12:0 + 14:0 + 16:0 + 18:0).

[8] (18:2n-6 + 18:3n-3 + 20:3n-6 + 20:4n-6 + 20:5n-3 + 22:4n-6 + 22:5n-3 + 22:6n-3)/(12:0 + 14:0 + 16:0 + 18:0).

[9] (C20:3n-6 + C20:5n-3)/C20:4n-6.

P:S1 and P:S2 ratios, negatively correlated with total fat measurements, are found. Most of the variation reflected by Factor 2 (19%) is due to ATT index and n-3 (total and in percentage). Therefore, the considered "fat" breeds (Aberdeen Angus, Highland, Holstein, Danish Red and Jersey), are plotted opposite to the "lean" breeds such as Piedmontese and Asturiana de los Valles.

4. Discussion

The results from this European project published up to now focused either on associations between molecular markers and different beef production traits (Dunner et al., 2013a, 2013b; Sevane et al., 2013; Sevane et al., in press), or on phenotype analysis including live weight, body size and carcass characteristics (Albertí et al., 2008), and relationship between collagen characteristics, total lipid content and texture (Christensen et al., 2011). However, none of these studies assessed individual profiles or different lipid ratios on the 15 European cattle breeds included in the project.

4.1. Muscle fatty acid composition

Since adipose tissue is where the bulk of FAs are located, early work on meat FA composition focused on this tissue. However recently muscle has been gaining more attention due to its greater significance as food and as a result of an increasing consumers' aversion to visible fat.

PL is an essential component of cell membranes and its amount remains fairly constant as the animal fattens, whereas NL increases in overall FA composition. Long chain PUFAs are mainly stored in muscle PL in cattle, and as muscle lipid and the proportion of NL, with its higher content of SFA and MUFA, increases, the proportion of PUFAs declines (Wood et al., 2008). This is in concordance with the negative correlation obtained here between the percentage of PUFA and fat measurements, as well as the weaker correlation between total PL and total lipid muscle content compared with NL (Fig. 2).

Oleic acid (18:1cis9) is the major FA in meat and is much more predominant in NL. It forms from stearic acid (18:0) through the enzyme stearoyl Co-A desaturase, and in ruminants the same enzyme also produces CLA from 18:1 trans-vaccenic FA (t18:1) in adipose tissue (Scollan et al., 2006; Wood et al., 2008). These metabolic relationships are reflected in the higher levels of 18:1cis9, 18:0, t18:1 and CLA FAs in the NL fraction compared with PL (Table S1). Concerning CLA amount, differences in fat content and a possible higher desaturase activity in fatter animals, as found by Siebert et al. (2003), may explain the higher CLA content in fatter animals in comparison to leaner animals (Aldai et al., 2006) found here (Table 1).

The correlations between total muscle lipid content (fatness score, fat percentage, total lipids, SFA), and absolute and proportional amounts of PUFA, n-6 and n-3 FAs were negative (Fig. 2) (Dinh, 2007; Hoehne et al., 2012). This means increasing carcass fat leads to an increasing amount of FAs in triglycerides, but at the same time the relative amount (%) of PUFA decreases (Wood et al., 2008).

Please cite this article as: Sevane, N., et al., Muscle lipid composition in bulls from 15 European breeds. Livestock Science (2013), http://dx.doi.org/10.1016/j.livsci.2013.11.001

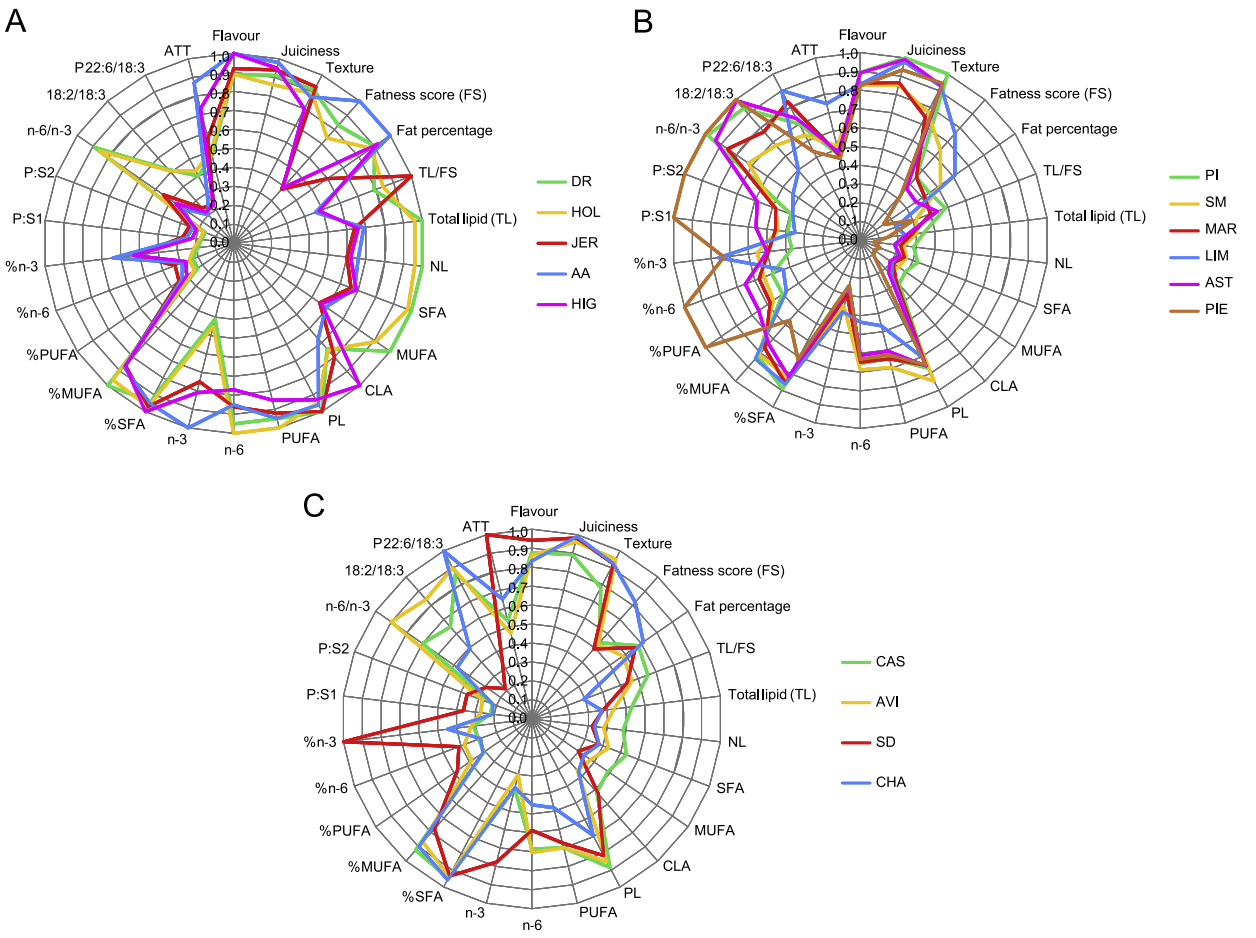

Fig. 1. Web drawing of main lipid traits measured on: (A) five fat breeds (DR Danish Red, HOL Holstein, JER Jersey, AA Aberdeen Angus, HIG Highland); (B) six lean breeds (PI Pirenaica, SM Simmental, MAR Marchigiana, LIM Limousin, AST Asturiana de los Valles, PIE Piedmontese); and (C) four intermediate breeds (CAS Asturiana de la Montaña, AVI Avileña-Negra Ibérica, SD South Devon, CHA Charolais). In order to obtain the web, each variable was transformed so that the breed having the highest value for a specific variable was set at 1.0 on the radial scale and values for the other breeds were expressed relative to that.

4.2. Breed differences on lipid profile

Lipid differences among breeds may be caused by their different history, production purpose and beef characteristic selection in response to commercial or cultural requirements that vary geographically (Albertí et al., 2008; Felius et al., 2011). Among the 15 European cattle breeds analyzed in this study, most are beef breeds, either local – South Devon, Highland, Aberdeen Angus, Asturiana de los Valles, Pirenaica, Marchigiana, Asturiana de la Montaña, and Avileña-Negra Ibérica – or worldwide used such as Limousin, Charolais, Piemontese, and Simmental, and three were dairy breeds – Jersey, Holstein, and Danish Red-.

Concerning total lipid content of meat, results show there were five fat (Danish Red ~ Holstein > Jersey ~ Aberdeen Angus ~ Highland), six lean (Pirenaica > Simmental ~ Marchigiana > Limousin ~ Asturiana de los Valles > Piedmontese), and four intermediate (Asturiana de la Montaña > Avileña-Negra Ibérica > South Devon ~ Charolais) breeds (Fig. 1), classification which is in agreement with the results reported by Pitchford et al. (2002) on Jersey, South Devon, and Limousin intramuscular fat crossbreed comparison. In agreement also with Wood et al. (2008), Aberdeen Angus had the highest subcutaneous fat content (fatness score). However, muscle lipid concentration did not mirror subcutaneous fat, and the partitioning of body fat between dairy and beef breeds was different, with dairy breeds having more internal and less external fat (Truscott et al., 1983; Wood et al., 2008), which was translated in a higher ratio of muscle lipid to fatness score (TL/FS) in dairy breeds compared to specialized beef breeds (Table 1), characterized by their ability to transform the nutrients mainly into proteins (Kempster et al., 1982). In agreement also with other studies (Huerta-Leidenz et al., 1993; Johnson, 1987; Siebert et al., 1996), large, lean breeds, such as Charolais, Piedmontese or Asturiana de los Valles, had lower levels of MUFA than smaller, early maturing breeds (Aberdeen Angus or Jersey).

The phospholipid 22:6 n-3/18:3 n-3 ratio, which theoretically correlates with greater activity or expression of Δ5 and Δ6 desaturase enzymes (Wood et al., 2008), was significantly higher in Charolais, Limousin, Avileña-Negra Ibérica, Asturiana de la Montaña and Marchigiana, whereas Jersey and Highland displayed the lowest ones,

Please cite this article as: Sevane, N., et al., Muscle lipid composition in bulls from 15 European breeds. Livestock Science (2013), http://dx.doi.org/10.1016/j.livsci.2013.11.001

Table 2
Means for lipid traits of breeds with different genotypes for the *GDF8* gene. Values are expressed as means (mg/100 g of total fatty acids) ± standard error.

Breed	**SD**[1]			**CHA**[1]	
GDF8 genotype[2]	+/+ (10)	+/*mh* (10)	*mh*/*mh* (3)	+/+ (21)	+/*mh* (9)
Fatness score[3]	6.56 ± 1.13^{bc}	5.6 ± 0.45^{cd}	1.67 ± 0.33^{e}	9.29 ± 0.16^{a}	8.44 ± 0.24^{ab}
Fat percentage[4]	17.6 ± 1.66^{a}	13.4 ± 1.06^{abc}	7.73 ± 1.37^{cd}	16.5 ± 0.48^{ab}	13 ± 0.72^{abc}
Flavour	3.83 ± 0.18	4.01 ± 0.12	3.4 ± 0.2	3.39 ± 0.09	3.4 ± 0.15
Juiciness	4.83 ± 0.1	5.17 ± 0.11	4.65 ± 0.08	4.92 ± 0.12	5.22 ± 0.27
Texture	4.94 ± 0.27^{ab}	5.32 ± 0.18^{ab}	5.07 ± 0.35^{ab}	4.94 ± 0.15^{ab}	5.78 ± 0.23^{ab}
Total lipid	2841 ± 304^{ab}	1666 ± 174^{bc}	1179 ± 296^{c}	2276 ± 144^{abc}	1506 ± 183^{bc}
PL[5]	534 ± 25	496 ± 19.8	472 ± 33.1	436 ± 7.66	426 ± 14.3
NL[6]	2307 ± 286^{ab}	1170 ± 174^{bc}	707 ± 294^{c}	1841 ± 140^{abc}	1080 ± 174^{bc}
CLA	12.4 ± 2.29^{a}	5.5 ± 0.91^{b}	2.88 ± 1.5^{b}	6.43 ± 0.57^{b}	3.86 ± 0.59^{b}
18:1cis9	748 ± 109^{ab}	400 ± 50.8^{bc}	226 ± 77.9^{c}	706 ± 50.6^{abc}	442 ± 60.2^{bc}
18:2 n-6	163 ± 14^{ab}	150 ± 6.64^{ab}	156 ± 10.7^{ab}	114 ± 5.27^{bc}	97.5 ± 3.99^{c}
18:3 n-3	28 ± 3.3^{a}	23 ± 2.36^{ab}	17.7 ± 1.21^{b}	8.08 ± 0.82^{c}	5.95 ± 0.53^{c}
20:5 n-3	8.53 ± 0.98^{a}	8.01 ± 0.5^{a}	8.05 ± 1.86^{a}	4.81 ± 0.4^{b}	4.62 ± 0.6^{b}
22:6 n-3	1.6 ± 0.35^{a}	1.27 ± 0.12^{ab}	1.22 ± 0.34^{ab}	1.23 ± 0.1^{ab}	1.03 ± 0.13^{ab}
SFA	1143 ± 152^{ab}	634 ± 75.1^{bc}	407 ± 136^{c}	918 ± 64^{abc}	592 ± 84.9^{bc}
MUFA	955 ± 138^{ab}	527 ± 67.4^{bc}	336 ± 106^{c}	863 ± 61^{abc}	541 ± 75^{bc}
PUFA	254 ± 20.1^{a}	231 ± 10.7^{ab}	233 ± 17.7^{ab}	178 ± 7.08^{bc}	155 ± 6.31^{c}
n-3 PUFA	52.4 ± 4.85^{a}	46.3 ± 3.2^{a}	40.6 ± 4.71^{a}	23.8 ± 1.45^{b}	20.6 ± 1.81^{b}
n-6 PUFA	202 ± 15.8^{ab}	184 ± 7.73^{abc}	192 ± 14.6^{ab}	154 ± 6.09^{bc}	135 ± 5.12^{c}
P:S1[7]	0.18 ± 0.02^{b}	0.3 ± 0.03^{ab}	0.51 ± 0.13^{a}	0.14 ± 0.01^{b}	0.19 ± 0.02^{b}
P:S2[8]	0.25 ± 0.03^{c}	0.4 ± 0.04^{abc}	0.69 ± 0.18^{ab}	0.21 ± 0.01^{c}	0.29 ± 0.03^{bc}
n-6/n:3	3.9 ± 0.19^{b}	4.08 ± 0.17^{b}	4.8 ± 0.48^{b}	6.68 ± 0.3^{b}	6.91 ± 0.58^{b}
18:2/18:3	5.98 ± 0.33^{c}	6.84 ± 0.39^{c}	8.8 ± 0.2^{c}	15.3 ± 0.67^{bc}	17 ± 1.09^{bc}
ATT[9]	0.60 ± 0.03^{a}	0.60 ± 0.03^{a}	0.60 ± 0.03^{a}	0.39 ± 0.01^{bc}	0.41 ± 0.02^{b}

Breed	**AST**[1]			**PI**[1]				
GDF8 genotype[2]	+/+ (2)	+/mh (15)	mh/mh (13)	+/+ (11)	A (10)	B (4)	C (3)	D (3)
Fatness score[3]	5 ± 0^{cd}	4.87 ± 0.38^{cd}	3 ± 0.28^{de}	4.91 ± 0.21^{cd}	5 ± 0.15^{cd}	4.5 ± 0.29^{cd}	5 ± 0^{cd}	5.33 ± 0.33^{cd}
Fat percentage[4]	7.96 ± 0.62^{cd}	10.3 ± 1.29^{bcd}	4.78 ± 0.49^{d}	8.97 ± 0.63^{cd}	10.1 ± 0.93^{cd}	8.05 ± 1.24^{cd}	9.65 ± 1.47^{cd}	12.8 ± 2.53^{abc}
Flavour	3.55 ± 0.15	3.69 ± 0.11	3.57 ± 0.11	3.7 ± 0.1	3.52 ± 0.12	3.45 ± 0.12	3.8 ± 0.21	3.93 ± 0.03
Juiciness	4.2 ± 1.1	5.23 ± 0.17	4.9 ± 0.19	5.18 ± 0.23	4.69 ± 0.28	4.87 ± 0.5	5.58 ± 0.66	5.59 ± 0.49
Texture	4.7 ± 0.3^{b}	5.43 ± 0.32^{ab}	5.07 ± 0.3^{ab}	5.62 ± 0.21^{ab}	5.41 ± 0.31^{ab}	5.56 ± 0.44^{ab}	5.43 ± 0.73^{ab}	6.59 ± 0.52^{a}
Total lipid	1196 ± 187^{c}	1674 ± 203^{bc}	1039 ± 124^{c}	1627 ± 171^{bc}	2010 ± 322^{abc}	1492 ± 410^{bc}	1595 ± 494^{bc}	3066 ± 394^{a}
PL[5]	450 ± 48.2	473 ± 14.2	475 ± 22.1	483 ± 27.8	482 ± 17	447 ± 28.1	490 ± 34.7	482 ± 19.9
NL[6]	746 ± 139^{c}	1201 ± 200^{bc}	564 ± 119^{c}	1144 ± 162^{bc}	1527 ± 312^{abc}	1045 ± 388^{bc}	1105 ± 514^{bc}	2583 ± 376^{a}
CLA	2.09 ± 0.53^{b}	4.54 ± 0.67^{b}	2.52 ± 0.51^{b}	3.88 ± 0.45^{b}	5.05 ± 0.98^{b}	5.34 ± 2.47^{b}	3.21 ± 1.13^{b}	7.92 ± 2.07^{ab}
18:1cis9	292 ± 39.6^{bc}	476 ± 77^{bc}	223 ± 36.5^{c}	447 ± 61.4^{bc}	589 ± 121^{abc}	405 ± 137^{bc}	441 ± 191^{bc}	1031 ± 163^{a}
18:2 n-6	143 ± 17^{abc}	154 ± 5.06^{ab}	143 ± 7.4^{abc}	151.4 ± 10^{ab}	160 ± 8.75^{ab}	150 ± 9.45^{ab}	179 ± 13.5^{a}	177 ± 18.2^{a}
18:3 n-3	4.2 ± 0.85^{c}	5.68 ± 0.47^{c}	4.27 ± 0.23^{c}	5.4 ± 0.48^{c}	5.67 ± 0.62^{c}	5.03 ± 1.04^{c}	5.65 ± 1.41^{c}	7.36 ± 0.96^{c}
20:5 n-3	2.47 ± 0.53^{b}	3.14 ± 0.32^{b}	2.9 ± 0.16^{b}	3.41 ± 0.47^{b}	2.41 ± 0.21^{b}	2.68 ± 0.32^{b}	2.83 ± 0.71^{b}	3.31 ± 0.66^{b}
22:6 n-3	0.55 ± 0.08^{b}	0.63 ± 0.05^{b}	0.7 ± 0.06^{ab}	0.71 ± 0.08^{ab}	0.59 ± 0.06^{b}	0.56 ± 0.12^{b}	0.51 ± 0.13^{b}	0.48 ± 0.05^{b}
SFA	428 ± 74.8^{c}	632 ± 88.1^{bc}	326 ± 47.5^{c}	614 ± 79.4^{bc}	768 ± 136^{abc}	539 ± 160^{c}	571 ± 194^{bc}	1231 ± 153^{a}
MUFA	368 ± 60.1^{c}	587 ± 90.5^{bc}	290 ± 44^{c}	549 ± 70.7^{bc}	726 ± 144^{abc}	513 ± 173^{bc}	554 ± 237^{bc}	1239 ± 196^{a}
PUFA	207 ± 27.7^{abc}	221 ± 6.74^{abc}	211 ± 9.29^{abc}	223 ± 12.1^{abc}	231 ± 10.1^{ab}	213 ± 15.2^{abc}	255 ± 6.97^{a}	247 ± 23.5^{ab}
n-3 PUFA	13.2 ± 2.28^{b}	16 ± 0.91^{b}	15.3 ± 0.72^{b}	16.9 ± 1.48^{b}	15 ± 1.07^{b}	15 ± 2.3^{b}	15.5 ± 0.24^{b}	17 ± 0.99^{b}

Table 2 (*continued*)

Breed	AST[1]			PI[1]				
GDF8 genotype[2]	+/+ (2)	+/mh (15)	mh/mh (13)	+/+ (11)	A (10)	B (4)	C (3)	D (3)
n-6 PUFA	194 ± 25.4^{ab}	205 ± 6.09^{ab}	195 ± 9.02a^{b}	206 ± 11.3^{ab}	216 ± 9.34^{a}	198 ± 13.3^{ab}	239.2 ± 6.87^{a}	230 ± 22.6^{a}
P:S1[7]	0.35 ± 0.02^{ab}	0.34 ± 0.06^{ab}	0.55 ± 0.07^{a}	0.29 ± 0.04^{ab}	0.29 ± 0.05^{ab}	0.34 ± 0.07^{ab}	0.42 ± 0.15^{ab}	0.15 ± 0.02^{b}
P:S2[8]	0.49 ± 0.02^{abc}	0.48 ± 0.08^{abc}	0.79 ± 0.1^{a}	0.42 ± 0.05^{abc}	0.4 ± 0.07^{abc}	0.46 ± 0.08^{abc}	0.6 ± 0.24^{abc}	0.2 ± 0.02^{c}
n-6/n:3	14.8 ± 0.62^{a}	13.2 ± 0.59^{a}	13 ± 0.66^{a}	12.8 ± 0.85^{a}	14.8 ± 0.72^{a}	13.8 ± 1.32^{a}	15.5 ± 0.41^{a}	13.5 ± 0.73^{a}
18:2/18:3	34.6 ± 2.99^{a}	29.4 ± 2.16^{a}	34.5 ± 2.38^{a}	29.3 ± 1.89^{a}	30.4 ± 2.35^{a}	32.4 ± 4.33^{a}	34.6 ± 5.8^{a}	24.4 ± 1.82^{ab}
ATT[9]	0.28 ± 0.05^{d}	0.29 ± 0.01^{cd}	029 ± 0.01^{cd}	0.30 ± 0.01^{cd}	0.27 ± 0.01^{d}	0.30 ± 0.02^{cd}	0.25 ± 0.01^{d}	0.30 ± 0.02^{cd}

$^{a-i}$Within row, values with the same letter are not significantly different ($P > 0.005$).

[1] Complete breed names: South Devon (SD), Charolais (CHA), Asturiana de los Valles (AST), Pirenaica (PI).

[2] +: non-hypertrophic. *mh*: hypertrophic. *GDF8* mutations: SD and AST nt821-del11; CHA Q204X; PI nt821-del11 and F94L (A ++/++F94L; B +del11/++; C ++/F94L-F94L; D +del11/+F94L). Between brackets: number of individuals.

[3] Visual fatness cover estimated by UE standard. 1: very low–15: very high.

[4] Proportion of subcutaneous and intermuscular fat in the rib dissection.

[5] Total phospholipids.

[6] Total neutral lipids.

[7] (18:2n-6+18:3n-3)/(12:0+14:0+16:0+18:0).

[8] (18:2n-6+18:3n-3+20:3n-6+20:4n-6+20:5n-3+22:4n-6+22:5n-3+22:6n-3)/(12:0+14:0+16:0+18:0).

[9] (C20:3n-6+C20:5n-3)/C20:4n-6.

Fig. 2. BiPlot of factor pattern for factors 1 and 2 of 15 European breeds showing the correlations to traits (*in italics*) with the two principal components (JER Jersey; SD South Devon; AA Aberdeen Angus; HIG Highland; HOL Holstein; DR Danish Red; SM Simmental; LIM Limousin; CHA Charolais; PIE Piedmontese; MAR Marchigiana; AST Asturiana de los Valles; CAS Asturiana de la Montaña; AVI Avileña-Negra Ibérica; PI Pirenaica).

and in concordance with Warren et al. (2008), Holstein displayed higher values than Aberdeen Angus (Table 1). However, the relationships between 18:3 n-3, 20:5 n-3, and 22:6 n-3 described by Raes et al. (2001) and Aldai et al. (2006) according to *GDF8* genotype (*mh/mh* genotype converts a higher proportion of 18:3 n-3 to 20:5 n-3 but not to 22:6 n-3) were not consistently found here (Table 2).

Those breeds showing high frequency of mutated *GDF8* genotypes will have a low concentration of total lipid in muscle and have a higher proportion of PL and, hence, higher proportions of PUFA in total lipid (Table 1). Therefore, as previously reported by several authors (Aldai et al., 2006, 2007; Esmailizadeh et al., 2008; Raes et al., 2001), double-muscled animals had lower total fat, SFA and MUFA, and higher relative proportions of PUFA, likely related to the muscle hyperplasia that increases the number of cells and thus the proportion of phospholipids, mainly present in cell membranes.

The distribution of breeds plotted by PCA analysis (Fig. 2) mainly reflected their absolute lipid composition vs. relative proportion of PUFA, both n-6 and n-3, as well as the different n-6 to n-3 ratios. Therefore, breeds naturally fell into three main groups: one group defined as having a high muscle absolute fat content (total lipid, NL, PL, CLA, SFA, MUFA, PUFA) – Aberdeen Angus, Highland and the dairy breeds; a second group with lower fat content and higher proportion of PUFAs, as well as P:S ratios (healthier meat) – Piedmontese and Asturiana de los Valles; and a large group gathering the rest of breeds with intermediate fat content. And lastly, Factor 2 highlights the

high values of South Devon for % n-3 and ATT (index higher values better for health).

All animals included in this project were fed a similar diet and reared intensively under comparable management conditions between countries. The effects of all factors other than breed (country, diet, slaughter) were controlled to minimize differences and were confounded with the breed effect. Inevitably, some variations might have occurred but special emphasis has been put to respect the diet composition in the different countries. The higher absolute n-3 PUFA muscle content found in the UK breeds specially in the Aberdeen Angus breed cannot be due to a grass-based diet generally used in UK (Scollan et al., 2006) inexistent in this study, but rather to a specific characteristic of this fat breed.

4.3. Implications for human nutrition

The ratio of PUFA to SFA (P:S) in beef (approximately 0.11) is lower than the desired dietary ratio of 0.4, which has led to focus research efforts on ways to improve this ratio within beef (Howell et al., 1997; Scollan et al., 2001, 2006). Given that the amount of SFA and MUFA increases faster (resulting in a decrease in the P:S ratio) with increasing fatness than does the content of PUFA, lowering the fat level of beef is thus more efficient in increasing the P:S ratio than dietary interventions (DeSmet et al., 2004). Thereof fat breeds have a lower P:S ratio whereas lean breeds, and specially double-muscled animals, approached or even exceeded P:S nutritional recommendations (Aldai et al., 2006; DeSmet et al., 2004). This variation is much larger than what can actually be achieved in beef by alterations of the diet (Scollan et al., 2003).

Regarding the ratio of n-6 to n-3 PUFA, none of the animal groups' ratio was as low as the nutritionally recommended value (4.0), however opposed trends have arisen in recent years. Although several studies have related the lowering of n-6 to n-3 ratio of diet with lower CVD risk (Scollan et al., 2006; Wood and Enser, 1997), the usefulness of this ratio has recently been questioned given that it detracts from actual amounts of both n-3 and n-6 that are essential for human health (Givens and Gibbs, 2008; see McAfee et al. (2010) for revision), and the focus is now moving towards the individual consideration of 18:3 n-3 and n-3 PUFA (Stanley et al., 2007). Beef can make an important contribution to the diet given that, whereas increases in dietary n-6 can readily be obtained from several foods, there are scarce sources of n-3, including eggs, fish, and ruminant meats, and although concentrations of n-3 found in beef are lower than those within oily fish (0.28 mg/g vs. 19.9 mg/g), red meat may be an important source of n-3 since its intake is generally greater than that of oily fish (Cosgrove et al., 2004; McAfee et al., 2010; SACN/COT, 2004). Moreover, red meat is the main dietary source of 22:5 n-3 (Givens and Gibbs, 2008), which has comparable health benefits to those of 20:5 n-3 and 22:6 n-3 (Hino et al., 2004; Howe et al., 2007; Rissanen et al., 2000), and CLA – with higher values in Highland, which has health benefits in the human diet (Hargrave-Barnes et al., 2008; Palmquist et al., 2005) and for which ruminant meat and milk are its major dietary sources (Turpeinen et al., 2002).

5. Conclusions

Beef producers in many countries are searching for ways to raise the nutritional value and quality of meat to make it more attractive to consumers. Our research has characterized the FA composition, an important factor in both nutritional and quality values, of 15 European cattle breeds, a representative set which provides most of the cattle meat consumed in Europe. The wide range of breeds studied and the significant differences on lipid profile described here provide a broad characterization of beef meat, which allows giving a better response to the variety of consumers' preferences. Taking all these data into account, the breeds that stand out regarding their meat health properties are: Piedmontese and Asturiana de los Valles due to the high P:S ratios; Limousin and Charolais with a significantly higher conversion of 18:3 n-3 to 22:6 n-3.

Conflict of interest statement

None of the authors of the manuscript entitled “Muscle lipid composition in bulls from 15 European breeds” have potential conflicts of interest which should be disclosed.

Acknowledgements

This work was supported in part by an EC grant QLK5 – CT2000-0147.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.livsci.2013.11.001.

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Please cite this article as: Sevane, N., et al., Muscle lipid composition in bulls from 15 European breeds. Livestock Science (2013), http://dx.doi.org/10.1016/j.livsci.2013.11.001

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