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1 **Heritability estimates for processing and quality traits in common** 2 **carp (*Cyprinus carpio* L.) using a molecular pedigree**

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12

13 **Abstract**

14 Heritability estimates with a microsatellite parentage assignment based pedigree are of special interest
15 in common carp cultured under traditional pond conditions. This method reduces common environment
16 effects as all families can be grown immediately after hatching mixed in the same pond. We applied this
17 method to study genetics of growth and processing traits in common carp at market size (1.5 kg and
18 more). The experimental progeny was established by crossing 147 two-year old males and 8 females
19 (six to eight-year old) of Hungarian synthetic mirror carp population. The fish grew up through three
20 vegetation seasons and at the end a sample of 331 fish was examined for biometrical traits (standard
21 length, body weight, relative head length, relative body height, relative body width), percent fat and
22 processing traits (% processed body, % fillets with skin, % fillets without skin). It was shown that sex
23 had a significant effect on most traits: females were larger and fatter than males, and they had both
24 higher percent processed body and percent fillet with skin. Standard length, body weight, percent fat
25 and relative head length had a high heritability (N0.5), while relative body height, relative body width,
26 percent processed body and fillet yields had a medium heritability (0.2–0.5). We found relatively high
27 positive genetic correlations between body size (standard length and body weight) and percent fat (0.71
28 and 0.59, respectively), favourable genetic correlations between body size and percent processed body

29 (0.69 for standard length and 0.74 for body weight) and between body size and fillet yields (0.50–0.77).
30 Genetic correlations between body size and body shape (relative head length, relative body height and
31 relative body width) were weak to moderate, thus selection for better growth should have little impact
32 towards more rotund shape. Relative head length had strong negative correlation (–0.7 to –0.9) with
33 percent fat, percent processed body and percent fillet yields. This means that indirect selection for
34 reduced relative head length should be effective in improving of fillet yield.

35

36 **Keywords:** Common carp; *Cyprinus carpio*; Heritability; Muscular fat; Processing; Dressout;
37 Slaughtering; Growth; Genetic correlations; Parentage assignment; Microsatellites

38

39

40 **1. Introduction**

41

42 The common carp, *Cyprinus carpio*, is a major fish species in the world aquaculture production (FAO,
43 2005). It is exclusively farmed in traditional extensive or semi-intensive ponds, where fish growth is
44 highly dependent (50% and more) on natural food (plankton and benthos). Hence, environmental
45 conditions have a major impact on the performance of common carp, and high attention has been given
46 to optimization of pond management. The pond management technology is well documented (Horváth
47 et al., 1992) and benefits from centuries of farming knowledge. Genetic improvement could be a
48 complementary way to increase the effectiveness of carp culture.

49 Studies on the genetic improvement of common carp have been performed by several authors (e.g. Moav
50 and Wohlfarth, 1976; Bakos and Gorda, 1995; Cherfas et al., 1996; Gela et al., 2003; Linhart et al., 2002;
51 Kocouret al., 2005a,b) and reviewed e.g. by Hulata (1995) and Horváth and Orban (1995). Presently,
52 the only widely applied method in common carp culture is intraspecific crossbreeding (Kocour et al.,
53 2005a). Utilization of all female population, produced from gynogenetic sex reversed offspring and
54 normal females, promises 5–8% higher performance (Cherfas et al., 1996; Kocouret al., 2005b), but is
55 not widely applied due to technical difficulties. In a well-documented experiment, mass selection for
56 growth related traits was found ineffective (Moav and Wohlfarth, 1976) and estimated heritabilities for
57 growth traits range from 0.0 to 0.5 (Vandeputte, 2003, for a review). However, some of the past

58 experiments could have been biased due to small number of breeders used, and/or inability to separate
59 common environment and genetic effects (Vandeputte,2003).

60 In a previous study with common carp, Vandeputte et al. (2004) used microsatellites for parentage
61 assignment of 240 families produced from 10 dams and 24 sires. Heritability estimates for weight,
62 standard length and Fulton's coefficient of body condition were found to range from 0.33 to 0.37.
63 However, these estimates were obtained from juvenile fish at the age of 8 weeks. Since such results
64 were encouraging and showed a potential for mass selection on growth in common carp, we have under-
65 taken the present study to estimate heritabilities in growth traits at market size. To account for potential
66 future marketing strategy and changing market demands, heritability values were also estimated for
67 quality and processing traits (% fat, % processed body, % fillets with and without skin). The aim of this
68 study was to estimate genetic parameters (heritabilities, correlations) for growth and processing traits in
69 the common carp at three summers of age, using microsatellite parentage assignment to avoid
70 environmental effects common to full-sib families.

71

72 **2. Materials and methods**

73

74 *2.1. Constitution of a pedigreed population of experimental fish*

75

76 The reproduction and culture of common carp was carried out at the experimental facilities of the
77 University of South Bohemia, Research Institute of Fish Culture and Hydrobiology (Vodňany, Czech
78 Republic). The traits of interest were recorded from generation 2 (G2) fish. G1 offspring were produced
79 in May 2001 using a full factorial cross between 24 G0 males and 10 G0 females of the HSM (Hungarian
80 Synthetic Mirror) line (Vandeputte et al., 2004). Fin samples (1 cm²) were taken on all 34 G0 parents
81 and kept in Eppendorf tubes filled in with 98% ethanol at laboratory temperature. In May 2003, 147
82 fluent males were collected from the G1 population, and crossed simultaneously with eight suitable G0
83 HSM females in a full factorial cross to establish the G2. Fin samples were collected on all 155 parents
84 (147 G1 males and 8 G0 females), and stored in 98% ethanol. Only one G0 female was used in both
85 2001 and 2003 crosses. The full factorial cross was done by pooling an equal quantity of striped eggs
86 from all 8 females. The pool of eggs was then divided into 147 equal aliquots. Each aliquot was fertilized

87 individually by the sperm of the 147 males. This was done in three separate fertilization batches, with
88 49 egg aliquots fertilized in each batch. The duration between the first and the third fertilization did not
89 exceed an hour. One minute after fertilization all aliquots from one fertilization batch were pooled and
90 egg stickiness was eliminated prior to incubating the eggs in one Zuger jar. Altogether, we incubated
91 eggs in three Zuger jars (three fertilization batches) and nursed larvae in three incubation cradles in the
92 same conditions. At swimming stage, we stocked the larvae in a pond after mixing equal numbers of
93 larvae from each of the three incubation cradles. For more details on the crossing, incubation and larval
94 rearing methodologies used see Vandeputte et al. (2004). The G2 population was reared as a single batch
95 in the same conditions in the same pond under semi-intensive pond management. In September 2003, a
96 random sample of 2000 yearlings of G2 population was individually PIT tagged and fin sampled.
97 G2 population was reared in earthen ponds until October 2005 (through three growing seasons), when
98 they reached market size. From the 2000 collected fin samples of G2, a random subset of 812 fish was
99 genotyped for parentage assignment.

100

101 *2.2. Parentage assignment*

102

103 The selected 812 G2 individuals were genotyped for five to eleven microsatellites described by
104 Crooijmans et al. (1997): MFW7, MFW9, MFW11, MFW16, MFW18 and MFW26 for all fish, MFW3,
105 MFW12, MFW20, MFW29 and MFW40 for some fish only. Parentage assignment was performed by
106 exclusion with one mismatch tolerated using VITASSIGN (Vandeputte et al., 2006). Among the 147 G1
107 sires, 126 (85.7%) could be assigned to a single G0 parental pair, there remaining 21 being assigned to
108 two or more pairs. These 21 sires were considered unrelated in the additive relationship matrix. Among
109 the 812 G2 offspring, 615 (75.7%) could be assigned to a single parental pair. One G2 fish was not
110 assigned, and 197 were assigned to several parental pairs. These 198 fish were excluded from the
111 analysis.

112

113 *2.3. Selection of slaughtered fish and phenotyping*

114

115 The 2000 G2 fish were landed and controlled in April 2004, October 2004 and April 2005. In April 2005,
116 445 of the 615 uniquely assigned fish were still alive. Unfortunately, many fish had mouth deformities.
117 Twenty six fish with strong mouth deformities (scores 2 and 3 in Kocour et al., 2006) were discarded.
118 Out of the remaining 419 fish, we eliminated 25, which were the only offspring of their sire, as they
119 have a very low interest for heritability estimation. The remaining fish were put back in the pond, and
120 harvested in October 2005.

121 A total of 331 fish, 218 without mouth deformities and 123 with mild mouth deformity (score 1 in
122 Kocour et al., 2006), were processed in November 2005 in the following way: fish were killed by hitting
123 on the head, and mean muscle percent fat was evaluated by Torry Fish Fatmeter®. The percent fat value
124 was the mean of our measurements on the left side of fish body performed evenly on the whole surface
125 (two on the back part and two on the body cavity part). Although we did not estimate the repeatability
126 of the fat meter values, the correlation between each of the four measurements on the same fish ranged
127 from 0.77 to 0.87. Additionally, the estimated correlation between the mean percent fat and a chemical
128 measurement of fillet fat content on 92 randomly sampled fish was 0.62. After the fat percent evaluation
129 the fish were measured for standard length, head length, (maximal) body height, (maximal) body width
130 and body weight. Then the scales were removed, and the fish were gutted and filleted. Gonads were
131 isolated and skin from both fillets was separated. The head was cut from the skeleton by a circular cut
132 in front of the pectoral fin girdle so that the fin girdle remained on the body (Gela and Linhart, 2000).
133 Finally, all different body parts were weighed to nearest 0.1 g. The following traits, important in
134 common carp culture, were calculated from the data:

135 1) Relative head length = head length / standard length

136 2) Relative body height = maximal height / standard length

137 3) Relative body width = maximal width / standard length

138 4) Percent processed body = (fillet weight + skin weight + weight of skeleton with remnants) / body
139 weight × 100

140 5) Percent fillets with skin = (fillet weight + skin weight) / body weight × 100

141 6) Percent fillets without skin = fillet weight / body weight × 100

142 Relative head length, relative body height and relative body width are traits describing body shape,
143 percent processed body and both percent fillets represent main edible parts. Percent fillets without skin is

144 a fundamental trait, as it represents pure flesh with intramuscular bones only. However, fillets without
145 skin are not yet the most demanded commodity on the market of common carp.

146

147 *2.4. Statistical analyses*

148

149 For each of the 331 G2 fish slaughtered, the G1 sire and the dam were unambiguously identified. For
150 280G2 fish, the G1 sire identified was itself unambiguously assigned to a G0 sire and dam. For 51 G2
151 fish, the G0 sire and dam were not identified, and therefore the pedigree was only one generation deep.
152 No adequate phenotypes were available for the G0 and G1 fish, and they were only used to complete the
153 pedigree. This practice resulted in a design with 264 full-sibs families produced from 92 sires and 8
154 dams, with an average full-sibs family size of 1.25 (range 1–5), an average paternal half-sibs family size
155 of 3.6 (range 2–11) and an average maternal half-sibs family size of 41.5 (range 29–52).

156 The pedigree was used together with the performance records and the fixed effects matrix to estimate
157 heritabilities and genetic correlations with VCE 5.1.2 (Kovac and Groeneveld, 2003). A multivariate
158 animal model included sex (male, female) and mouth deformity status (normal, deformed) as fixed
159 effects, and animal genetic factor as a random effect. Significance of fixed effects was assessed with a
160 single generation sire and dam model without interactions, using SAS®-Mixed procedure. Phenotypic
161 correlations were estimated using SAS® as Pearson correlation coefficients between the variables
162 tested, and their standard errors were estimated according to Sokal and Rohlf (1981).

163

164 **3. Results**

165

166 *3.1. Phenotypic data and fixed effects*

167

168 The fish were on average 1549 g (Table 1) with a coefficient of variation of 22% for body weight. Sex
169 had a significant effect on all traits except relative body height and percent fillet without skin. Females
170 were larger and fatter than males, and they had higher percent processed body and percent fillet with
171 skin. Percent fillet without skin displayed a pattern similar to fillet with skin, but the difference did not
172 reach statistical significance. This is likely because unequal skinning among individuals increases error

173 variance. Mouth deformities had a significant impact on all traits except relative head length and percent
174 processed body. Fish with deformed mouth were lighter, thinner and had lower fillet yields than normal
175 fish.

176

177 *3.2. Heritability estimates*

178

179 Heritabilities of the traits studied are listed in Table 2. Body weight, standard length, percent fat and
180 relative head length had high heritability (>0.5), relative body height, percent processed body and fillet
181 yields had medium heritability ($0.2-0.5$), and relative body width had low heritability (<0.2).

182

183 *3.3. Correlations between quantitative traits*

184

185 As usual there were very high genetic and phenotypic correlations between length and body weight
186 ($r_A=0.97$, $r_P=0.92$). Correlations between percent fillet with skin and without skin were also very high
187 ($r_A=0.96$, $r_P=0.87$), but interestingly the heritability of fillet yield with skin is almost twice as high as
188 that of fillet yield without skin (0.38 vs. 0.21). The rest of phenotypic correlations are mostly moderate
189 (below 0.5 in absolute value) except between yields. We found relatively high positive genetic
190 correlations between body size (standard length and body weight) and percent fat (0.71 and 0.59 ,
191 respectively), favourable correlations between body size and percent processed body (0.69 with standard
192 length and 0.74 with bodyweight) and body size and fillet yields ($0.50-0.77$). Genetic correlations
193 between body size and body shape (relative head length, relative body height and relative body width)
194 were weak to moderate. Relative head length seems quite informative, as it had strong negative
195 correlations (-0.7 to -0.9) with percent fat, percent processed body and percent fillet yields (Table 2).

196

197 **4. Discussion**

198

199 *4.1. Phenotypic data*

200

201 The fish reached commercial size in three growing seasons, as usual in the Czech Republic. The
202 phenotypic variation in fish body weight was within expected range, with a CV of 22%. Sex had a
203 significant effect on growth, but also on yields. The effect was especially important on percent processed
204 body (66.2% in males, 67.9% in females), mostly caused by the fact that more males than females mature
205 in the 3rd spring, giving a gonadosomatic index of 2.4% in males vs. 1.1% in females. Similar results
206 were found in the three summers old common carp by Kocour et al. (2005b) in a study comparing all
207 female and mixed sex populations. It shows one possible practical use of all-female populations at that
208 age in the local climate. However, this advantage of females disappeared at four-summer-old carps due
209 to female maturation leading to an increase of their gonadosomatic index (Kocour et al., 2005b).

210 As expected, there was a negative effect of mouth deformities on growth. This was already demonstrated
211 at earlier growth stages (Kocour et al., 2006) together with the fact that mouth deformities are brought
212 about essentially by (unidentified) environmental factors. Here, we assumed that the mouth deformity
213 had a purely environmental effect on the traits studied, which can be accounted for by its inclusion as a
214 fixed effect in the statistical model. The syndrome provoked by the mouth deformity was quite coherent
215 with a lower ability to feed. Deformed fish had lower bodyweight and length, lower percent muscle fat,
216 thinner body (lower relative body height) and lower fillet yields.

217

218 *4.2. Genetic parameters*

219

220 First of all, we would like to point out that due to the single batch rearing of the progenies from the
221 larval stage, genetic parameters are not likely to be strongly biased by common environmental effects.
222 Still, the heritability estimate obtained for bodyweight is high (0.70). All previous studies in common
223 carp have found lower estimates, between 0 and 0.48 (Nenashev, 1966; Nenashev, 1969; Nagy et al.,
224 1980; Smíšek, 1981; Tanck et al., 2001). Our previous heritability estimates for juvenile weight, which
225 was done on a sample of the G1 population, was also lower (0.30–0.33; Vandeputte et al., 2004). The
226 present dataset is small (331 fish) and this may be thought as a reason for lack of precision. Nevertheless,
227 the standard error estimate shows that the heritability of body weight clearly differs from zero.

228 The heritability of percent fat obtained using Torry Fish Fatmeter was also high (0.58), and in
229 accordance with what is seen in other species (0.55 in chinook salmon, Jopson et al., 2002; 0.36–0.72

230 in rainbow trout, Chevassus et al., 2002; 0.25 realized h^2 in rainbow trout, Quillet et al., 2005). This
231 high heritability shows that selection for increased or decreased lipid content is feasible. However, the
232 favourable direction for selection is not necessarily clear, as consumers may ask for less fat products,
233 but fat deposits may be an asset for overwintering survival in carp (Steffens, 1996). Two trait selection
234 for weight and lower fat content would also decrease the genetic gain to be obtained for grow thin carp,
235 as there is a positive genetic correlation (0.59) between percent fat and body weight. The heritability of
236 relative body height (0.32) is of similar magnitude to the realized heritability given by Ankorion et al.
237 (1992) (0.47 for upwards selection, 0.33 for downwards selection) and to an average 0.36 heritability of
238 body shape in rainbow trout (Kause et al., 2004). This confirms the ability to select for body shape in
239 common carp, which is also confirmed by the fact that another body shape parameter, the relative head
240 length, seems to be heritable ($h^2 = 0.54$).

241 Interestingly, percent processed body and fillet yields were heritable ($h^2 = 0.21-0.38$). This is in
242 accordance with data on other species ($h^2 = 0.45$ for gutted yield and 0.33 for fillet yield in rainbow trout,
243 Kause et al., 2002; 0.36 for gutted yield in rainbow trout, Gjerde and Schaeffer, 1989; 0.30 for fillet yield
244 in black sea bream, Doupe and Lymbery, 2005). The heritability of percent fillet with skin is higher than
245 that of percent fillet without skin (0.38 vs. 0.21), but the genetic correlation between the two is close to
246 unity (0.96). This is probably due to a lower repeatability of the fillet without skin due to variations in
247 the efficiency of skin removal. Percent fillet without skin is commercially more important trait. To
248 increase this trait, it would be however advisable to select on percent fillet with skin. These results show
249 the theoretical feasibility of selection for improved yields in common carp. However, because the
250 evaluation of fillet yield is lethal for breeding candidates, this implies that selection should be done on
251 the basis of slaughtering traits of their relatives. This practise would require identification of families,
252 either by separate rearing or by genotyping. In this context, the highly negative genetic correlation
253 between relative head length and fillet yield without skin (-0.86) is interesting, because relative head
254 length can easily be measured on the live breeding candidates. Moreover, relative head length is more
255 heritable than fillet yield, so for the same intensity, the relative response between indirect selection on
256 relative head length and direct selection on fillet yield should be $r \frac{1}{4} h_X r_{A\delta X}$; $Y_{Ph} Y_{1:37}$ (Falconer,
257 1960). Therefore, indirect selection for reduced relative head length should be effective in improving
258 fillet yield in common carp. Cibert et al. (1999), with more sophisticated morphometric analysis but

259 with a smaller sample size($n=42$) proposed that the best morphotype for fillet yield should have a lower
260 anterior dorsal height. It does not seem to be the case here, as both genetic and phenotypic correlations
261 between relative body height and fillet yields, although negative, are small and hardly different from
262 zero. One interesting point is the fact that genotypes with high fillet yield seems to have also high
263 muscular percent fat ($r_A=0.64$), despite a quite low phenotypic correlation ($r_P=0.20$). Therefore,
264 selection for increased fillet yield may also lead to fatter animals, which may or may not be an advantage
265 as already pointed out.

266 The genetic correlation between body weight and relative body height was weak (0.08), and the one
267 between body weight and relative body width was positive but moderate (0.34). Therefore, selection for
268 increased body weight should slowly change body shape towards more “rotund” fish, similar to what
269 was demonstrated in rainbow trout (Kause et al., 2003). If selection is undertaken on standard length,
270 the effects on shape should be even reduced ($r_A=0.18$ with relative body width and -0.14 with relative
271 body height). Additionally, rotund fish in common carp are not necessarily unwanted and may even
272 sometimes be specifically selected for. Finally, we would like to stress that although our results are
273 interesting as they are the first data on genetic parameters of processing and quality traits in the common
274 carp, they should be taken with care, because of the small sample size used. Moreover, there are many
275 strains of common carp, and these results are only valid for the HSM strain held at USB RIFCH,
276 Vodňany. We feel that the heritability estimated for body weight is very high, and not fully compatible
277 with previous estimations as well as the failure of mass selection for growth reported by Moav and
278 Wohlfarth (1976). Therefore, the current results should be validated by a selection experiment.

279

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281

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Table 1
Growth and processing traits of common carp at the end of the 3rd growing season ($n=331$), with effects of sex and mouth deformity

	Mean±S.D.	Sex effect			Mouth deformity effect		
		Male LS mean±S.E.	Female LS mean±S.E.	Sig. level	Normal LS mean±S.E.	Deformed LS mean±S.E.	Sig. level
Standard length	352.8±27.0	345.6±2.8	355.0±2.6	***	355.0±2.5	345.6±2.9	***
Body weight	1549±341.9	1449±35.1	1571±33.1	***	1602±32.1	1419±36.4	***
Mean % fat	5.20±1.91	4.57±0.20	5.58±0.19	***	5.38±0.19	4.77±0.21	***
Relative head length	0.292±0.015	0.289±0.002	0.294±0.001	***	0.293±0.001	0.291±0.002	NS
Relative body height	0.398±0.022	0.396±0.004	0.397±0.004	NS	0.400±0.003	0.394±0.004	**
Relative body width	0.204±0.011	0.202±0.001	0.200±0.001	*	0.205±0.001	0.201±0.001	***
% Processed body	67.2±2.2	66.2±0.2	67.9±0.2	***	67.1±0.2	67.0±0.2	NS
% Fillet with skin	41.1±2.2	40.6±0.2	41.4±0.2	**	41.2±0.2	40.7±0.2	*
% Fillet without skin	32.1±2.0	31.8±0.2	32.2±0.1	NS	32.3±0.2	31.7±0.2	*

*** $P<0.001$, ** $P<0.01$, * $P<0.05$, NS: not significant.

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Table 2
Heritabilities (bold, diagonal), genetic correlations (below diagonal) and phenotypic correlations (italics, above diagonal) for growth and processing traits in common carp after 3rd growing season ($n=331$)

	Standard length	Body weight	Mean % fat	Rel. head length	Rel. body height	Rel. body width	% Processed body	% Fillet with skin	% Fillet without skin
Standard length	0.69 ± 0.10	<i>0.92 ± 0.02</i>	<i>0.34 ± 0.05</i>	<i>-0.18 ± 0.05</i>	<i>-0.17 ± 0.05</i>	<i>-0.03 ± 0.06</i>	<i>0.35 ± 0.05</i>	<i>0.46 ± 0.05</i>	<i>0.42 ± 0.05</i>
Body weight	<i>0.97 ± 0.01</i>	0.70 ± 0.08	<i>0.40 ± 0.05</i>	<i>-0.05 ± 0.06</i>	<i>0.15 ± 0.05</i>	<i>0.28 ± 0.05</i>	<i>0.35 ± 0.05</i>	<i>0.43 ± 0.05</i>	<i>0.41 ± 0.05</i>
Mean % fat	<i>0.71 ± 0.16</i>	<i>0.59 ± 0.14</i>	0.58 ± 0.09	<i>-0.14 ± 0.05</i>	<i>-0.01 ± 0.06</i>	<i>0.17 ± 0.05</i>	<i>0.20 ± 0.05</i>	<i>0.31 ± 0.05</i>	<i>0.20 ± 0.05</i>
Relative head length	<i>-0.36 ± 0.12</i>	<i>-0.26 ± 0.12</i>	<i>-0.82 ± 0.15</i>	0.54 ± 0.12	<i>0.42 ± 0.05</i>	<i>0.39 ± 0.05</i>	<i>-0.09 ± 0.05</i>	<i>-0.25 ± 0.05</i>	<i>-0.23 ± 0.05</i>
Relative body height	<i>-0.14 ± 0.17</i>	<i>0.08 ± 0.11</i>	<i>-0.63 ± 0.08</i>	<i>0.53 ± 0.11</i>	0.32 ± 0.06	<i>0.74 ± 0.04</i>	<i>0.02 ± 0.06</i>	<i>-0.15 ± 0.05</i>	<i>-0.11 ± 0.05</i>
Relative body width	<i>0.18 ± 0.23</i>	<i>0.34 ± 0.11</i>	<i>-0.14 ± 0.18</i>	<i>0.18 ± 0.21</i>	<i>0.62 ± 0.12</i>	0.15 ± 0.05	<i>0.00 ± 0.06</i>	<i>-0.11 ± 0.05</i>	<i>-0.08 ± 0.05</i>
% Processed body	<i>0.69 ± 0.12</i>	<i>0.74 ± 0.12</i>	<i>0.66 ± 0.15</i>	<i>-0.75 ± 0.13</i>	<i>0.00 ± 0.17</i>	<i>0.10 ± 0.22</i>	0.28 ± 0.06	<i>0.63 ± 0.04</i>	<i>0.54 ± 0.05</i>
% Fillet with skin	<i>0.77 ± 0.10</i>	<i>0.73 ± 0.11</i>	<i>0.76 ± 0.10</i>	<i>-0.83 ± 0.08</i>	<i>-0.14 ± 0.16</i>	<i>0.00 ± 0.22</i>	<i>0.79 ± 0.13</i>	0.38 ± 0.09	<i>0.87 ± 0.03</i>
% Fillet without skin	<i>0.50 ± 0.19</i>	<i>0.60 ± 0.16</i>	<i>0.64 ± 0.11</i>	<i>-0.86 ± 0.05</i>	<i>-0.07 ± 0.16</i>	<i>-0.14 ± 0.21</i>	<i>0.75 ± 0.18</i>	<i>0.96 ± 0.04</i>	0.21 ± 0.07

All estimates given±standard error.

371