INDIVIDUAL VARIATION IN GROWTH PERFORMANCE
AND HETEROZYGOSITY OF ATLANTIC SALMON

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SUMMARY

The aim of this paper is to present and review published data on individual variation in growth, growth efficiency and protein turnover in fish. Individual fish which have lower rates of protein turnover tend to have higher growth efficiencies. It has been proposed that this relates to a reduction in the comparatively high energetic costs of protein turnover. Data is also presented on the relationships between individual heterozygosity and indicators of growth performance in Atlantic salmon. Six heterozygous loci were screened in farmed Atlantic salmon for which there was information on growth and growth efficiency. At high rations growth and growth efficiency were not significantly correlated with individual heterozygosity. At low rations there were indications that individual heterozygosity was negatively correlated with growth efficiency (P < 0.02), protein synthesis and protein degradation.

INTRODUCTION

The intensive culture of salmonid species such as Atlantic salmon (Salmo salar), Arctic char (Salvelinus alpinus), Pacific salmon (e.g. Oncorhynchus kisutch) and rainbow trout (O. mykiss) is comparatively recent. However, several commercial strains are identified for each of these species and in most cases a fast growth rate has been the main characteristic used for selection (Gjedrem 1983; Hershberger et al. 1990). There has been some investigation into the physiological and genetic basis of differences between strains. For example, different strains of rainbow trout show differences in the efficiency of utilisation of dietary protein for growth (Austreng and Refstie 1979; Ming 1985). Enzyme heterozygosity (e.g. Ferguson, 1990; Nakajima et al. 1991) and the presence of specific alleles (e.g. Grobler et al. 1992; Torrissen and Shearer 1992; Jordan et al. 1990) have also been linked to differences in phenotypic indicators of growth performance. Individual differences in protein turnover are correlated with heterozygosity in the mussel (Mytilus edulis) (Hawkins et al. 1989).

Individual differences in growth have been investigated in fish held in groups and recently research has focused on individual differences in growth efficiency and protein turnover (e.g. Carter et al. 1992a, 1992b, 1993a, 1993b; McCarthy et al. 1994). The use of X-radiography (Talbot and Higgins 1983) to measure individual rates of feed consumption by fish held in groups has been an important development (reviewed by McCarthy et al. 1993). It is apparent that feed consumption rates vary between individual fish. As would be expected, most of the variation in growth rate relates to the variation in feed consumption rate (Carter et al. 1992a, 1992b, 1993a, 1993b; McCarthy et al. 1994). However, some fish, apparently consuming a similar amount of feed, have different growth rates and therefore different growth efficiencies. The physiological basis of these differences has been investigated in relation to protein turnover. An aim of this paper is to summarise our findings on the relationships between individual variation in protein turnover and growth efficiency of fish. A second aim is to present some preliminary
data on genetic variation in individual Atlantic salmon (Carter and Pringle unpublished) for which information on growth rates, growth efficiency and protein turnover is also available. This analysis is the final part of a study on Atlantic salmon in which the physiological basis of individual variation in growth and growth efficiency was investigated (Carter et al. 1993b, 1994a; Thompson 1993).

MATERIALS AND METHODS

Measurement of feed consumption, growth and growth efficiency

The details of the experiment are given by Carter et al. (1993b, 1994a). Briefly, seven groups of 25 Atlantic salmon (95.8 ± 1.4 g) were held in 4500-l tanks supplied with fresh seawater at a rate of 40 l/min. Six groups were fed one of three feeds (C1, C2, C3) at a ration at 25 mg dry feed per g wet weight fish per day (mg / g / d) for 76 days. The seventh group was fed a low ration of C1 of 12.5 mg / g / d. Towards the end of the experiment a further 20 fish were starved for 20 days. Feed consumption rates were measured using X-radiography after a feed containing radio-opaque glass beads (2% by weight) had been substituted for the normal feed. Carcasses were analysed for dry material and protein and growth rate was calculated as specific growth rate for wet weight or protein. Growth efficiency was calculated as the proportion of consumed dry material or protein which was retained as wet weight growth or protein growth.

Measurement of physiological variation

Rates of protein synthesis were calculated following a flooding dose of L-[2,6-3H] phenylalanine (Garlick et al. 1983). All fish were fed C1, 10 fish from the low ration and 10 from the high ration groups were used. Protein turnover was investigated in whole body samples in relation to fractional rates (% / d) of protein consumption (kr), growth (kg), synthesis (ks) and degradation (kd); RNA activity (mg RNA / g protein) and RNA capacity (g protein synthesised / g RNA / d); efficiency of anabolic stimulation (ks / kr, %), protein growth (kg / kr, %) and synthesis retention (kg / ks, %) (Carter et al. 1993b).

Measurement of genetic variation

The following 6 heterozygous loci were screened in 181 fish according to Pringle (1995): aspartate aminotransferase (AAT; EC 2.6.1.1); L-idol dehydrogenase (IDDH; EC 1.1.1.14); isocitrate dehydrogenase (IDH; EC 1.1.1.42); lactate dehydrogenase (LDH; EC 1.1.1.27); malic enzyme (ME-2; 1.1.1.40); superoxide dismutase (SOD; EC 1.15.1.1). The number of heterozygous loci were summed for each fish (No. heterozygous loci / fish) and could have ranged between 0 and 6. The relationship between the number of heterozygous loci and selected physiological variables was investigated by calculation of the Pearson correlation coefficient (Ferguson 1990).

RESULTS

Heterozygous loci

The salmon were taken from the stock of a commercial salmon farm, Otter Ferry Salmon Ltd., Argyll. The farm had an established stock and a brood stock program; the farm acted as a supplier of salmon eggs to other salmon farms.
Table 1. The mean (±sd) feed consumption, growth and growth efficiency of Atlantic salmon fed the same feed at the same group ration and divided according to the number of heterozygous loci / fish. Means compared by ANOVA.

<table>
<thead>
<tr>
<th>No. heterozygous loci / fish</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>consumption (mg/g/d)</td>
<td>0.90 ± 0.12</td>
<td>0.89 ± 0.09</td>
<td>0.91 ± 0.10</td>
<td>0.84 ± 0.13</td>
<td>0.70</td>
<td>0.56</td>
</tr>
<tr>
<td>growth (%)</td>
<td>7.11 ± 1.63</td>
<td>6.89 ± 1.32</td>
<td>6.71 ± 1.73</td>
<td>6.49 ± 1.18</td>
<td>0.24</td>
<td>0.87</td>
</tr>
<tr>
<td>growth efficiency (%)</td>
<td>125 ± 24</td>
<td>128 ± 26</td>
<td>138 ± 38</td>
<td>129 ± 34</td>
<td>0.34</td>
<td>0.80</td>
</tr>
<tr>
<td>number of fish</td>
<td>6</td>
<td>19</td>
<td>13</td>
<td>7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The proportion of salmon which were heterozygous differed at each loci: iddh-2, 40.9%; Idh-4, 16.0%; aat-4, 13.8%; sod, 13.8%; idh-4, 2.8%; me-2, 48.1%. The proportions of the 181 salmon with 0, 1, 2, 3, 4, 5 or 6 heterozygous loci were 21.0%, 39.8%, 23.4%, 12.7%, 1.1%, 0% and 0%, respectively. Feed consumption, growth and growth efficiency of salmon fed the same feed (C1) at the same group ration were not significantly different for salmon with different numbers of heterozygous loci (Table 1). The low and high ration groups were analysed separately. There were no significant correlations between individual heterozygosity and growth for either ration group or for growth efficiency (P > 0.05) for the high ration group. The correlations between individual heterozygosity and growth efficiency was significant (r = -0.547; n = 20; p < 0.02).

Of the 20 fish for which protein turnover was measured 7, 6, 4, 2 and 1 fish were heterozygous at 0, 1, 2, 3 and 4 loci, respectively. There were no significant correlations between indices of protein turnover and the number of heterozygous loci / fish (Table 2). However, the trends suggested that at high rations protein growth and growth efficiency decreased with increasing heterozygosity. At low rations the negative correlations between heterozygosity and protein synthesis and degradation were approaching significance and suggested that the more heterozygous individuals had lower rates of synthesis and degradation under these conditions.
Table 2. The Pearson correlation coefficient ($r = 0.632$ significant at 5 % level) between number of heterozygous loci / fish and indices of protein turnover for Atlantic salmon ($n = 10$).

<table>
<thead>
<tr>
<th>Indices of protein turnover</th>
<th>Pearson correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>low ration</td>
</tr>
<tr>
<td>protein consumption (kr)</td>
<td>0.370</td>
</tr>
<tr>
<td>protein growth (kg)</td>
<td>-0.082</td>
</tr>
<tr>
<td>protein synthesis (ks)</td>
<td>-0.622</td>
</tr>
<tr>
<td>protein degradation (kd)</td>
<td>-0.631</td>
</tr>
<tr>
<td>RNA capacity</td>
<td>0.072</td>
</tr>
<tr>
<td>RNA activity</td>
<td>-0.367</td>
</tr>
<tr>
<td>protein growth efficiency</td>
<td>-0.149</td>
</tr>
<tr>
<td>anabolic stimulation</td>
<td>-0.477</td>
</tr>
<tr>
<td>synthesis retention efficiency</td>
<td>0.385</td>
</tr>
</tbody>
</table>

DISCUSSION

It has been proposed that more heterozygous individuals are metabolically more efficient than homozygous individuals (Koehn and Shumway 1982). The basis of the argument is that heterozygous individuals have lower maintenance costs and can therefore partition a greater proportion of consumed energy into growth (Danzmann et al. 1987). However, in the present study the negative correlations between individual heterozygosity and growth and growth efficiency suggested that increasing heterozygosity did not result in increased growth. This trend was apparent in all groups (i.e. low and high rations: wet weight and protein growth) but only significant in some. Ferguson (1990) measured variation at 9 heterozygous loci in rainbow trout and found that there was a significant negative regression between heterozygosity and size when high rations were fed but not when low rations were fed. Individual heterozygosity was negatively correlated with protein synthesis in the mussel (Hawkins et al. 1989) although the relationship was very weak ($r = -0.192; n = 60; P < 0.20$). A similar trend was observed in this study for Atlantic salmon fed a low group ration but not for those fed a high group ration.

Table 3. The relationships between fractional rates of protein consumption and protein growth as described by the model $Y = a + bX$.

<table>
<thead>
<tr>
<th>Species</th>
<th>a</th>
<th>b</th>
<th>$R^2$</th>
<th>P</th>
<th>reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass carp</td>
<td>-0.291</td>
<td>0.338</td>
<td>0.66</td>
<td>&lt;0.001</td>
<td>Carter et al. 1993a</td>
</tr>
<tr>
<td>Atlantic salmon</td>
<td>-0.186</td>
<td>0.306</td>
<td>0.67</td>
<td>&lt;0.001</td>
<td>Carter et al. 1993b</td>
</tr>
<tr>
<td>Rainbow trout</td>
<td>-0.347</td>
<td>0.366</td>
<td>0.74</td>
<td>&lt;0.001</td>
<td>McCarthy et al. 1994</td>
</tr>
</tbody>
</table>

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Individual variation in growth rates is apparent in groups of cultured fish and has been termed growth depensation. The causes of growth depensation has long been the subject of research (reviewed by McCarthy et al. 1993). The measurement of individual feed consumption rates has enabled the variation in growth to be related to the variation in feed consumption. The simple linear models (shown to be better than curvi-linear models) demonstrate that variation in feed consumption accounts for the majority of variation in growth rates (Table 3).

Individual variation in protein turnover has a significant effect on growth efficiency. The cost of protein turnover is comparatively high and protein synthesis can account for 15% of the energy intake of a fish (Houlihan et al. 1995). Costs associated with degradation have not been determined but they are likely to be significant (Hawkins et al. 1989; Houlihan et al. 1995). Fish which are inefficient at retaining synthesised protein will, therefore, incur increased energetic costs compared with more efficient individuals. Negative correlations between protein turnover (protein degradation) and growth efficiency have been demonstrated in grass carp and rainbow trout (Table 4) as well as for poultry (Tomas et al. 1991) and mussels (Hawkins et al. 1989). A positive correlation has been observed between the efficiency of retention of synthesised protein and growth efficiency in grass carp and Atlantic salmon (Table 4).

Table 4. Relationships between growth efficiency (kg/kr) and protein turnover (kt) or synthesis retention efficiency (kg/ks) for different species.

<table>
<thead>
<tr>
<th>Species</th>
<th>correlation</th>
<th>r, correlation coefficient</th>
<th>P</th>
<th>reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass carp</td>
<td>kt vs kg/kr</td>
<td>-0.67</td>
<td>&lt;0.01</td>
<td>Carter et al. 1993a</td>
</tr>
<tr>
<td></td>
<td>kg/ks vs kg/kr</td>
<td>0.73</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Atlantic salmon</td>
<td>kg/ks vs kg/kr</td>
<td>0.50</td>
<td>&lt;0.05</td>
<td>Carter et al. 1993b</td>
</tr>
<tr>
<td>Rainbow trout</td>
<td>kt vs kg/kr</td>
<td>-0.77</td>
<td>&lt;0.001</td>
<td>McCarthy et al. 1994</td>
</tr>
</tbody>
</table>

These observations have been made for individuals grown for comparatively short periods of time (1 to 3 months). The next step is to examine whether individual differences in protein turnover are maintained over long periods which equate to complete production cycles. These questions require the development of new techniques such as the use of stable isotopes to measure protein synthesis several times on the same fish (Carter et al. 1994b).

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