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A morphometric study on four land-locked salmonid species

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Lakes in Vuoksi drainage area in eastern Finland are inhabited by four salmonid species: the grayling (*Thymallus thymallus*), the Atlantic salmon (*Salmo salar* m. *sebago*), the brown trout (*Salmo trutta* m. *lacustris*), and the arctic charr (*Salvelinus alpinus*). We studied second-generation hatchery-reared juveniles of these freshwater salmonids from two age groups: (0+)-year-old fish, and (1+)-year-old fish; and compared their morphology in order to assess both intra- and interspecific variation in morphometric characters, and changes associated with growth. We observed that the (0+)-year-old salmonids are morphologically very similar, but as they grow, the interspecific differences become more pronounced. The characters that best discriminate among the studied species are body height and head dimensions as well as pectoral fin length. The grayling and the arctic charr are streamlined, whereas the salmon and the brown trout are more robust in their body shape. The shape of the studied species reflects also their adaptation to their native habitats.

1. Introduction

We compared the morphology (i.e., selected morphometric characters) of four land-locked freshwater salmonid species: the grayling (*Thymallus thymallus*), the Atlantic salmon (*Salmo salar* m. *sebago*), the brown trout (*Salmo trutta* m. *lacustris*), and the arctic charr (*Salvelinus alpinus*), that all live in lakes of Vuoksi drainage area in eastern Finland. The salmon and the brown trout are anadromous freshwater species that reproduce in rivers or rapids, where the juveniles spend their first years of life. The arctic charr and the studied grayling stock live and reproduce in lakes (there are also river-reproducing stocks of the grayling), and the juveniles spend their first summer in the littoral area. All the species spawn in autumn except the grayling, that spawns in spring, but the eggs of all these species hatch in spring. They all thrive in cool or cold, clean, well-oxygenated water, but due to waterway constructions, and other man-made changes in their native environment as well as overfishing these species have became locally endangered. Phylogenetically salmonids are con-

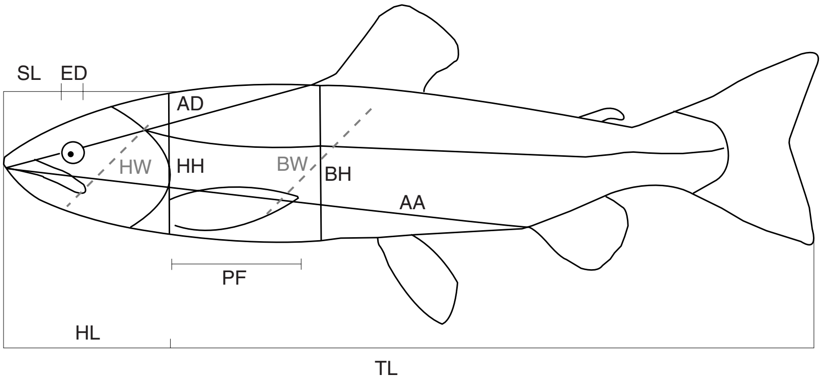

Fig. 1. The measurements taken from the salmonids: TL = total length of the fish, BH = body height, HL = head length, HH = head height, SL = snout length, HW = head width, ED = eye diameter, BW = body width, PF = pectoral fin length, AD = anterodorsal length, and AA = anteroanal length.

sidered primitive teleost fishes (Wootton 1990), and the study species share certain common characteristics, for example, relatively late maturation age that is one reason contributing to the decline of many stocks. Therefore hatchery-rearing is extensive, and cultured fish are continuously restocked to their original environment.

In the present study, we wanted to find out which morphometric characters best discriminate amongst juveniles of these salmonid species. We were also interested in inter- and intraspecific morphometric changes associated with growth, and therefore we studied two age groups. We also wanted to study to what extent morphometric attributes of a fish species reflect its adaptation to the environment.

2. Materials and methods

The study specimens were second-generation hatchery-reared juvenile salmonids: the grayling, salmon, brown trout, and arctic charr. We studied two age groups, (0+)-year-old and (1+)-year-old fish. Sample sizes are given in Appendix 1. Both studied age groups originated from the same populations, that represent the maximum genetic variation of parental hatchery stocks. (0+)-year-old fish were sampled in June–July 1996 and (1+)-year-old fish in March 1997.

The study specimens were sampled randomly from hatchery basins, each species having their own basin. After catching, they were killed with an overdose of anaesthetic agent (MS-222, tricaine methanesulphonate), and then frozen in a small amount of water and preserved at –18°C. All the fish were weighed (0.01 g) immediately after thawing. Subsequently, larger fish ((1+)-year old) were measured with electrical callipers (0.01 mm), whereas, smaller fish ((0+)-year-old) were measured with the same instrument but after about 24-hour fixing in 70% ethanol; otherwise they would have been too soft and difficult to handle. Altogether 11 morphometric characters per fish were measured, and all the measurements were taken from the left side of the fish. To reduce measurement bias, all the individuals were measured by S. Pakkasmaa in a randomised order. The measured characters reflected body form, size and placement of the fins as well as the eye position, and they were chosen to represent those of ecological importance according to the studies of Parmanne (1990) and Sandlund *et al.* (1992). The characters (Fig. 1) were the total length of the fish (TL), the body height (BH) in front of the dorsal fin, the head length (HL) from the snout tip to the operculum edge, the head height (HH) at the operculum edge, the snout length (SL) from the snout tip to the eye edge, the head width (HW) behind the eyes, the eye diameter (ED) measured horizontally, the body width (BW) in front of dorsal fin, the pectoral fin length (PF), the anterodorsal length (AD) from the snout tip to the base of the first fin ray of the dorsal fin, and the anteroanal length (AA) from the snout tip to the base of the first fin ray of the anal fin (Appendix 1).

Multivariate methods were applied in the data analyses. They offer the advantage of taking into account all the variables in a single analysis, and therefore, it is possible to assess intraspecific variation between the age groups as well as interspecific variation. Because of differences in size (TL), we found it reasonable to use size-adjusted values in data analyses. Thus, the first step in analysing the data was to calculate linear regressions against TL of the fish for all the other measured characters. This method effectively removed allometric variation due to differences in fish size. The standardised regression residuals were then applied in statistical analyses. First, we made the principal component analysis (PCA) to create uncorrelated principal components from the original variables. Note that despite the residual technique used, variables that are highly correlated still remained, thus making the multivariate analyses feasible. PCA was based on the correlation matrices (Table 1). The data were further analysed with discriminant analysis exploring the variables most useful for discriminating amongst the species and the age groups. Also the discriminant analysis was computed from regression residuals.

Table 1. Correlations between size-adjusted morphological variables in the 0+ and 1+ age groups of the four studied species (correlations are truncated to three digits; TL = total length of the fish, BH = body height, HL = head length, HH = head height, SL = snout length, HW = head width, ED = eye diameter, BW = body width, PF = pectoral fin length, AD = anterodorsal length, and AA = anteroanal length).

	BH	HL	HH	SL	HW	ED	BW	PF	AD
Grayling 0+									
HL	0.03								
HH	0.41	–0.04							
SL	0.39	0.00	0.16						
HW	0.51	0.30	0.31	–0.01					
ED	0.04	0.06	0.10	0.00	0.17				
BW	0.35	0.23	0.23	0.13	0.50	0.02			
PF	–0.31	0.08	–0.20	–0.38	–0.06	0.10	–0.08		
AD	0.00	0.17	0.28	–0.24	0.17	0.27	0.25	0.28	
AA	–0.03	–0.28	0.29	0.08	–0.10	0.11	0.03	–0.14	0.09
Grayling 1+									
HL	0.35								
HH	0.77	0.42							
SL	0.19	0.12	–0.00						
HW	–0.17	0.18	–0.12	–0.23					
ED	–0.47	–0.09	–0.11	–0.38	0.56				
BW	0.59	0.23	0.21	0.17	–0.00	–0.49			
PF	0.19	0.18	0.38	0.03	–0.10	0.06	–0.08		
AD	–0.41	0.19	–0.06	–0.38	0.42	0.61	–0.63	–0.09	
AA	0.16	–0.22	0.12	0.29	–0.38	–0.46	0.35	–0.22	–0.31
Salmon 0+									
HL	0.25								
HH	0.72	0.34							
SL	0.17	0.33	0.22						
HW	0.16	0.14	0.41	0.35					
ED	0.30	0.38	0.53	0.37	0.52				
BW	–0.08	0.30	0.08	0.31	0.64	0.42			
PF	0.27	0.13	0.26	0.15	0.50	0.45	0.54		
AD	0.28	0.52	0.30	0.25	0.27	0.38	0.41	0.22	
AA	0.13	0.07	0.08	0.14	–0.15	0.02	–0.35	–0.27	–0.08
Salmon 1+									
HL	–0.52								
HH	0.83	–0.41							
SL	–0.16	0.09	–0.17						
HW	–0.76	0.66	–0.55	0.13					
ED	–0.81	0.65	–0.62	0.07	0.80				
BW	0.83	–0.24	0.87	–0.02	–0.49	–0.58			
PF	–0.48	0.16	–0.34	0.30	0.41	0.42	–0.32		
AD	–0.01	–0.10	–0.27	–0.07	–0.00	0.11	–0.25	0.22	
AA	–0.17	0.07	0.01	–0.43	0.13	0.29	–0.12	0.09	–0.02
Brown trout 0+									
HL	0.23								
HH	0.58	0.34							
SL	0.06	0.22	0.12						
HW	0.12	–0.28	0.09	–0.08					
ED	–0.13	0.25	–0.11	–0.02	–0.35				
BW	–0.01	–0.20	–0.11	0.10	0.63	–0.22			
PF	0.06	–0.03	0.07	–0.01	0.12	–0.03	0.20		
AD	0.35	0.07	0.08	0.02	0.08	0.02	0.02	–0.19	
AA	0.31	0.13	0.43	0.07	0.12	–0.14	0.04	0.10	0.05

Continues

Table 1. Continued.

	BH	HL	HH	SL	HW	ED	BW	PF	AD
Brown trout 1+									
HL	–0.02								
HH	0.72	0.27							
SL	0.64	0.24	0.73						
HW	0.13	–0.14	0.00	0.14					
ED	–0.41	–0.08	–0.33	–0.48	–0.22				
BW	0.59	0.10	0.58	0.38	–0.23	–0.28			
PF	–0.28	0.12	–0.27	–0.22	–0.52	0.19	0.18		
AD	0.27	0.41	0.28	0.43	–0.14	–0.07	0.23	0.21	
AA	0.34	–0.14	0.22	0.37	0.49	–0.31	0.16	–0.23	0.13
Arctic charr 0+									
HL	0.30								
HH	0.69	0.48							
SL	0.15	0.49	0.37						
HW	–0.01	0.47	0.39	0.42					
ED	0.00	0.23	0.36	0.10	0.02				
BW	–0.05	0.36	0.31	0.01	0.39	0.34			
PF	–0.07	–0.04	–0.03	–0.25	–0.07	0.13	0.06		
AD	0.47	0.48	0.22	0.26	0.32	–0.05	0.03	–0.04	
AA	0.04	0.12	0.26	–0.16	0.14	0.15	0.09	–0.03	0.37
Arctic charr 1+									
HL	0.26								
HH	0.62	0.54							
SL	0.24	0.38	0.26						
HW	0.00	0.38	0.19	0.20					
ED	–0.06	0.04	–0.05	–0.14	0.60				
BW	0.05	0.10	0.23	0.23	0.36	0.41			
PF	–0.50	–0.04	–0.29	0.01	0.07	0.11	–0.16		
AD	0.60	0.26	0.11	0.35	–0.14	–0.22	–0.26	–0.21	
AA	0.17	0.34	–0.13	0.38	–0.00	0.16	–0.00	–0.09	0.49

3. Results

We considered principal components with eigenvalues higher than 1.00 of importance (e.g., Chatfield & Collins 1983). According to this criterion, three components remained, explaining about 70% of the variation of the original size-adjusted body-morphology variables (Table 2). The first component was composed mainly of the head and body heights as well as the pectoral fin lenght. We interpret PC1 pooling characters associated with the swimming ability of the fish. The second component consisted of the head and body widths, as well as the eye diameter, characters associated with both feeding and swimming. The third component consisted of the head and snout lengths, characters of importance in foraging.

The first principal component (PC1) clearly separates the grayling from the rest of the studied salmonid species, but also the arctic charr appears to differ from the two *Salmo* species (Fig. 2). The grayling and arctic charr have shallower head and body than the salmon and brown trout, but the salmon and brown trout have relatively larger pectoral fins.

The second principal component (PC2) differentiates the arctic charr from the other species. It has narrower body and head, and smaller eyes than the three other species. Also the 1+ salmon differ from the 1+ brown trout in PC2. Finally, despite that the PC3 characterises weakly the four species, 1+ age groups of the brown trout and arctic charr differ from 1+ age groups of the grayling and salmon by having — in terms of body shape — longer snout and head than the others. Interestingly enough, on the three principal components the two age groups of each species are clearly different (Fig. 2; with the exception of salmon on the PC2).

We used discriminant analysis (DCA) to look for, in more detail, the body-shape variables which are most explicitly differentiating amongst the four salmonid species in the two age groups. The DCA was based on the correlation matrix of the size-adjusted variables, thus giving equal weight for variation in all variables (Table 3).

Jack-knifed classification resulted in a very high degree of correct classifications, in other words, how large percentage of the species and the age groups retained their grouping status upon applying the DCA-based classification functions (Table 4). Most often (6 out of 9 cases) the miss-classified fish ended up in a wrong age group within a species. Thus, the obtained discriminant functions are very powerful in identifying the species and age groups. Note, however, that the functions emphasise differently the body-shape variables than the principal component analysis does (Table 3).

The three discriminant functions reveal an interesting feature: in the early phase of their life ((0+)-year old) the studied species closely resemble each other as shown by the discriminant scores near the origin in all pairwise plots of the DC1–DC3 (Fig. 3). When the fish grow ((1+)-year old) they begin to differentiate more in body shape.

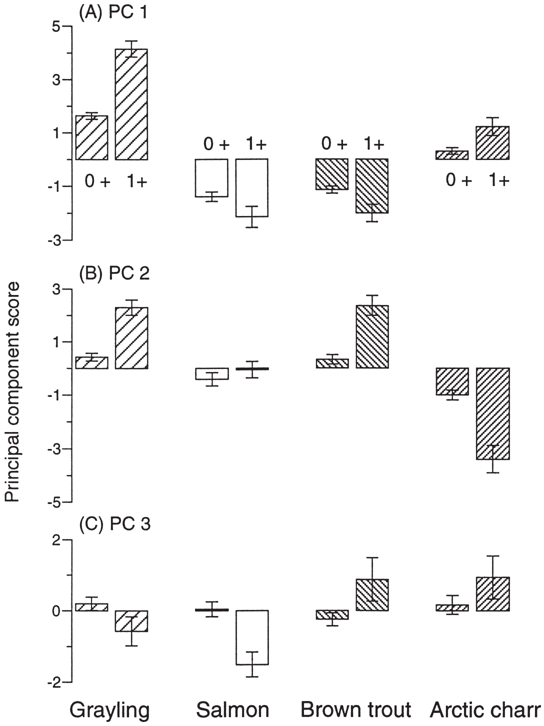

Fig. 2. Species and age group specific principal component scores (mean with 95% confidence limits) for the four salmonid species studied. For identification of the principal components, *see* Table 2).

The first discriminant function is positively correlated with the size of the pectoral fin, and it is good in telling apart a grayling from the other

Table 2. Principal component analysis for both age groups. PCA was computed from correlation matrix using regression residuals as the initial variables. The PCA loadings are listed together with the variable correlations (*r*) with the component scores. The variables are arranged after their principal component loadings; the highest component loadings are indicated with boldface.

Component	PC1	*r*	PC2	*r*	PC3	*r*
Head height	**–0.455**	0.844	0.243	0.381	0.070	0.074
Pectoral fin	**–0.438**	–0.814	–0.100	–0.157	–0.249	–0.266
Body height	**–0.435**	–0.808	0.264	0.413	–0.001	–0.001
Body width	–0.225	–0.418	**0.466**	0.729	–0.129	–0.137
Head width	–0.162	–0.302	**0.439**	0.687	0.200	0.213
Eye diameter	0.178	0.331	**0.400**	0.626	–0.035	–0.038
Anteroanal length	0.305	0.567	**0.381**	0.596	0.196	0.209
Snout length	0.210	0.390	0.130	0.203	**0.610**	0.650
Head length	–0.257	–0.477	–0.179	–0.281	**0.592**	0.631
Anterodorsal length	–0.313	–0.581	–0.308	–0.483	**0.334**	0.356
Eigenvalues	3.45	2.49	1.14			
% of variance	34.5	24.5	11.4			
Cumul. % of var.	34.5	59	70.3			

species in both age groups (Fig. 3A). In this respect, both age groups of the arctic charr and brown trout appear similar, but the older salmon are different from them.

The second function clearly separates the arctic charr from the other studied species, indicating that it has a shallower body and smaller eyes than the other species. The third function, on its part, reflects head dimensions, and in that respect the brown trout differs from the others having a relatively shorter and larger head. One should note that the first discriminant function explains 63% of the variation in body shape, the second about 25%, and the third only about 10%.

4. Discussion

The existence of variation is a principal issue in evolutionary ecology (e.g., Futuyma 1986). In fish, there is a clear relationship between the form and function (Robinson & Wilson 1996); morphology reflects an adaptation to the habitat and feeding niche of a species (e.g., Wootton 1990).

Table 3. Canonical discriminant functions (DC), standardised by within variances, and correlations (*r*) with the size-adjusted body shape variables. Eigenvalues, canonical correlations and cumulative variance explained is indicated with some basic statistics of the discrimination. Largest coefficients (absolute values) for each variable are indicated in bold, the variables are arranged in decreasing order of the coefficients on each discriminant function.

	DC1	*r*	DC2	*r*	DC3	*r*
Pectoral-fin length	**0.793**	0.292	0.383	0.025	–0.368	0.165
Anteroanal length	**–0.310**	–0.276	0.142	0.221	0.208	–0.060
Body width	**–0.161**	–0.037	0.052	0.306	0.035	0.122
Anterodorsal length	0.394	–0.087	**–0.860**	–0.198	0.292	0.066
Body height	0.135	–0.072	**0.570**	0.218	0.136	0.160
Eye diameter	–0.293	–0.224	**0.370**	0.197	0.254	–0.085
Head height	0.385	–0.120	–0.001	0.116	**0.622**	0.135
Head length	–0.048	–0.061	–0.029	–0.123	**–0.320**	–0.033
Head width	0.026	–0.188	0.109	0.213	**0.314**	–0.022
Snout length	–0.116	–0.087	–0.086	0.015	**–0.215**	–0.194
Eigenvalue	22.11		8.50		3.41	
Canonical correlation	0.977		0.946		0.879	
Cumulative variance explained (%)	63.0		88.3		98.5	

Wilks' $\lambda = 0.001$, $F_{70,1587} = 56.6$, $p < 0.0000$
Pillai's trace = 3.053, $F_{70,1939} = 21.4$, $p < 0.000$
Lawley-Hotelling trace = 33.5, $F_{70,1885} = 128.935$, $p < 0.000$.

Table 4. Jackknifed classification matrix for all the species and both age groups.

	G0+	G1+	S0+	S1+	Bt0+	Bt1+	Ac0+	Ac1+	%
Grayling 0+	53	0	0	0	0	0	0	0	100
Grayling 1+	0	21	0	0	0	0	0	0	100
Salmon 0+	0	0	40	1	2	0	1	0	91
Salmon 1+	0	0	0	21	0	0	0	0	100
Brown trout 0+	0	0	1	0	55	2	1	0	93
Brown trout 1+	0	0	0	0	1	20	0	0	95
Arctic charr 0+	0	0	0	0	0	0	48	0	100
Arctic charr 1+	0	0	0	0	0	0	1	20	95
Total	53	21	41	22	58	22	51	20	97

Morphological differences among coexisting species are considered to result from a divergent evolution to minimise competition by exploiting different resources (Ehlinger & Wilson 1988, Skúlason *et al.* 1989).

We studied juveniles of four freshwater salmonid species inhabiting lakes of Vuoksi drainage area in eastern Finland. We were interested in their morphometric characters: how do they differ between species, and between age groups of the same species. With multivariate statistics (PCA and DCA) we could identify the characters that best discriminated the studied species. Especially the head and body heights as well as the pectoral fin size appeared to differentiate the species. Those characters reflect the swimming ability of the fish.

The head and body widths as well as the eye diameter were also important in discriminating amongst the species. However, in this sense the brown trout and arctic charr appeared more similar than the salmon and grayling. The body width obviously also reflects the swimming ability of the fish. The eye diameter can also reflect the light conditions of where the fish is living. On the other hand, Finnish waters are often rather dark and humic, and light does not penetrate very deep (Ilmavirta 1990). Juvenile salmon and brown trout live in shallow rivers, where water is quite clear, and they have large eyes, whereas juveniles of the arctic charr inhabit shallow littoral areas, but have small eyes. Baumgartner *et al.* (1988) suggested that the eye size may as well be related to feeding behaviour.

The head morphology also reflects a species' feeding habits (Skúlason *et al.* 1989). The diets of juvenile salmonids are relatively similar, all of them feed mainly on zooplankton and benthic animals. The third principal component consisted of head dimensions, but it was rather a weak classificator, indicating that foraging habits of the studied salmonids are not very different. In 0+ age group, the species were almost similar, but in 1+ age group there was more differentiation. The brown trout and arctic charr had relatively longer head and snout as compared with the grayling and salmon. Elongated snout may also enhance the capture of small prey (Baumgartner *et al.* 1988).

Though all the studied species live in lakes in the same geographic area, their habitats are somewhat different. Arctic charr and grayling are lake-resident, and the juveniles live in the littoral area in still water. The brown trout and salmon, on the other hand, are anadromous migrating between the feeding habitat, i.e., lakes, and streams, in which their reproduction occurs. The adaptation to living in streams is reflected in their body morphology; they are relatively robust, having long

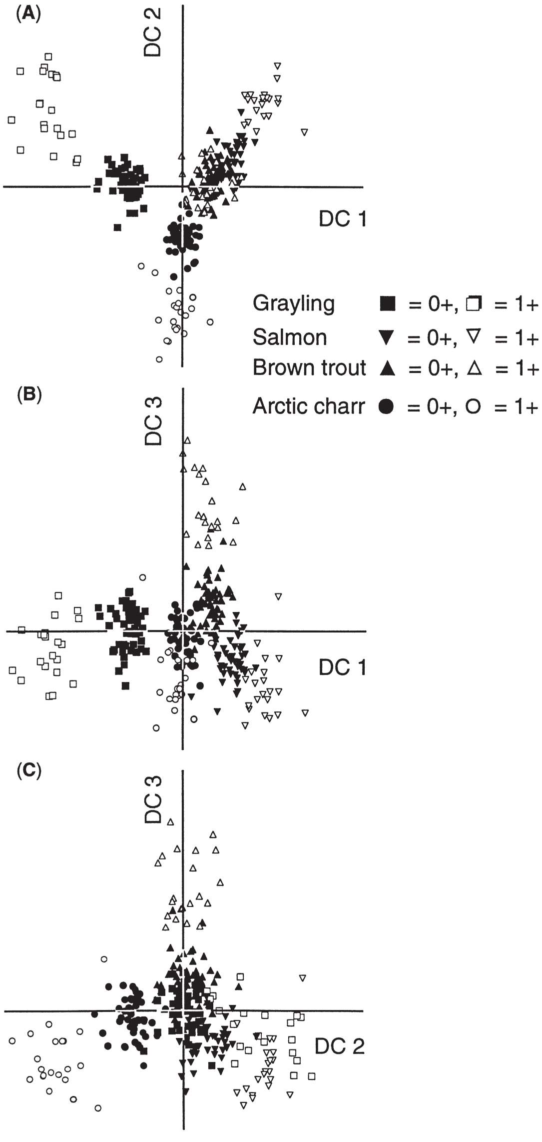

Fig. 3. Pairwise scatterplots of function loadings of the three discriminant functions (DC1–DC3, *see* Table 3 for details). The four species and the two age groups are plotted with different symbols. The axes go through the origin (range of DC 1 is from –15 to 15, from –10 to 10 for DC 2 and from –5 to 10 for DC 3).

pectoral fins. A deeper body improves burst swimming performance (Webb 1978), and it is advantageous in navigating through structurally complex habitats (Robinson & Wilson 1996). Long pectoral fins are related to slow and precise movements (Ehlinger 1990), and large fins are also effective in maintaining one's position in the river (Riddell & Leggett 1981). The size of pectoral fins has also been found to correlate with the habitat use: benthic and generalist brook charr (*Salvelinus fontinalis*) have on average longer pectoral fins than pelagic individuals (Bourke *et al.* 1997).

The grayling and arctic charr are streamlined and fusiform species. That kind of body shape allows efficient cruising, reduces the drag (Webb 1982), and it is also efficient in foraging for patchily distributed prey in large volumes of open water, or when migrating (Taylor & McPhail 1985, Baumgartner *et al.* 1988, Swain *et al.* 1991, Robinson & Wilson 1996).

We observed ontogenetic divergence in the morphology of the studied salmonid species: (0+)-year-old freshwater salmonids appear rather similar morphometrically, but as the fish grow, the differences become more marked. Also, the two age groups of each species appeared clearly different morphometrically. Interestingly, salmon is an exception: both the studied age groups are rather similar. Freshwater territorial form of the Atlantic salmon (*Salmo salar*) has a deep-bodied morphology, but when it migrates it becomes more streamlined (Nicieza 1995). Migration is associated with smoltification, that takes place in salmon at two years of age, and it involves both physiological and morphological changes: the juvenile changes into a more streamlined, silvery and active pelagic form, and simultaneously also its metabolism changes (Hoar 1988). Also the brown trout smoltifies, but its morphological and physiological changes are less prominent (Hoar 1988).

We can also speculate about as to what extent the hatchery environment has modified the morphology of the studied fish apart from their 'natural' morphology. Compared to the conditions in the wild, hatchery environment is much more homogenous. It is known that hatchery-rearing of the Atlantic salmon leads to an evolutionary divergence of the cultured strain from the natural phenotypic norm (Petersson *et al.* 1996), and the body form of the Atlantic salmon may change within a single generation in culture (Fleming *et al.* 1994). Hatchery-rearing has also been observed to cause changes in the body morphology of coho salmon (*Oncorhynchus kisutch*) as compared with wild fish (Taylor 1986, Swain *et al.* 1991). This hatchery effect may derive from phenotypic plasticity or selective mortality in the wild (Swain *et al.* 1991). Fleming and Gross (1989) observed that hatchery-reared coho salmon were more streamlined than wild fish, and this was suggested to be due to reduced selection for burst swimming performance. Hatchery-reared Atlantic salmon have smaller fins and heads as compared with their wild conspecifics (Fleming *et al.* 1994). Relative habitat homogeneity or heterogeneity may be reflected in the amount of variation in body morphology, and loss of genetic variation in the hatchery population may lead to reduced morphological variation. In the hatchery the morphology of coho salmon has been observed to be less variable than in nature (Taylor 1986). However, there is no reason to assume that morphological differences in the studied salmonid species would have been smaller if we had studied wild fish.

The studied fish were immature and we did not determine their sex. One can speculate about possible sex-associated morphometric differences, because mature salmonids are known to be sexually dimorphic (e.g., salmon, Fleming *et al.* 1994; brown trout, Reyes-Gavilán *et al.* 1997; arctic charr, Bjøru and Sandlund 1995). However, Fleming *et al.* (1994) observed that immature female and male salmon parrs do not differ in their morphology. Thus intersexual morphometric divergence probably appears not earlier than at maturity.

Some researchers (e.g., Pavlov 1980) have reported that the results of morphometric investigations are influenced by whether fresh or preserved fish specimens are used. We were aware of this problem, but because all (0+)-year-old fish were measured as preserved, and all (1+)-year-old fish immediately after thawing, we considered this problem negligible. Furthermore, the preservation time for (0+)-year-old fish was relatively short, and thus shrinking was probably insignificant.

It is argued that differences between hatchery-reared species may not be representative for wild fish (Hedenskog *et al.* 1997). However, most studies have concerned adult or mature fish, and it is reasonable to assume that the larger the fish are, the greater the effect of hatchery-rearing on their body morphology is. If the rearing environment has, as suggested, a considerable effect on the morphology of an individual, the differences in the field may be even larger than we found in this study. In the present study, we succeeded to find out which characters best discriminate amongst the studied species. Therefore we believe that our study gives new and valuable information about the between-species differences in freshwater salmonids, and though the phenomenon of ontogenetic divergence in salmonids may be well-known among fishermen, this is to our knowledge the first time it was scientifically documented.

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References

Baumgartner, J. V., Bell, M. A. & Weinberg, P. H. 1988: Body form differences between the Enos Lake species pair of threespine sticklebacks (Gasterosteus aculeatus complex). — Can. J. Zool. 66: 467–474.

Bjøru, B. & Sandlund, O.T. 1995: Differences in morphology and ecology within a stunted arctic char population. — Nordic J. Freshwat. Res. 71: 163–172.

Bourke, P., Magnan, P. & Rodríguez, M. A. 1997: Individual variations in habitat use and morphology in brook charr. — J. Fish Biol. 51: 783–794.

Chatfield, C. & Collins, A. J. 1983: Introduction to multivariate analysis. — Chapman & Hall Ltd., London.

Ehlinger, E. J. & Wilson, D. S. 1988: Complex foraging polymorphism in bluegill sunfish. — Proc. Nat. Acad. Sci. (USA) 85: 1878–1882.

Ehlinger, T. J. 1990: Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. — Ecology 71: 886–896.

Fleming, I. A. & Gross, M. R. 1989: Evolution of adult female life history and morphology in a Pacific salmon (coho: Oncorhynchus kisutch). — Evolution 43: 141–157.

Fleming, I. A., Jonsson, B. & Gross, M. R. 1994: Phenotypic divergence of sea-ranched, farmed, and wild salmon. — Can. J. Fish. Aquat. Sci. 51: 2808–2824.

Futuyma, D. J. 1986: Evolutionary biology. 2nd ed. — Sinauer Ass., Sunderland, MA.

Hedenskog, M., Petersson, E., Järvi, T. & Khamis, M. 1997: Morphological comparison of natural produced Atlantic salmon (Salmo salar L.), anadromous brown trout (S. trutta L.) and their hybrids. — Nordic J. Freshw. Res. 73: 35–43.

Hoar, W. S. 1988: The physiology of smolting salmonids. — In: Hoar, W. S. & Randall, D. J. (eds), Fish physiology. Vol. XI B: 275–343. Academic Press, Inc.

Ilmavirta, V. (ed.) 1990: Järvien kunnostuksen ja hoidon perusteet. — Yliopistopaino, Helsinki.

Nicieza, A. G. 1995: Morphological variation between geographically disjunct populations of Atlantic salmon: the effects of ontogeny and habitat shift. — Funct. Ecol. 9: 448–456.

Parmanne, R. 1990: Growth, morphological variation and migrations of herring (Clupea harengus L.) in the northern Baltic. — Finnish Fish. Res. 10: 1–48.

Pavlov, A. F. 1980: A morphometric description of the tugun, Coregonus tugun, of the Severnaya Sos'va River basin. — Journal of Ichthyology 20: 24–34.

Petersson, E., Järvi, T., Steffner, N. G. & Ragnarsson, B. 1996: The effect of domestication on some life history traits of sea trout and Atlantic salmon. — J. Fish Biology 48: 776–791.

Reyes-Gavilán, F. G., Ojanguren, A. F. & Braña, F. 1997: The ontogenetic development of body segments and sexual dimorphism in brown trout (Salmo trutta L.). — Can. J. Zool. 75: 651–655.

Robinson, B. W. & Wilson, D. S. 1996: Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (Lepomis gibbosus). — Evol. Ecol. 10: 631–652.

Riddell, B. E. & Leggett, W. C. 1981: Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (Salmo salar). — Can. J. Fish. Aquat. Sci. 38: 321–333.

Sandlund, O. T., Gunnarsson, K., Jónasson, P. M., Jonsson, B., Lindem, T., Magnússon, K. P., Malmquist, H. J., Sigurjónsdóttir, H., Skúlason, S. & Snorrason S. S. 1992: The arctic charr Salvelinus alpinus in Thingvallavatn. — Oikos 64: 305–351.

Skúlason, S., Noakes, D. L. & Snorrason, S. S. 1989: Ontogeny of trophic morphology in four sympatric morphs of arctic charr Salvelinus alpinus in Thingvallavatn, Iceland. — Biol. J. Linn. Soc. 38: 281–301.

Swain, D. P., Riddell, B. E. & Murray C. B. 1991: Morphological differences between hatchery and wild populations of coho salmon (Oncorhynchus kisutch): Environmental versus genetic origin. — Can. J. Fish. Aquat. Sci. 48: 1783–1791.

Taylor, E. B. 1986: Differences in morphology between wild and hatchery populations of juvenile coho salmon. — Prog. Fish-Cult. 48: 171–176.

Taylor, E. B. & McPhail, J. D. 1985: Variation in body morphology among British Columbia populations of coho salmon, Oncorhynchus kisutch. — Can. J. Fish. Aquat. Sci. 42: 2020–2028.

Webb, P. W. 1978: Fast-start performance and body form in seven species of teleost fish. — J. Exp. Biol. 74: 211–226.

Webb, P. W. 1982: Locomotor patterns in the evolution of actinoptherygian fishes. — Am. Zool. 22: 329–342.

Wootton, R. J. 1990: Ecology of teleost fishes. — Chapman & Hall, London.

Appendix 1. Descriptive statistics for fish of the two age groups. Abbreviations: TL = total length of the fish, BH = body height, HL = head length, HH = head height, SL = snout length, HW = head width, ED = eye diameter, BW = body width, PF = pectoral fin length, AD = anterodorsal length, and AA = anteroanal length.

	0+ year old					1+ year old				
Variable	*n*	Mean	CV%	Min.	Max.	*n*	Mean	CV%	Min.	Max.
Grayling										
TL	63	40.7	12.0	26.2	52.1	21	100.3	16.9	67.9	126.5
BH	59	6.5	17.0	3.8	8.4	21	15.9	21.2	9.9	20.7
HL	62	9.3	10.5	6.9	11.4	21	20.3	16.4	13.8	25.6
HH	61	5.9	10.8	4.2	7.6	21	14.0	18.9	9.1	18.0
SL	63	2.0	23.4	1.1	2.9	21	4.8	22.1	2.9	6.5
HW	61	4.4	12.3	2.7	5.4	21	10.4	13.7	7.6	12.9
ED	63	3.1	9.2	2.3	3.6	21	6.2	8.5	5.1	6.9
BW	58	3.9	15.1	2.7	5.6	21	11.1	21.5	6.7	14.6
PF	62	4.3	15.6	2.5	6.2	21	10.3	22.2	6.5	13.8
AD	63	15.1	10.7	9.7	18.6	21	34.5	15.6	24.4	42.2
AA	58	26.8	10.8	19.6	34.3	21	67.0	17.2	45.1	84.6
Salmon										
TL	44	43.2	9.2	33.5	52.2	21	110.4	18.5	71.7	143.2
BH	44	8.6	13.4	6.3	11.3	21	21.2	24.2	1.7	29.4
HL	44	10.3	7.7	8.3	12.2	21	23.3	16.4	5.7	29.2
HH	44	7.3	10.1	5.9	9.2	21	17.8	20.6	0.9	24.0
SL	44	1.9	16.5	1.1	2.6	21	4.5	21.6	3.0	6.2
HW	44	4.7	12.4	3.5	6.1	21	11.0	14.3	7.6	13.2
ED	44	2.7	14.3	1.8	3.4	21	6.0	8.1	5.0	6.8
BW	44	4.3	19.1	2.4	6.1	21	12.7	23.4	7.1	17.5
PF	44	8.6	11.0	6.4	10.7	21	19.0	12.0	14.5	23.7
AD	44	17.6	9.0	13.7	21.3	21	43.3	18.6	28.2	57.4
AA	44	26.1	9.4	20.4	31.5	21	69.0	18.8	44.8	89.1
Brown trout										
TL	60	47.1	8.9	34.4	57.3	21	114.3	13.0	84.4	144.8
BH	60	9.4	14.1	6.1	11.8	21	23.3	15.8	16.2	30.2
HL	60	10.6	8.9	8.7	12.9	21	24.2	12.7	18.7	29.6
HH	60	8.3	11.1	5.7	10.4	21	19.6	14.3	14.4	25.3
SL	60	1.9	15.2	1.3	2.7	21	4.9	22.5	3.4	7.2
HW	59	5.4	12.7	3.9	7.1	21	12.5	11.7	9.5	15.6
ED	60	3.0	9.5	2.3	3.5	21	6.5	8.6	5.5	7.8
BW	59	4.9	13.6	3.5	6.4	21	13.3	15.5	9.6	17.1
PF	60	7.6	10.0	5.4	9.6	21	15.2	11.8	12.0	18.7
AD	60	19.5	9.1	14.7	23.1	21	47.6	12.7	35.1	59.6
AA	60	29.1	10.0	20.9	37.3	21	74.9	13.3	54.8	95.2
Arctic charr										
TL	50	44.5	9.7	28.9	52.6	21	128.5	11.1	97.6	162.0
BH	49	7.1	15.2	2.7	9.3	21	20.3	14.9	11.8	25.4
HL	50	10.2	10.0	6.3	11.9	21	27.3	10.0	21.3	32.8
HH	50	6.6	10.7	4.3	7.7	21	18.5	12.9	13.0	23.7
SL	50	1.9	19.5	0.9	2.8	21	5.7	12.6	4.0	7.1
HW	50	4.7	14.2	2.3	6.3	21	12.3	8.7	9.7	14.2
ED	50	2.7	10.4	1.8	3.4	21	6.3	6.0	5.7	7.0
BW	49	4.1	13.6	2.0	5.3	21	12.8	12.6	9.9	16.7
PF	50	6.2	10.5	3.8	7.3	21	16.0	10.6	12.4	20.0
AD	50	19.3	9.8	12.3	22.6	21	54.0	11.0	39.5	65.8
AA	50	27.7	9.5	18.1	34.1	21	81.5	11.2	60.7	102.9