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Features of the Changes in External Morphology and Axial Skeleton in Juvenile Salmonid Fishes (Salmonidae) Associated with Smoltification

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Abstract—Changes in external morphological characters and relative lengths of vertebral centra from different regions of the vertebral column are analyzed during smoltification in wild juveniles of five salmonid fish species: Atlantic salmon *Salmo salar*, brown trout *S. trutta*, mikizha *Parasalmo mykiss*, coho salmon *Oncorhynchus kisutch*, and northern Dolly Varden *Salvelinus malma*. The changes in the body proportions and external morphology are similar in different salmonid species, but the patterns of differentiation of the vertebral column's postanal part are different. In Atlantic salmon, all vertebral centra of the postanal part are subject to elongation; in mikizha and brown trout, a small number of the centra are elongated only in the anterior region of the postanal part; in coho salmon, the centra are elongated in the posterior region of the postanal part; in Dolly Varden, the centra are elongated in the middle region of the postanal part. Thus, despite observed universal changes in external morphology associated with smoltification in the family Salmonidae, the development of future marine migrants' phenotypes is species-specific due to different growth of various groups of vertebral centra in the vertebral column's postanal part. The possible reasons for the species diversity in the growth of various groups of vertebral centra are discussed.

Keywords: Atlantic salmon *Salmo salar*, brown trout *S. trutta*, mikizha *Parasalmo mykiss*, coho salmon *Oncorhynchus kisutch*, northern Dolly Varden *Salvelinus malma*, smoltification, smolt, parr, morphology, skeleton, vertebrae, morphogenesis

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INTRODUCTION

Smoltification in salmonid fishes (Salmonidae) is an important step in the life cycle of anadromous species associated with complex morphofunctional changes of the organism leading to the development of adaptations for the marine environment. Smoltification begins in fresh water long before downstream migration of juveniles to the sea, and substantial transformations are observed in almost all systems of the organism. The analysis of the features and mechanisms of smoltification is a subject of special attention for scientists due to the theoretical and practical importance of this process. The investigation of the changes in certain characters or systems of characters is important for the understanding of the entire process. The changes in external morphology of juvenile salmonids during smoltification are studied comparatively well in Atlantic salmon *Salmo salar* (Vernidub, 1977; Martynov, 1983; Kazakov, 1987; Kuzishchin and Novikov, 1994), while to a lesser degree in brown trout *S. trutta* (Chernitskii, 1993, 1994; Kuzishchin, 1997), mikizha *Parasalmo mykiss* (Kuzishchin et al., 2002), and coho salmon *Oncorhynchus kisutch* (Winans and Nishioka, 1987). The data on other salmonid fish species are fragmental or absent. In general, these studies have a descriptive nature, and a connection between habitus changes and transformations of other structures of the organism has not been analyzed in the majority of cases. Only single studies are devoted to the transformation and mineralization of vertebrae in Atlantic salmon smolts during the transition to saline water in aquaculture conditions (Fjelldal et al., 2005, 2006, 2007).

The goal of this study is to analyze the relationship between the changes in external morphology of the fish and vertebral column structure in five salmonid fish species during smoltification.

MATERIALS AND METHODS

The material included riverine juveniles (parr) and migrants (smolts) of Atlantic salmon from the Nilma River (Karelian coast of the Kandalaksha Bay, the White Sea) and brown trout from the Vorob'ev Stream

Table 1. Number of exemplars in the samples (*n*) and parameters of the parr and smolts of the studied species of the Salmonidae family

Species	Parr				Smolts			
	n	age, years	body length (*FL*), mm	body weight, g	*n*	age, years	body length (*FL*), mm	body weight, g
Salmo salar	40	3+	169.4 ± 0.5 139–180	42.6 ± 0.9 30–56	40	3+	173.5 ± 0.5 142–188	50.2 ± 1.0 32–61
S. trutta	30	3+	169.3 ± 0.6 159–189	51.2 ± 0.4 41–68	32	3+	171.3 ± 0.6 156–195	58.1 ± 0.6 40–77
Parasalmo mykiss	50	3+	179.3 ± 0.5 154–198	58.7 ± 0.8 38–84	50	3+	185.4 ± 0.4 153–202	65.6 ± 0.8 37–92
Oncorhynchus kisutch	50	2+	102.3 ± 0.5 90–150	12.7 ± 0.8 9–20	50	2+	107.5 ± 0.4 93–153	14.6 ± 0.9 10–21
Salvelinus malma	50	3+	147.7 ± 0.8 135–188	34.8 ± 1.1 21.3–50.8	50	3+	151.2 ± 0.7 138–185	31.3 ± 0.8 22.6–48.7

Here and in Tables 2–4: above the line is mean value and standard error; below the line is the range of the values.

(the same region) collected in June 1995, mikizha and coho salmon from the Saichik River (western coast of Kamchatka) collected in June and July 1998, and northern Dolly Varden *Salvelinus malma* from the Kol River basin (western coast of Kamchatka) collected in July 2004. All juveniles used for the study belonged exclusively to wild populations. The catches were conducted in early summer during the mass downstream migration of the young to the sea. The smolts of Atlantic salmon and brown trout were caught with rods and lines and fish traps installed in the sea near river mouths in the intertidal zones. All smolts intensively fed just before the capture. The Atlantic salmon fed on mysids (Mysidae) and White Sea herring *Clupea pallasii marisalbi* juveniles, while brown trout fed on mysids, White Sea herring juveniles, and ninespine stickleback *Pungitius pungitius*. Large fat deposits were observed in the intestine and internal organs of the smolts of both species. The smolts of mikizha and coho salmon were collected with rods and lines in a brackish estuary (salinity 6–11‰) of the Saichik River. All smolts of mikizha actively fed on chum salmon *Oncorhynchus keta* juveniles that migrated to the sea and large mysids, while the smolts of coho salmon fed on mainly mysids. The smolts of Dolly Varden were collected in the Kol River delta at a distance of approximately 800 m from the sea. They actively fed on mysids and (less intensively) chum salmon juvenile migrants. Thus, the smolts of the five species used in this study were sampled after their downstream migration from fresh water; they formed schools and were at a final stage of smoltification, so-called "silvery fishes with easily falling scales" according to the terminology of some authors (Kazakov, 1982, 1987, 1992; Kuzishchin et al., 2002).

The parr were collected in the streams and rivers in the typical freshwater biotopes described in the previous studies (Kuzishchin and Novikov, 1994; Kuzishchin et al., 2002; Pavlov et al., 2009) with a Smith-Root 24L electrical fishing device during the time of the smolts' sampling. The individuals with typical protective coloration without indications of smoltification were used for the analysis.

In all fishes, the fork length (*FL*), total body weight, and eviscerated body weight were determined. The morphometric analysis was conducted according to a shortened and modified scheme of Pravdin (Fig. 1a) (Pavlov et al., 2001). For the analysis of the body length–body weight relationship and approximation of regression lines, the parr and smolts of different age classes were used; the number of individuals of each species is indicated in the figures.

The individuals of parr and smolts in the catches had different age, body length, and body weight. Nevertheless, for each species used for the analysis of external morphology and axial skeleton, the parr and smolts belonging to the same age class and characterized by similar body length and body weight were chosen (Table 1). A selection of the parr and smolts of coho salmon at the age 2+ applied in this study was connected with an extremely low abundance of fishes at the age 3+ in the rivers of Western Kamchatka (Zorbidi, 2010). Only the males and females with the gonads at maturity stage II were used for the study.

All morphometric characters were obtained on fresh individuals, and the measurements and calculations were conducted by the same operator. After the biological and morphometric analyses, the fishes were placed into boiling water for several seconds, then vertebral columns together with the last urostilar centra

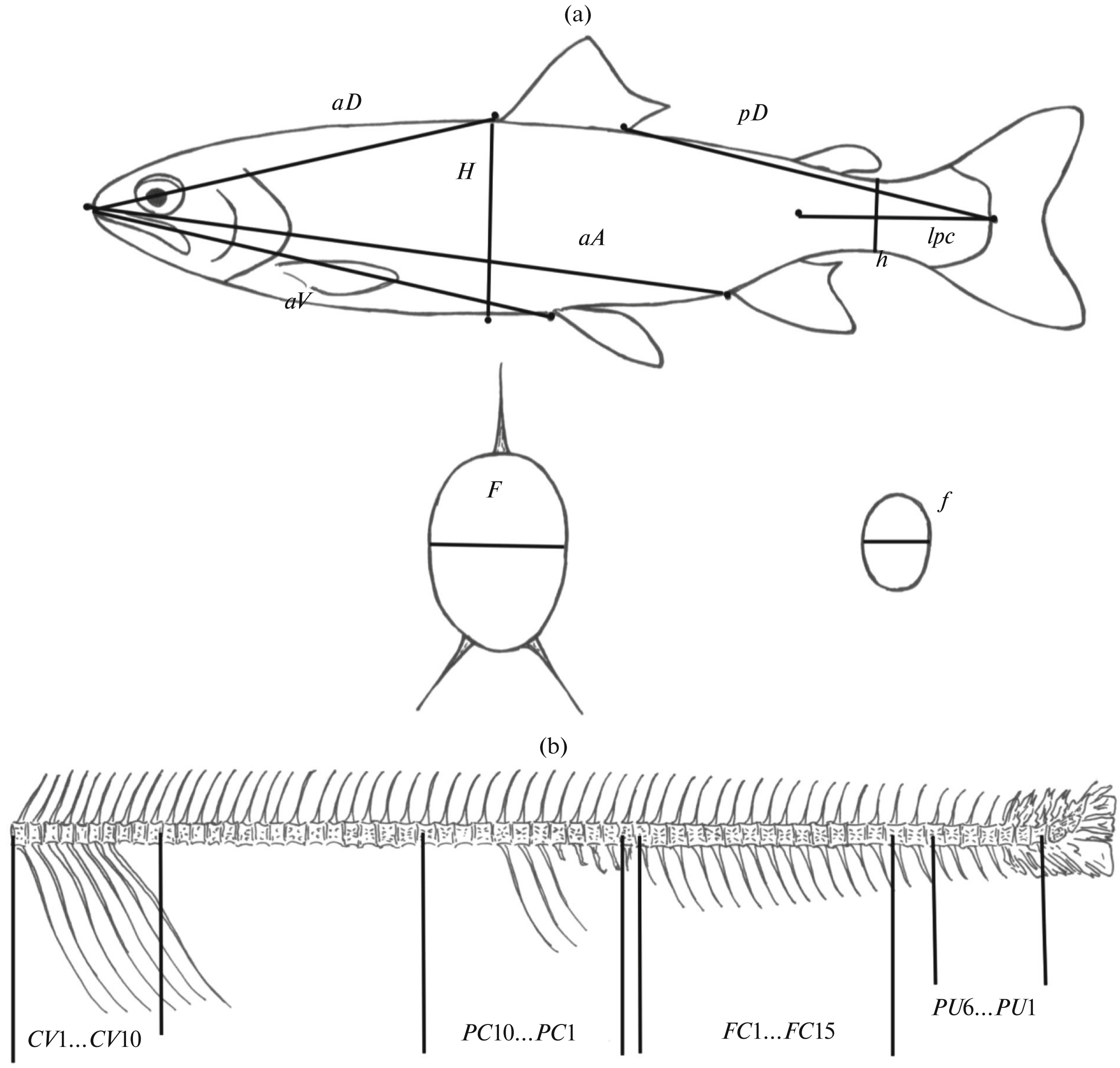

Fig. 1. (a) Scheme of morphometric measurements and (b) vertebral groups in the studied species of the family Salmonidae: *aD*, *pD*, *aV*, *aA*, antedorsal, postdorsal, anteventral, and anteanal distances, respectively; *lpc*, caudal peduncle length; *H*, largest body depth; *h*, caudal peduncle depth; *F*, largest body width at a level of a vertical before the dorsal fin base's origin; *f*, caudal peduncle width at a level of its lowest depth; *CV*1–*CV*10, vertebral centra of the anterior region of the vertebral column (the numbers begin from the basioccipital); *PC*1–*PC*10, vertebral centra of the posterior region of the preanal part of the vertebral column (the numbers begin from the end of the part); *FC*1–*FC*15, anterior vertebral centra with neural spines of the vertebral column's postanal part (the numbers begin from the onset of the part); *PU*1–*PU*6, last vertebral centra before the urostilar centra (the numbers begin from the end of the part).

and basioccipital of the axial skull were dissected. After the preparation, the vertebral columns were preserved by a fresh-dry method, and all vertebral centra were placed along a straight line. The total number of the preanal and postanal centra were counted. The length of the vertebral column and its parts was measured with a caliper to the nearest 0.1 mm, and the vertebral centra were separated. The centra were measured with a micrometer to the nearest 0.01 mm. The length of each centrum was expressed in percent of the vertebral column length (without urostilar centra). The results of centra measurements are given for the following vertebral column regions: ten first and ten last centra of the preanal part and 15 anterior and six posterior centra of the postanal part (without urostilar centra). These measurements correspond with the measurements conducted in the parr and smolts of Atlantic salmon (Kacem et al., 1998; Fjelldal et al.,

Table 2. Meristic characters of the parr and smolts of the studied species of the Salmonidae family

Species	Group	Character		
		vert.	*vert.c.*	*ll*
Salmo salar	Parr	59.4 ± 0.23 58–61	23.15 ± 0.17 21–25	125.7 ± 1.11 114–130
	Smolts	59.5 ± 0.27 58–61	23.18 ± 0.18 21–25	126.3 ± 1.08 115–128
S. trutta	Parr	59.6 ± 0.21 58–61	22.36 ± 0.18 20–24	116.9 ± 0.97 104–127
	Smolts	59.7 ± 0.20 58–61	22.53 ± 0.19 20–24	115.6 ± 1.08 105–126
Parasalmo mykiss	Parr	63.21 ± 0.22 60–65	22.33 ± 0.16 21–25	127.05 ± 0.80 121–130
	Smolts	63.25 ± 0.24 60–65	22.39 ± 0.18 21–25	127.71 ± 0.86 124–132
Oncorhynchus kisutch	Parr	67.45 ± 0.26 64–69	23.64 ± 0.26 21–25	134.93 ± 1.01 129–143
	Smolts	67.46 ± 0.28 64–69	23.27 ± 0.24 21–25	135.01 ± 1.10 130–143
Salvelinus malma	Parr	65.21 ± 0.29 61–71	24.43 ± 0.21 22–26	131.84 ± 1.22 123–158
	Smolts	65.19 ± 0.30 62–70	24.52 ± 0.22 22–26	131.28 ± 1.28 122–155

vert., total vertebral number; *vert.c.*, vertebral number in the vertebral column's postanal part; *ll*, number of pointed scales in the lateral line.

2005, 2006, 2007). The groups of the centra analyzed in this study are illustrated in Fig. 1b (according to Arratia and Schultze (1992)).

The material was treated by the methods of standard univariant statistical analysis (Lakin, 1990). The frequency distribution for the values of morphometric characters in parr and smolts did not differ from the normal (Gaussian) distribution in any samples. Therefore, the parametric Student's *t*-test (t_{st}) was applied for the analysis.

RESULTS

Similar changes in body coloration and external morphology were observed in all five studied salmonid fish species during smoltification. The most notable morphological transformations were connected with body proportions: the relative length of the caudal peduncle had abruptly increased, and the position of the paired and unpaired fins had substantially changed. The smolts differed from the parr in the displacement of the dorsal, pelvic, and anal fins to the head. However, the differences between the parr and smolts in the number of pointed scales in the lateral line, total vertebral number, and number of postanal vertebrae were not registered in all five species (Table 2). During smoltification, the body depth and caudal peduncle depth became notably lower, and the largest body width and caudal peduncle width became substantially larger (Table 3). The smolts differed in almost rounded body (at a transversal section) vs. laterally compressed body in the parr. It is important to note that the transgression in the frequency distributions of the values of the morphometric characters was absent (i.e., the hiatuses were observed) in the majority of cases. These characters were as follows: body width (*F*), caudal peduncle width (*f*), body depth—body width ratio (H/F), and caudal peduncle depth—caudal peduncle width ratio (h/f). The changes associated with smoltification were similar in salmonid fish juveniles from different species and genera.

The analysis of the body length—eviscerated body weight ratio showed that the relative body weight in the smolts of all studied species was larger than that in the parr (Fig. 2). These data support that the development of oval or almost rounded body shape (at a transversal section) in the smolts entering into brackish waters was reached due to the increase of muscle mass.

Table 3. Morphometric characters and indices of the parr and smolts of the studied species of the Salmonidae family

Species	Group	Character, % *FL*									Index	
		aD	*pD*	*aV*	*aA*	*H*	*h*	*lpc*	*F*	*f*	*H/F*	*h/f*
Salmo salar	p	42.4 ± 0.14 39.2–45.7	41.8 ± 0.19 38.3–43.4	49.4 ± 0.14 47.5–51.8	68.3 ± 0.18 66.7–72.3	20.7 ± 0.23 19.7–22.8	7.8 ± 0.10 7.1–8.6	19.5 ± 0.12 17.5–21.8	15.1 ± 0.22 13.5–17.4	5.9 ± 0.10 5.1–7.2	1.45 ± 0.08 1.38–1.51	1.33 ± 0.07 1.21–1.55
	s	40.5 ± 0.26 37.1–42.0	45.1 ± 0.18 42.2–47.6	47.6 ± 0.18 45.2–49.6	66.8 ± 0.27 64.7–70.1	18.6 ± 0.21 17.2–20.4	6.7 ± 0.11 6.1–7.4	22.2 ± 0.19 20.4–24.7	18.5 ± 0.23 17.2–19.7	6.7 ± 0.11 6.1–7.3	1.01 ± 0.05 0.99–1.04	1.00 ± 0.08 0.98–1.01
	t_{st}	6.43***	12.6***	7.89***	4.62***	6.74***	7.39***	12.01***	10.68***	5.38***	*X*	*X*
S. trutta	p	43.2 ± 0.25 41.1–46.4	40.4 ± 0.21 39.4–43.7	49.9 ± 0.26 46.4–51.5	68.8 ± 0.31 67.1–71.3	21.9 ± 0.25 19.8–24.0	8.5 ± 0.11 7.5–10.3	17.7 ± 0.16 16.2–19.1	12.3 ± 0.11 10.6–14.8	4.5 ± 0.12 4.1–5.6	1.82 ± 0.04 1.66–1.93	1.87 ± 0.11 1.72–1.92
	s	41.8 ± 0.24 40.2–44.5	42.1 ± 0.19 40.8–44.6	47.7 ± 0.21 45.3–50.7	67.2 ± 0.25 66.4–70.2	19.4 ± 0.26 18.4–20.8	7.9 ± 0.10 7.2–8.9	19.3 ± 0.15 18.6–21.7	18.8 ± 0.15 16.8–19.9	6.4 ± 0.13 5.9–8.0	1.05 ± 0.03 1.03–1.07	1.23 ± 0.10 1.20–1.28
	t_{st}	4.04***	6.00***	6.58***	4.02***	6.93***	4.04***	7.29***	*X*	*X*	*X*	*X*
Parasalmo mykiss	p	45.4 ± 0.20 42.8–48.1	38.8 ± 0.23 33.8–43.8	50.3 ± 0.23 46.7–53.1	68.5 ± 0.24 63.7–70.9	21.7 ± 0.28 18.5–25.4	8.2 ± 0.10 7.2–9.1	17.8 ± 0.15 16.1–19.4	13.6 ± 0.20 12.3–15.8	5.5 ± 0.13 4.9–6.7	1.58 ± 0.10 1.49–1.70	1.48 ± 0.09 1.42–1.55
	s	44.1 ± 0.18 42.0–46.4	40.6 ± 0.14 38.0–41.7	49.1 ± 0.16 46.6–51.4	67.4 ± 0.19 66.1–71.4	18.7 ± 0.19 17.2–20.6	7.6 ± 0.10 6.9–8.6	19.6 ± 0.13 18.6–21.8	17.9 ± 0.19 16.8–19.7	7.1 ± 0.11 6.3–8.0	1.04 ± 0.11 1.02–1.07	1.08 ± 0.09 1.03–1.11
	t_{st}	4.83***	6.68***	4.28***	3.59***	8.86***	4.24***	9.07***	*X*	9.39***	*X*	*X*
Oncorhynchus kisutch	p	45.6 ± 0.27 41.2–48.1	38.7 ± 0.24 35.4–41.8	48.0 ± 0.19 45.3–50.6	64.2 ± 0.21 61.5–67.1	21.4 ± 0.16 19.5–23.8	8.2 ± 0.08 7.1–9.6	17.4 ± 0.17 14.9–19.3	13.7 ± 0.12 11.6–13.5	4.8 ± 0.08 4.0–5.7	1.69 ± 0.07 1.56–1.84	1.71 ± 0.08 1.62–1.88
	s	44.4 ± 0.22 40.5–46.1	41.0 ± 0.25 37.9–43.8	46.8 ± 0.17 44.8–48.9	63.3 ± 0.20 60.0–65.9	19.0 ± 0.14 17.3–20.6	7.8 ± 0.09 6.8–8.9	18.7 ± 0.18 16.4–20.1	17.8 ± 0.15 15.7–19.1	7.2 ± 0.09 6.8–8.5	1.07 ± 0.07 1.04–1.12	1.08 ± 0.06 1.05–1.13
	t_{st}	3.44***	6.64***	4.71***	3.10**	11.28***	3.32**	5.25***	*X*	*X*	*X*	*X*
Salvelinus malma	p	42.6 ± 0.28 40.1–45.4	39.9 ± 0.22 38.2–42.4	48.0 ± 0.24 46.8–49.8	67.8 ± 0.24 65.6–69.7	21.5 ± 0.21 19.8–24.5	8.8 ± 0.18 8.1–9.4	17.8 ± 0.20 16.7–19.0	16.5 ± 0.13 14.8–17.7	5.8 ± 0.10 5.0–7.1	1.30 ± 0.08 1.25–1.37	1.52 ± 0.05 1.48–1.51
	s	40.8 ± 0.23 39.7–43.1	43.5 ± 0.26 42.0–44.8	46.5 ± 0.27 44.1–48.7	66.1 ± 0.26 64.3–67.7	17.3 ± 0.19 15.7–18.7	7.4 ± 0.11 7.2–8.6	20.5 ± 0.23 18.7–21.5	17.2 ± 0.15 16.2–17.9	7.2 ± 0.11 6.7–7.4	1.00 ± 0.06 0.96–1.02	1.02 ± 0.04 1.00–1.04
	t_{st}	4.96***	10.6***	4.15***	4.80***	*X*	6.64***	8.85***	3.53***	9.41***	*X*	*X*

FL, fork length; *aD*, *pD*, *aV*, *aA*, antedorsal, postdorsal, anteventral, and anteanal distasnces, respectively; *lpc*, caudal peduncle length; *H*, largest body depth; *h*, caudal peduncle depth; *F*, largest body width at a level of a vertical before the dorsal fin base origin; *f*, caudal peduncle width at a level of its lowest depth; t_{st}, Student's *t*-test for the differences between the parr (p) and smolts (s); *X*, a presence of the hiatus in the distribution of the values, $t_{st} \ll 0.001$. $^{**}p < 0.01$, $^{***}p < 0.001$.

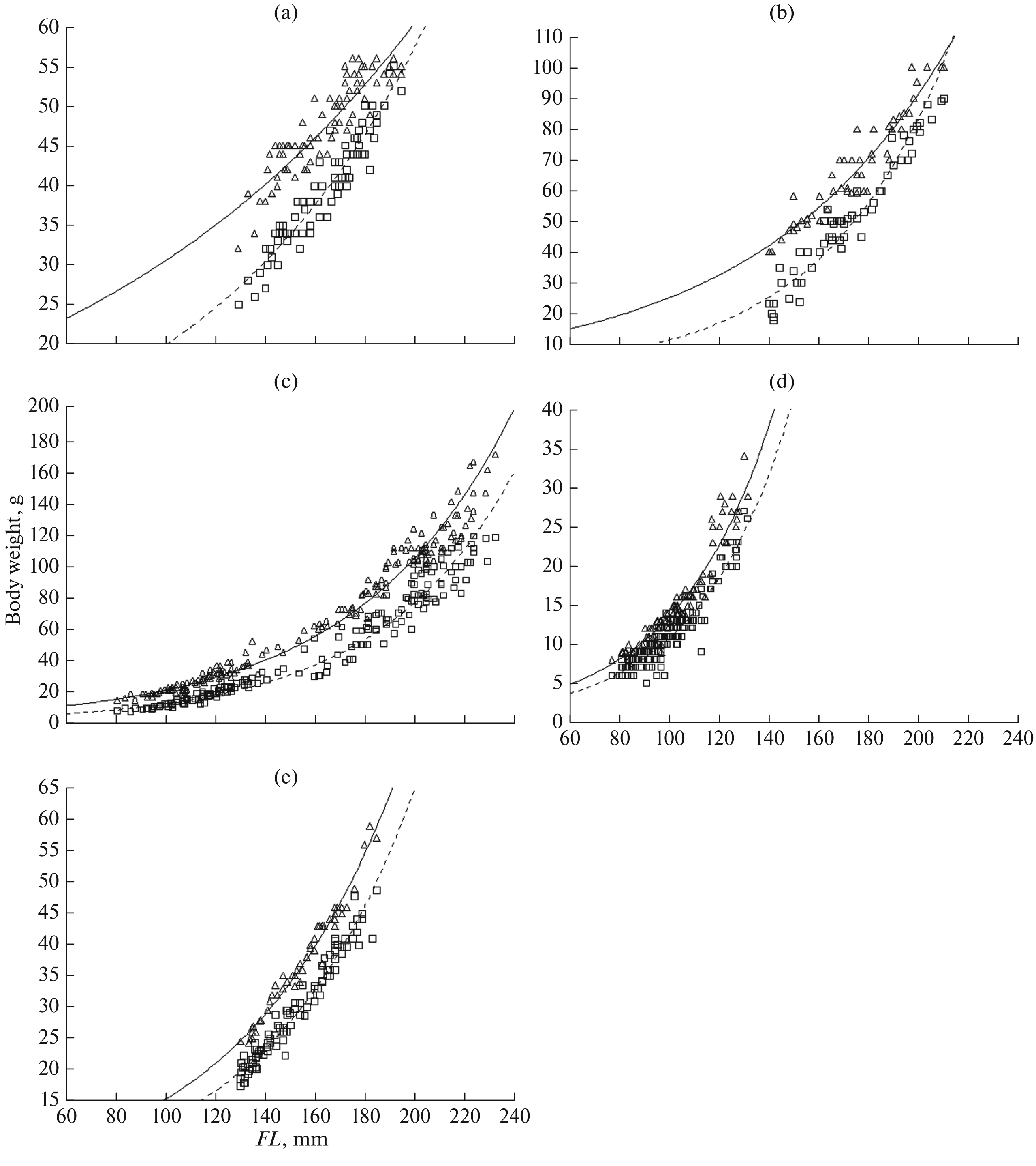

Fig. 2. Relationship between eviscerated body weight and body length (*FL*) in the (□) parr and (△) smolts: (a) Atlantic salmon *Salmo salar* (parr, $n = 115$; smolts, $n = 163$); (b) brown trout *S. trutta* ($n = 98$ and 172); (c) mikizha *Parasalmo mykiss* ($n = 177$ and 224); (d) coho salmon *Oncorhynchus kisutch* ($n = 131$ and 208); (e) northern Dolly Varden *Salvelinus malma* ($n = 75$ and 100).

The analysis of relative lengths of the vertebral centra showed that the smolts did not differ from the parr in the lengths of the anterior and posterior centra of the preanal part of the vertebral column. However, the differences in the proportion of the centra in the vertebral column's postanal part were well expressed. In different species, these differences were observed in various groups of the centra of the postanal part (Table 4). The parr and smolts of Atlantic salmon significantly differed in relative lengths of all vertebral centra with hemal spines of the vertebral column's postanal part. The parr and smolts of brown trout and mikizha significantly differed in relative lengths of the centra in the anterior region of the vertebral column's postanal part. In particular, the relative length of only 9–10 anterior centra had increased in brown trout smolts, and the relative length of 14–15 anterior centra had increased in mikizha smolts. In the smolts of coho salmon, the relative length of the last 9–11 postanal centra (before urostilar centra) had increased; in the smolts of Dolly Varden, the relative length of the centra in the middle region of the vertebral column's postanal part had increased. In five studied salmonid fish species, the lowest number of vertebral centra subjected to transformations associated with smoltification (≤10) was observed in brown trout, and the largest number (23–25) was registered in Atlantic salmon; the other studied species were characterized by intermediate values.

DISCUSSION

In salmonid fishes, smoltification is a complex and multifactor integral process characterized by coordinated biochemical, physiological, and morphological transformations of the organism directed to development of preadaptations to life in the new pelagic environment of the sea (Hoar, 1976, 1988; Farmer et al., 1978; Folmar and Dickhoff, 1980; Kazakov, 1982; Chernitskii, 1994; Thorpe, 1994; *Atlanticheskii*..., 1998). Based on the strength of morphophysiological changers in the organism, smoltification in salmonid fishes can be regarded as a variant of a well-expressed metamorphosis similar to that observed in flatfishes (Pleuronectiformes) or even in amphibians (Amphibia) during the development of their definitive body shapes (Barrington, 1961; Dickhoff et al., 1990; Paris and Laudet, 2008; Björnsson et al., 2012). In particular, a notable change of body shape in salmonid juveniles during smoltification is connected with substantial differentiation of various body parts' growth, including the effect of different gene expression (Fjelldal et al., 2005; Seear et al., 2010).

The changes in external morphology associated with smoltification and described in this study for Atlantic salmon, brown trout, mikizha, coho salmon, and Dolly Varden are, in general, similar to those observed in these species by other authors. In particular, the change in the position of fins, decrease of the body depth and caudal peduncle depth, and elongation of the postanal part of the body are reported for the juveniles of Atlantic salmon (Vernidub, 1977; Kazakov, 1982; Fjelldal et al., 2005), brown trout (Chernitskii, 1993, 1994), mikizha (Beeman et al., 1995), and coho salmon (Winans and Nishioka, 1987). We have not found the description of similar transformations of body proportions in northern Dolly Varden in available literature. However, the changes described in this study are similar to those described in a relative species, Arctic charr *Salvelinus alpinus* (Damsgard, 1991). Thus, the results of this study and literature data show an occurrence of universal and parallel adaptations of salmonid fishes directed to the development of optimal hydrodynamic body shape, which is necessary for active life in the water mass and migrations.

During the downstream migration of smolts in fresh water and their transition to brackish water, the transformation of the digestive system and forced starvation of the juveniles are observed, which leads to the decrease in relative body weight, and the smallest body weight is reached just before the migration to saline water (Mahnken, 1973; Barannikova et al., 1976; Clarke and Nagahama, 1977; Hoar, 1988; Soivio et al., 1988; Virtanen et al., 1988). Nevertheless, an increased food intake is observed in the juveniles leaving the rivers and foraging in brackish waters and the marine environment. The relative body weight of the smolts of all studied salmonid fish species is always larger than that in the parr (Fig. 2), which indicates a so-called growth jump or growth spurt (Fjelldal et al., 2007). Similar data are obtained during the study of body length and weight increments in the smolts of steelhead trout (mikizha) in the rivers of Oregon: their relative body weight has abruptly increased for a short time (~1 week) followed by the downstream migration that is especially well expressed in large smolts 140–209 mm *FL* (Fessler, 1969).

In the discussions of the habitus change of the fishes during smoltification, different authors pay special attention to the increase in relative length of the caudal peduncle. According to a general opinion, the elongation of the caudal peduncle is an important parameter showing the onset of a transition from the maneuvering in turbulent water currents in freshwater biotopes to prolonged cruising movement in pelagic marine waters (Lundqvist and Eriksson, 1985; Taylor and McPhail, 1985a, 1985b, Hoar, 1988). Based on the data of this study, the development of the elongated caudal peduncle is a universal event, which is usual for the salmonid species belonging to different genera and living in the water bodies of various types, from small streams to large rivers.

It seems obvious that the increase in relative length of the caudal peduncle in the salmonid fish species' smolts is a consequence of exclusively unequal growth in different parts of the vertebral column, and, therefore, unequal growth of certain groups of vertebral centra. Nevertheless, this aspect of smoltification is poorly studied, which is emphasized in a few studies devoted to this subject (Fjelldal et al., 2005, 2006, 2007). Attempts of analyzing the change in vertebral morphology associated with smoltification have been conducted for Atlantic salmon in connection with the features of its cultivation in the conditions of intensive aquaculture (Fjelldal et al., 2005, 2006, 2007). Based on the study of the cited authors, the lengths of the postanal vertebral centra (from 35th to 58th), including the last centrum (before urostilar centra), have

Table 4. Relative length of the vertebral centra (% of the vertebral column length) of the parr and smolts of the studied species of the Salmonidae family

Centrum	*Salmo salar*		*S. trutta*		*Parasalmo mykiss*		*Oncorhynchus kisutch*		*Salvelinus malma*	
	parr	smolts	parr	smolts	parr	smolts	parr	smolts	parr	smolts
	Centra of the anterior part of the vertebral column									
*CV*1	1.401 ± 0.006 1.38–1.42	1.400 ± 0.008 1.38–1.42	1.413 ± 0.006 1.39–1.42	1.414 ± 0.008 1.39–1.42	1.392 ± 0.007 1.37–1.41	1.396 ± 0.008 1.37–1.41	1.288 ± 0.006 1.26–1.31	1.291 ± 0.007 1.27–1.31	1.315 ± 0.007 1.29–1.33	1.317 ± 0.009 1.29–1.33
*CV*2	1.415 ± 0.006 1.39–1.43	1.417 ± 0.008 1.39–1.44	1.421 ± 0.008 1.40–1.50	1.422 ± 0.009 1.40–1.51	1.405 ± 0.009 1.39–1.42	1.406 ± 0.009 1.37–1.41	1.306 ± 0.008 1.28–1.32	1.308 ± 0.009 1.28–1.32	1.322 ± 0.009 1.31–1.35	1.323 ± 0.010 1.30–1.35
*CV*3	1.427 ± 0.007 1.41–1.44	1.427 ± 0.008 1.39–1.47	1.443 ± 0.007 1.41–1.52	1.447 ± 0.008 1.41–1.52	1.411 ± 0.009 1.39–1.43	1.411 ± 0.009 1.39–1.43	1.315 ± 0.009 1.28–1.33	1.317 ± 0.010 1.29–1.33	1.347 ± 0.009 1.32–1.36	1.350 ± 0.010 1.33–1.38
*CV*4	1.431 ± 0.008 1.41–1.48	1.433 ± 0.009 1.41–1.50	1.482 ± 0.009 1.47–1.52	1.480 ± 0.008 1.46–1.53	1.412 ± 0.010 1.39–1.43	1.411 ± 0.010 1.39–1.42	1.326 ± 0.009 1.30–1.34	1.325 ± 0.010 1.31–1.34	1.355 ± 0.010 1.33–1.37	1.356 ± 0.011 1.33–1.38
*CV*5	1.456 ± 0.007 1.43–1.50	1.452 ± 0.009 1.42–1.51	1.483 ± 0.009 1.47–1.53	1.482 ± 0.009 1.46–1.53	1.413 ± 0.010 1.39–1.43	1.414 ± 0.010 1.39–1.43	1.326 ± 0.010 1.30–1.35	1.327 ± 0.010 1.31–1.35	1.357 ± 0.010 1.33–1.38	1.360 ± 0.011 1.34–1.39
*CV*6	1.464 ± 0.008 1.44–1.51	1.466 ± 0.009 1.43–1.51	1.488 ± 0.009 1.47–1.53	1.485 ± 0.010 1.46–1.53	1.414 ± 0.009 1.39–1.43	1.413 ± 0.011 1.39–1.43	1.327 ± 0.010 1.31–1.35	1.327 ± 0.011 1.31–1.35	1.358 ± 0.010 1.33–1.38	1.360 ± 0.012 1.34–1.39
*CV*7	1.464 ± 0.008 1.44–1.52	1.465 ± 0.009 1.43–1.52	1.484 ± 0.008 1.47–1.54	1.482 ± 0.011 1.46–1.52	1.413 ± 0.010 1.38–1.43	1.414 ± 0.011 1.39–1.43	1.328 ± 0.010 1.30–1.35	1.328 ± 0.011 1.31–1.36	1.359 ± 0.010 1.33–1.38	1.360 ± 0.012 1.34–1.38
*CV*8	1.465 ± 0.008 1.43–1.51	1.466 ± 0.010 1.43–1.52	1.487 ± 0.010 1.46–1.53	1.479 ± 0.009 1.46–1.53	1.415 ± 0.010 1.39–1.43	1.413 ± 0.011 1.38–1.43	1.326 ± 0.010 1.30–1.35	1.328 ± 0.011 1.31–1.35	1.358 ± 0.010 1.33–1.38	1.359 ± 0.012 1.34–1.38
*CV*9	1.472 ± 0.008 1.45–1.52	1.477 ± 0.008 1.45–1.52	1.485 ± 0.010 1.47–1.54	1.486 ± 0.010 1.47–1.53	1.413 ± 0.009 1.39–1.44	1.413 ± 0.012 1.38–1.43	1.327 ± 0.011 1.29–1.35	1.329 ± 0.011 1.30–1.35	1.359 ± 0.011 1.33–1.39	1.360 ± 0.012 1.33–1.38
*CV*10	1.475 ± 0.009 1.45–1.52	1.477 ± 0.008 1.45–1.53	1.482 ± 0.010 1.47–1.54	1.488 ± 0.011 1.46–1.54	1.414 ± 0.009 1.39–1.43	1.413 ± 0.011 1.39–1.43	1.328 ± 0.011 1.30–1.35	1.328 ± 0.011 1.30–1.35	1.358 ± 0.011 1.33–1.38	1.360 ± 0.012 1.32–1.38

Table 4. (Contd.)

Centrum	*Salmo salar*		*S. trutta*		*Parasalmo mykiss*		*Oncorhynchus kisutch*		*Salvelinus malma*	
	parr	smolts	parr	smolts	parr	smolts	parr	smolts	parr	smolts
	Posterior preanal centra									
*PC*10	1.772 ± 0.010 1.75–1.80	1.780 ± 0.010 1.76–1.80	1.765 ± 0.010 1.75–1.78	1.770 ± 0.011 1.75–1.79	1.526 ± 0.010 1.49–1.55	1.527 ± 0.011 1.50–1.55	1.528 ± 0.011 1.50–1.55	1.529 ± 0.012 1.51–1.55	1.501 ± 0.011 1.48–1.52	1.499 ± 0.012 1.47–1.51
*PC*9	1.776 ± 0.011 1.75–1.80	1.781 ± 0.010 1.76–1.81	1.772 ± 0.010 1.75–1.78	1.772 ± 0.011 1.76–1.79	1.527 ± 0.010 1.50–1.55	1.527 ± 0.012 1.50–1.55	1.529 ± 0.011 1.50–1.55	1.531 ± 0.012 1.51–1.55	1.488 ± 0.0110 1.46–1.5	1.487 ± 0.011 1.46–1.50
*PC*8	1.777 ± 0.010 1.75–1.81	1.781 ± 0.011 1.77–1.82	1.778 ± 0.011 1.75–1.80	1.780 ± 0.012 1.76–1.80	1.525 ± 0.011 1.50–1.56	1.526 ± 0.012 1.50–1.55	1.525 ± 0.011 1.50–1.56	1.527 ± 0.012 1.50–1.55	1.475 ± 0.012 1.45–1.50	1.476 ± 0.011 1.45–1.49
*PC*7	1.779 ± 0.011 1.76–1.81	1.781 ± 0.012 1.77–1.82	1.804 ± 0.011 1.78–1.81	1.800 ± 0.012 1.78–1.82	1.523 ± 0.011 1.50–1.55	1.522 ± 0.012 1.50–1.56	1.523 ± 0.011 1.50–1.55	1.526 ± 0.012 1.50–1.55	1.469 ± 0.011 1.44–1.50	1.470 ± 0.012 1.45–1.50
*PC*6	1.779 ± 0.012 1.76–1.82	1.782 ± 0.012 1.76–1.82	1.811 ± 0.012 1.80–1.83	1.808 ± 0.011 1.79–1.82	1.521 ± 0.011 1.50–1.55	1.522 ± 0.012 1.50–1.55	1.522 ± 0.011 1.50–1.54	1.524 ± 0.012 1.50–1.55	1.463 ± 0.011 1.44–1.50	1.462 ± 0.012 1.44–1.49
*PC*5	1.805 ± 0.010 1.78–1.83	1.808 ± 0.011 1.78–1.83	1.823 ± 0.012 1.81–1.84	1.818 ± 0.012 1.81–1.84	1.520 ± 0.011 1.50–1.53	1.522 ± 0.012 1.50–1.54	1.523 ± 0.011 1.50–1.54	1.524 ± 0.012 1.50–1.53	1.462 ± 0.011 1.44–1.49	1.462 ± 0.012 1.44–1.49
*PC*4	1.812 ± 0.011 1.78–1.83	1.811 ± 0.011 1.78–1.83	1.856 ± 0.011 1.84–1.87	1.858 ± 0.010 1.84–1.87	1.517 ± 0.012 1.49–1.53	1.520 ± 0.012 1.50–1.54	1.521 ± 0.012 1.50–1.55	1.523 ± 0.012 1.50–1.55	1.462 ± 0.011 1.44–1.50	1.462 ± 0.011 1.44–1.50
*PC*3	1.814 ± 0.011 1.78–1.83	1.813 ± 0.010 1.79–1.84	1.875 ± 0.012 1.86–1.88	1.880 ± 0.011 1.85–1.90	1.518 ± 0.012 1.49–1.53	1.519 ± 0.012 1.50–1.53	1.520 ± 0.010 1.50–1.55	1.520 ± 0.011 1.49–1.55	1.460 ± 0.012 1.44–1.50	1.461 ± 0.012 1.44–1.49
*PC*2	1.821 ± 0.012 1.79–1.85	1.819 ± 0.012 1.78–1.85	1.878 ± 0.011 1.86–1.89	1.882 ± 0.012 1.87–1.91	1.516 ± 0.012 1.49–1.53	1.518 ± 0.013 1.49–1.53	1.519 ± 0.011 1.49–1.53	1.520 ± 0.011 1.49–1.54	1.458 ± 0.011 1.43–1.50	1.460 ± 0.012 1.44–1.50
*PC*1	1.833 ± 0.012 1.80–1.86	1.828 ± 0.011 1.80–1.86	1.877 ± 0.012 1.86–1.90	1.900 ± 0.011 1.87–1.93	1.516 ± 0.012 1.49–1.53	1.518 ± 0.012 1.48–1.53	1.520 ± 0.011 1.49–1.53	1.520 ± 0.011 1.49–1.54	1.458 ± 0.012 1.43–1.49	1.457 ± 0.012 1.43–1.50

Table 4. (Contd.)

Centrum	*Salmo salar*		*S. trutta*		*Parasalmo mykiss*		*Oncorhynchus kisutch*		*Salvelinus malma*	
	parr	smolts	parr	smolts	parr	smolts	parr	smolts	parr	smolts
	Anterior postanal centra									
*FC*1	**1.873 ± 0.012** **1.84–1.91**	**1.955 ± 0.011** **1.93–1.98**	**1.883 ± 0.012** **1.87–1.91**	**1.960 ± 0.012** **1.93–2.00**	**1.514 ± 0.012** **1.49–1.53**	**1.548 ± 0.012** **1.52–1.57**	1.412 ± 0.012 1.39–1.43	1.413 ± 0.011 1.39–1.43	1.441 ± 0.012 1.42–1.47	1.471 ± 0.012 1.45–1.50
*FC*2	**1.879 ± 0.012** **1.85–1.92**	**1.960 ± 0.011** **1.93–1.99**	**1.884 ± 0.011** **1.87–1.92**	**1.962 ± 0.010** **1.93–1.99**	**1.515 ± 0.012** **1.49–1.53**	**1.548 ± 0.011** **1.52–1.57**	1.410 ± 0.0111 1.39–1.4	1.411 ± 0.012 1.39–1.42	1.440 ± 0.012 1.42–1.46	1.470 ± 0.012 1.45–1.50
*FC*3	**1.880 ± 0.011** **1.85–1.93**	**1.958 ± 0.012** **1.93–1.99**	**1.885 ± 0.010** **1.87–1.93**	**1.961 ± 0.011** **1.93–2.00**	**1.513 ± 0.012** **1.49–1.53**	**1.549 ± 0.012** **1.53–1.58**	1.398 ± 0.012 1.37–1.42	1.400 ± 0.011 1.38–1.41	1.438 ± 0.012 1.41–1.46	1.469 ± 0.011 1.45–1.50
*FC*4	**1.880 ± 0.011** **1.85–1.93**	**1.961 ± 0.011** **1.94–2.00**	**1.883 ± 0.010** **1.87–1.93**	**1.963 ± 0.012** **1.94–2.01**	**1.515 ± 0.013** **1.49–1.53**	**1.551 ± 0.012** **1.53–1.59**	1.391 ± 0.011 1.37–1.42	1.393 ± 0.012 1.38–1.42	1.438 ± 0.012 1.41–1.45	1.470 ± 0.012 1.45–1.50
*FC*5	**1.882 ± 0.011** **1.86–1.94**	**1.960 ± 0.012** **1.94–2.00**	**1.887 ± 0.011** **1.87–1.94**	**1.963 ± 0.012** **1.94–2.00**	**1.513 ± 0.013** **1.49–1.53**	**1.549 ± 0.011** **1.53–1.58**	1.388 ± 0.012 1.37–1.41	1.388 ± 0.012 1.37–1.41	1.437 ± 0.011 1.41–1.46	1.468 ± 0.012 1.45–1.50
*FC*6	**1.881 ± 0.012** **1.86–1.94**	**1.960 ± 0.011** **1.94–2.00**	**1.886 ± 0.010** **1.87–1.94**	**1.964 ± 0.011** **1.95–2.01**	**1.514 ± 0.011** **1.48–1.53**	**1.548 ± 0.011** **1.53–1.58**	1.384 ± 0.012 1.36–1.40	1.385 ± 0.011 1.37–1.41	**1.437 ± 0.011** **1.41–1.45**	**1.469 ± 0.011** **1.45–1.50**
*FC*7	**1.882 ± 0.011** **1.86–1.93**	**1.960 ± 0.011** **1.94–1.99**	**1.887 ± 0.011** **1.87–1.94**	**1.962 ± 0.012** **1.94–1.99**	**1.512 ± 0.010** **1.48–1.53**	**1.547 ± 0.012** **1.52–1.58**	1.380 ± 0.012 1.36–1.40	1.381 ± 0.011 1.36–1.40	**1.435 ± 0.010** **1.41–1.45**	**1.468 ± 0.012** **1.45–1.50**
*FC*8	**1.883 ± 0.011** **1.86–1.94**	**1.960 ± 0.011** **1.94–2.00**	**1.888 ± 0.011** **1.87–1.93**	**1.954 ± 0.010** **1.93–1.98**	**1.512 ± 0.012** **1.48–1.52**	**1.546 ± 0.012** **1.52–1.58**	1.380 ± 0.011 1.36–1.40	1.380 ± 0.012 1.36–1.40	**1.434 ± 0.011** **1.41–1.45**	**1.467 ± 0.013** **1.45–1.50**
*FC*9	**1.882 ± 0.010** **1.86–1.94**	**1.961 ± 0.012** **1.94–2.01**	**1.886 ± 0.010** **1.87–1.92**	**1.931 ± 0.010** **1.91–1.98**	**1.511 ± 0.012** **1.48–1.52**	**1.544 ± 0.010** **1.52–1.58**	1.381 ± 0.011 1.36–1.40	1.381 ± 0.012 1.36–1.40	**1.433 ± 0.011** **1.41–1.45**	**1.466 ± 0.012** **1.45–1.50**
*FC*10	**1.882 ± 0.010** **1.85–1.94**	**1.959 ± 0.011** **1.94–2.00**	**1.886 ± 0.010** **1.87–1.90**	**1.914 ± 0.011** **1.89–1.94**	**1.510 ± 0.011** **1.48–1.52**	**1.544 ± 0.012** **1.52–1.58**	1.379 ± 0.011 1.36–1.39	1.380 ± 0.012 1.36–1.40	**1.432 ± 0.011** **1.40–1.45**	**1.465 ± 0.011** **1.45–1.50**
	Postanal centra with neural spines									
*FC*11	**1.880 ± 0.010** **1.86–1.93**	**1.958 ± 0.012** **1.93–1.99**	1.885 ± 0.009 1.87–1.90	1.905 ± 0.010 1.88–1.93	**1.509 ± 0.010** **1.48–1.52**	**1.542 ± 0.011** **1.52–1.57**	1.378 ± 0.009 1.35–1.39	1.391 ± 0.010 1.37–1.41	**1.431 ± 0.011** **1.41–1.45**	**1.463 ± 0.011** **1.44–1.49**

Table 4. (Contd.)

Centrum	*Salmo salar*		*S. trutta*		*Parasalmo mykiss*		*Oncorhynchus kisutch*		*Salvelinus malma*	
	parr	smolts	parr	smolts	parr	smolts	parr	smolts	parr	smolts
*FC*12	**1.878 ± 0.010** **1.85–1.93**	**1.958 ± 0.012** **1.93–1.98**	1.880 ± 0.009 1.86–1.90	1.888 ± 0.009 1.87–1.91	**1.506 ± 0.010** **1.48–1.52**	**1.540 ± 0.012** **1.52–1.56**	**1.379 ± 0.008** **1.35–1.39**	**1.410 ± 0.010** **1.39–1.43**	**1.429 ± 0.011** **1.41–1.45**	**1.462 ± 0.011** **1.44–1.50**
*FC*13	**1.878 ± 0.011** **1.85–1.92**	**1.958 ± 0.011** **1.93–1.98**	1.878 ± 0.009 1.86–1.91	1.880 ± 0.009 1.87–1.90	**1.504 ± 0.010** **1.48–1.52**	**1.537 ± 0.012** **1.51–1.56**	**1.377 ± 0.009** **1.35–1.40**	**1.422 ± 0.011** **1.40–1.44**	**1.425 ± 0.012** **1.40–1.44**	**1.460 ± 0.011** **1.44–1.49**
*FC*14	**1.877 ± 0.011** **1.84–1.92**	**1.957 ± 0.011** **1.92–1.98**	1.880 ± 0.008 1.86–1.90	1.881 ± 0.009 1.86–1.90	**1.502 ± 0.010** **1.48–1.51**	**1.532 ± 0.011** **1.51–1.56**	**1.377 ± 0.008** **1.35–1.39**	**1.421 ± 0.011** **1.40–1.44**	**1.423 ± 0.011** **1.40–1.44**	**1.459 ± 0.011** **1.44–1.48**
*FC*15	**1.877 ± 0.010** **1.84–1.92**	**1.956 ± 0.010** **1.92–1.98**	1.875 ± 0.008 1.86–1.89	1.880 ± 0.008 1.86–1.90	**1.492 ± 0.010** **1.47–1.51**	**1.526 ± 0.011** **1.51–1.55**	**1.370 ± 0.008** **1.35–1.39**	**1.422 ± 0.010** **1.42–1.45**	**1.423 ± 0.011** **1.40–1.44**	**1.455 ± 0.010** **1.44–1.48**
	Six last postanal centra (before urostilar centra)									
*PU*6	**1.869 ± 0.011** **1.84–1.89**	**1.949 ± 0.012** **1.91–1.97**	1.870 ± 0.009 1.85–1.90	1.872 ± 0.010 1.86–1.90	1.470 ± 0.009 1.45–1.49	1.475 ± 0.010 1.45–1.50	**1.368 ± 0.010** **1.34–1.39**	**1.419 ± 0.012** **1.39–1.44**	**1.420 ± 0.010** **1.40–1.44**	**1.454 ± 0.012** **1.43–1.48**
*PU*5	**1.860 ± 0.010** **1.82–1.89**	**1.943 ± 0.011** **1.91–1.96**	1.868 ± 0.008 1.84–1.89	1.870 ± 0.009 1.85–1.90	1.462 ± 0.009 1.44–1.48	1.471 ± 0.010 1.44–1.49	**1.366 ± 0.010** **1.34–1.39**	**1.417 ± 0.011** **1.39–1.44**	**1.418 ± 0.010** **1.40–1.43**	**1.449 ± 0.011** **1.43–1.48**
*PU*4	**1.808 ± 0.010** **1.78–1.84**	**1.915 ± 0.010** **1.88–1.94**	1.800 ± 0.007 1.77–1.83	1.803 ± 0.009 1.78–1.86	1.461 ± 0.008 1.44–1.48	1.462 ± 0.010 1.44–1.48	**1.364 ± 0.009** **1.34–1.38**	**1.412 ± 0.011** **1.39–1.43**	1.415 ± 0.010 1.39–1.43	1.422 ± 0.011 1.40–1.44
*PU*3	**1.713 ± 0.009** **1.69–1.74**	**1.886 ± 0.010** **1.86–1.91**	1.706 ± 0.007 1.68–1.74	1.711 ± 0.008 1.69–1.77	1.458 ± 0.008 1.43–1.48	1.460 ± 0.010 1.44–1.48	**1.360 ± 0.009** **1.34–1.38**	**1.404 ± 0.010** **1.38–1.43**	1.411 ± 0.011 1.39–1.43	1.412 ± 0.011 1.39–1.43
*PU*2	**1.667 ± 0.008** **1.62–1.73**	**1.779 ± 0.008** **1.75–1.83**	1.614 ± 0.006 1.58–1.63	1.711 ± 0.008 1.69–1.77	1.449 ± 0.008 1.43–1.47	1.451 ± 0.009 1.43–1.47	**1.355 ± 0.010** **1.33–1.37**	**1.397 ± 0.010** **1.37–1.42**	1.402 ± 0.010 1.38–1.42	1.404 ± 0.010 1.38–1.42
*PU*1	**1.501 ± 0.006** **1.30–1.62**	**1.689 ± 0.008** **1.66–1.79**	1.429 ± 0.005 1.39–1.46	1.432 ± 0.006 1.41–1.47	1.402 ± 0.007 1.38–1.42	1.403 ± 0.009 1.38–1.42	**1.322 ± 0.009** **1.30–1.34**	**1.378 ± 0.010** **1.36–1.40**	1.385 ± 0.011 1.37–1.41	1.387 ± 0.010 1.37–1.41

See the sequence numbers of the centra in Fig. 1b; the values in bold mean the significant differences ($p < 0.05$) between the parr and smolts.

increased in the cultivated and wild juveniles subjected to smoltification. These data correspond with our results obtained on wild juveniles of Atlantic salmon (Tables 2, 4).

The nature of this transformation (i.e., a substantial increase in relative lengths of vertebral centra only in certain regions of the vertebral column) is not studied well (Fjelldal et al., 2006, 2007; Björnsson et al., 2012). According to some authors, the changes in vertebral centra proportions are connected with the level of their mineralization and calcium content in blood plasma (Björnsson et al., 1989, 2012; Helland et al., 2005). The vertebral centra and neural spines are substantially demineralizated in migrating smolts at the final steps of smoltification in the river but before their entrance to the sea (Björnsson et al., 1989; Fjelldal et al., 2005, 2006, 2007; Helland et al., 2005). In several cases, for example, at extremely high growth rate of the juveniles during intensive culture in the condition of continuous illumination, demineralization of vertebral centra is regarded as a reason for the appearance of abnormally flattened centra in the postanal part of the body (Fjelldal et al., 2005, 2006, 2007; Witten et al., 2005). However, similar abnormalities have not been observed in wild juveniles (Fjelldal et al., 2007). In our opinion, demineralized vertebrae developing in the beginning of smoltification in fresh water and described in the cited works should lead to decreasing hardness of bone tissues particularly by the period of the increasing pressure to the axial skeleton in saline water. This pressure can provoke the appearance of deformations of centra shapes, but, in reality, such deformations are not registered. We can suppose that demineralization does not spread to a whole centrum, but it occurs only in its internal part, and the hardness of its peripheral covers used for the attachment of the caudal peduncle muscles remains.

According to several authors, the growth of the vertebral centra in the preanal an postanal parts of the vertebral column can be regulated independently, but possible mechanisms of such regulation are poorly studied (Fjelldal et al., 2005; Nordvik et al., 2005). One of the mechanisms is a special rhythm of certain genes' (*Hox*) expression, which have a selective effect on different regions of the vertebral column, as has been demonstrated for zebrafish *Danio rerio* and threespine stickleback *Gasterosteus aculeatus* (Prince et al., 1998; Ahn and Gibson, 1999; Morin-Kensicki et al., 2002; Agathon et al., 2003). According to several studies, the elongation of the vertebral column's postanal part and, respectively, caudal peduncle is a consequence of a cumulative effect of vertebral demineralization and mechanical stimulation. The latter process is connected with prolonged swimming and increasing pressure to the postanal part of the body due to the transition of the juveniles from a sedentary mode of life in shelters (in a zone of hydrodynamic shadow) to active swimming in a pelagic environment (Björnsson et al., 1989, 2012; Fjelldal et al., 2005).

The complex heterochronous processes of the selective growth of different regions of the vertebral column associated with smoltification are most likely responsible for substantial changes in the smolts' phenotype. Nevertheless, based on the results of this study, the changes in body proportions and external morphology are identical in the studied salmonid species and genera, but the growth features in the postanal part of the body are substantially different. The following vertebral centra of the vertebral column's postanal part are subjected to elongation in different species: all centra in Atlantic salmon, a comparatively small number of centra only in the anterior region of the postanal part in mikizha and brown trout, the centra in the posterior region of the postanal part in coho salmon, and the centra in the middle region of the postanal part in Dolly Varden (Table 4, Fig. 3). Thus, despite observed universal changes of the external morphology associated with smoltification in the representatives of the family Salmonidae, the development of the phenotypes of marine migrants occurs by means of differentiated growth of various regions of the postanal part of the body, and this process is species-specific. The data obtained in this study can be regarded as preliminary because only one population of each species has been analyzed. To take into account a wide spectrum of environmental conditions within the range of each species, the intraspecific variation in the features of vertebral centra proportions' changes at a population level of species structure cannot be excluded.

Observed species specificity of the differentiated growth of vertebral centra in the vertebral column's postanal part could be connected with the extension of marine migrations in the life cycles of the studied species. In particular, the elongation of the caudal peduncle is expressed in brown trout and Dolly Varden at the lowest degree because a small vertebral centra number (less than ten) are subjected to the increase of their relative lengths. In brown trout, a small elongation of the caudal peduncle could be connected with restricted and short (for 1.5–2.5 months) migrations observed mainly in the coastal zones (Suslova, 1969; Ershov, 1985; Chernitskii, 1993, 1994; Kuzishchin, 1997). The life cycle of northern Dolly Varden is similar: the juveniles forage in the coastal shelf zones under the influence of continental flow (Armstrong, 1974; DeCicco, 1992; Morita et al., 2009). The largest number of vertebral centra subjected to transformations associated with smoltification is registered in Atlantic salmon. This species is characterized by a rapid movement from the coastal zones to te pelagic environment of the sea and prolonged and distant migrations in the open areas (Reddin, 1985, 1987; Reddin and Short, 1991; Reddin and Friedland, 1993). For example, the Atlantic salmon of the White Sea basin migrates into the Barents Sea for foraging during the first summer of marine life and does not remain in the White Sea for wintering (Kazakov, 1982; *Atlanticheskii*..., 1998).

Nevertheless, observed features of different species could be a consequence of specific development and calcification of the vertebral centra at early developmental steps, and the species specificity could remain until smoltification. The sequence of the development and formation of the rings of vertebral centra is directed from the head to the tail (with the exclusion of urostilar centra): the centra of the vertebral column's postanal part are the last to develop and mineralize. At an equal developmental speed of each centrum, the duration of growth, differentiation, and calcification of the centra of the postanal part is the largest. Therefore, the centra of the postanal part are characterized by initially low mineralization in comparison with that in the centra of the preanal part. A low mineralization is compensated by a substantial hardness of peripheral surfaces of the centra subjected to maximum pressure. This pressure is connected with the attachment of the caudal peduncle muscles.

In the early ontogeny of the studied species (excluding northern Dolly Varden), the anlages of the centra appear for 1–2 weeks, and their development is strictly associated with the emergence of the larvae into the water current and their initial spatial distribution (Pichugin, 2009; our data). The somatic growth, increase of muscular mass, and muscle differentiation connected with the developmental of the axial skeleton are observed during this short period. These processes coincide with the onset of complex and prolonged movements of the larvae in the water current (Pichugin, 2002, 2009, 2015). It is important to note that the development of the axial skeleton begins during the endogenous feeding of the progeny or just after the transition of the larvae to exogenous feeding, and this development terminates during the accelerated growth of the young (Pichugin, 2009, 2015). Similar events are observed during smoltification. The differentiated growth of the vertebral centra in the vertebral column's postanal part begins during the downstream migration and temporal starvation of the juveniles (i.e., it depends on accumulated fat reserves) (Fjelldal et al., 2007; Pavlov et al., 2011; our data), and the growth of the centra terminates during the growth spurt (the term according to Fjelldal et al. (2007)) and recovery of the feeding after the entrance of the juveniles into brackish water.

The development and growth of the vertebrae in the smolts of different salmonid fish species are observed at various temperature, and this factor is important for the rate of development, formation of the vertebral rings, neural and hemal spines, and calcification of the centra. In mikizha, the development of the centra anlages begins before the onset of the step of mixed feeding (SMF) at a temperature of 13–16°C (Pichugin, 2009; Pavlov et al., 2016). In coho salmon, this process begins before the SMF or in the beginning of the SMF at 6–11°C (Kirillova, 2008). In Atlantic Salmon of the Tuloma River, this process begins more than 2 weeks before the SMF at 10–12°C (Zubchenko et al., 1989). In anadromous brown trout from the streams of the White Sea basin, the development of the centra anlages begins just after the transition of the larvae to the SMF at 7–8°C (Pavlov, 1989). The most prolonged process in formation of the centra anlages not connected with the initial spatial distribution of the young is observed in northern Dolly Varden. The juveniles of this species remain at the spawning grounds for more than one year, and their initial distribution begins at advanced stages of morphological development (Pichugin, 2015). The pattern of vertebral centra formation in the early ontogeny, most likely, has an effect on the differentiated growth of the centra in the subsequent ontogeny during smoltification.

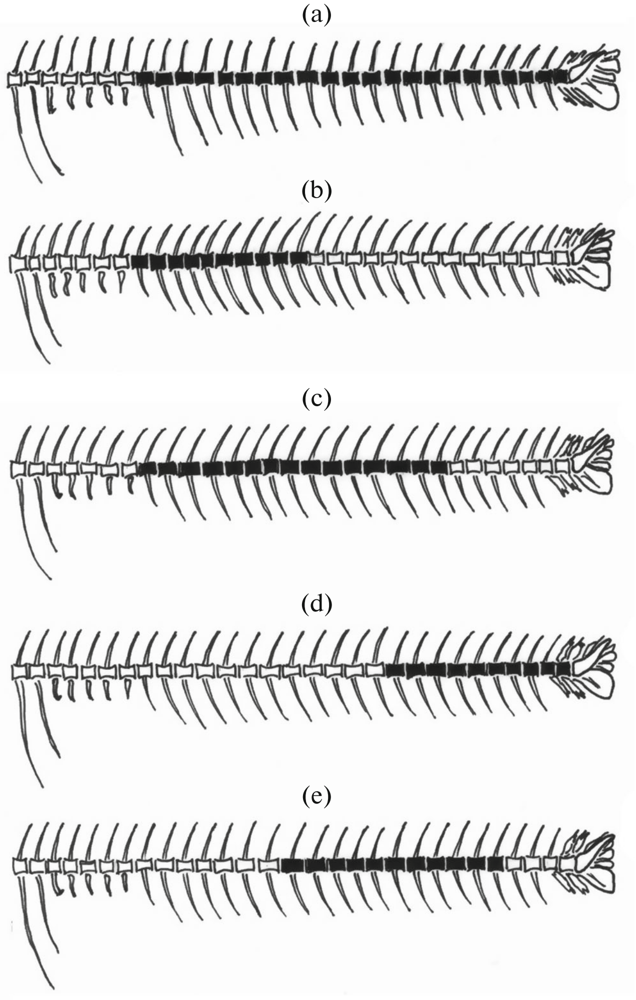

Fig. 3. Scheme of the vertebral column's postanal part; the vertebral centra significantly elongated in the smolts in comparison with the parr are black: (a) Atlantic salmon *Salmo salar*; (b) brown trout *S. trutta*; (c) mikizha *Parasalmo mykiss*; (d) coho salmon *Oncorhynchus kisutch*; (e) northern Dolly Varden *Salvelinus malma*.

Thus, based on the analysis of external morphological characters and relative lengths of the vertebral centra from different parts of the vertebral column during smoltification of wild juveniles from five salmonid fish species, parallel adaptations are revealed. These adaptations are connected with the change in the modes of life: from the territorial life in the biotopes with shelters and a complex system of turbulent currents in the river to active and prolonged migrations in the water mass in the sea. Despite observed universal changes of the body shape, the differentiated growth of the vertebral centra is species-specific. Nevertheless, the results of this study can be regarded as preliminary, and the analysis of intraspecific variation in other populations of the species should be conducted.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interests.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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