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Telomere length decreases during early life stages in peled

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ABSTRACT. The different type of the age-related dynamics of telomeric DNA in different species indicates the complex mechanisms for regulating telomere length. In fish, telomere length can decrease, be maintained or increase during ontogeny. The cause of this is still unclear, but we assume that the regulation of telomeric DNA length may depend on the activity of protective systems and distribution of energy resources between tissues. We studied age-related dynamics of telomeric DNA in muscles and fins of peled, *Coregonus peled*, a valuable commercial fish that is widespread in the Russian North and used for successful acclimatization. Using quantitative PCR, we revealed a shortening of telomeric DNA in both tissues during the first two years of life of peled. Perhaps, a pattern of telomeric DNA dynamics is associated with the species-specific features of growth and development since some other salmonids maintain telomere length in the first years of life.

Keywords: telomere length, telomere dynamics, age, *Coregonus peled*

1. Introduction

In the 1960s, L. Hayflick and co-authors published the data showing that human diploid cells divide approximately 50 times (Hayflick and Moorhead, 1961; Hayflick, 1965). This doubling limit of somatic cells is now called the Hayflick limit and associated with the end-replication problem (Olovnikov, 1971; 1973). At the ends of chromosomes, DNA has a special structure and together with proteins forms telomeres (de Lange, 2005). Telomeres protect the rest of DNA from degradation and prevent fusion of chromosomes with each other (Deng and Chang, 2007). Due to the end-replication problem, each cell division leads to a decrease in telomeres. This enables considering telomeres as a mitotic clock, on which the proliferative potential of cells depends (Harley et al., 1990; Allsopp et al., 1992). The obtained data allowed telomeres to be attributed to one of the nine key biomarkers of ageing (López-Otín et al., 2013). At the same time, there are some examples in various taxonomic groups when the age-related dynamics of telomeric DNA (tDNA) has a different type: in mollusks (Gruber et al., 2014; Maximova et al., 2017), fish (Gao and Munch, 2015), reptiles (Paitz et al., 2004), birds (Caprioli et al., 2013), etc. Normally, tDNA dynamics is associated with telomerase activity, an enzyme that maintains the telomere length (Greider and Blackburn, 1989). However, cases when telomeres can decrease in the presence of active telomerase indicate the more complex mechanism for regulating the length of tDNA (Hatakeyama et al., 2008; Hartmann et al., 2009). External and internal factors, such as UV and radiation, intense sound, temperature, or oxidative stress (Oikawa et al., 2001; Doroshuk et al., 2013; Injaian et al., 2019; Singh et al., 2019), can also influence the length of tDNA, which partly explains the loss of telomeric repeats in non-dividing cells.

tDNA of vertebrates consists of short TTAGGG repeats and has different lengths, depending on species (Meyne et al., 1989; Gomes et al., 2011; de Abechuco et al., 2016). Fish were the first vertebrates that showed a decrease in tDNA in the presence of active telomerase (Hatakeyama et al., 2008; Hartmann et al., 2009). Telomerase can perform functions that are not related to maintaining telomeres and be involved in the regulation of the cell cycle, proliferation, regeneration, apoptosis, and some other processes (Romaniuk et al., 2019). Therefore, the presence of active telomerase does not guarantee the maintenance of telomeres and, hence, the absence of the Hayflick limit. A decrease in telomeres is rather associated with tissue type and metabolic characteristics than proliferative potential, as shown for *Danio rerio* Hamilton 1822 (Carneiro et al., 2016). Fish belong to animals with a very high phenotypic plasticity, which is evolutionarily associated

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with their strong dependence on environmental conditions (Woodhead, 1998). On the one hand, the constant growth typical of fish along with a need to respond to stresses loads the replicative and preparative systems of cells in some tissues and can decrease tDNA (Hatakeyama et al., 2008; Carneiro et al., 2016). On the other hand, there are some examples when tDNA does not decrease in fish (Horn et al., 2008; Izzo et al., 2014; Gao and Munch, 2015). This can be due to the different activities of telomerase, which in one case maintains telomeres, and in other cases, it does not. Nevertheless, we should not exclude the more complex mechanism for regulating tDNA dynamics involving many factors.

Coregonus peled Gmelin 1789 is species of whitefish that is widespread in the Russian North. Peled tolerates significant fluctuations in temperature and water composition. It also has a wide nutrition spectrum, and with feed abundance, it can quickly gain weight. Owing to these abilities, this fish acclimatizes well and currently inhabits various water bodies of Russia and other countries (Mukhachev, 2003). Members of the order Salmoniformes, *Oncorhynchus kisutch* Walbaum 1792 and *Salmo trutta* Linnaeus 1758, maintain the telomere length during first years of life (Naslund et al., 2015; Pauliny et al., 2015). This study aimed to assess the age-related dynamics of tDNA in *C. peled*, other valuable salmonid species.

2. Materials and methods

The study material was brought from the Belsk fish hatchery (Irkutsk Region, Usolsky District, Baikalskaya Ryba LLC). Until the analysis, the material was kept in the unique facility “Experimental freshwater aquarium complex of Baikal hydrobionts” at Limnological Institute SB RAS. Eggs and larvae of peled were kept at a temperature of 4-5°C; fish – in a pool with a water temperature of ~15°C. Individuals in three stages of ontogeny were selected: eggs (five-six months, n = 29), larvae (one-two days after hatching, n = 26) and two-year individuals (n = 22). Among them, there were females and males in the maturity stages I-II. To analyze the length of telomeres, we used white muscles (for individuals in all three stages) and fins (for larvae and two-year adults).

Genomic DNA was extracted using the phenol/ chloroform method (Sambrook et al., 1989) because it allows obtaining DNA samples of high quality (Voropaeva et al., 2015). Relative telomere length (telomere DNA concentration/ DNA concentration of single copy-gene, T/S) was measured by qPCR as described in Cawthon, 2002. The qPCR was carried out using the Rotor-Gene Q 6000 (QIAGEN, Germany). The gene of GAPDH served as a reference gene. Primer pair was designed using the gene sequence of Atlantic salmon (BT045621). Primer sequences were GCACTCACACCCTCCATAAC (forward) and ACAGCCTACGACAGAGACTAA (reverse). qPCR was made in presence one-fold *Snp*-buffer, 0.25 мМ dNTPs, 0.2 U *Snp*-polymerase (Evrogen, Russia), 0.1-0.4 ng DNA, SYBR Green (1:20000) (Lumiprobe, Russia), 0.5 pmol primers for GAPDH gene. In the case of telomeric repeats during qPCR, 0.17 pmol Tel1 and 0.5 pmol Tel2 primers were added to the reaction mixture instead of primers for the GAPDH gene. Amplification conditions of telomere regions and the reference gene were different. The polymerase was activated at 95 °C for 3 min. The telomere reaction was immediately subject to 35-40 cycles at 95 °C for 15 s and 54 °C for 2 min. Touchdown PCR was used for the amplification of the reference gene fragment. The primer annealing temperature gradually decreased from 64 to 58 °C for the first seven cycles. One cycle included the following stages: 95 ºC for 10 s, 58 ºC for 15 s and 72 ºC for 15 s. It was repeated 35-40 times. To determine significant differences between telomere length in different age groups, Mann-Whitney U-test was used. T/S values are presented as mean ± SD with 95% CI. CI for means was estimated using the bootstrap method in R version 3.6.2 (Shitikov and Rosenberg, 2013). To estimate differences between samples in percent, we also calculated an inequality between means and 95% CI with the bootstrap method.

3. Results

In the muscle tissue, we analyzed relative telomere length (RTL or T/S) at the final stage of eggs development, in larvae and two-year individuals. The values were 1.01 ± 0.14 (95% CI 0.96 to 1.06), 0.97 ± 0.094 (95% CI 0.932 to 1.003) and 0.91 ± 0.103 (95% CI 0.864 to 0.95), respectively. In fins, RTL was analyzed in larvae and two-year individuals and amounted to 1.06 ± 0.102 (95% CI 1.02 to 1.097) and 0.88 ± 0.092 (95% CI 0.843 to 0.92), respectively. In larvae, RTL was much higher in fins than in muscles (T-test for Dependent Samples: $t = -3.38$, $df = 25$, $p = 0.002$), whereas two-year individuals already had no differences (T-test for Dependent Samples: $t = 0.99$, $df = 21$, $p = 0.333$). Subsequent analysis of the RTL age-related dynamics revealed a significant decrease in tDNA during the early life stage in both tissues (Fig. 1). In this fish, from larvae stage to two-year individuals, RTL decreases by 6% (95% CI 0.7% to 11.6%) in muscles (Mann-Whitney U Test: $U = 218.5$, $Z = 1.99$, $p = 0.046$; $R = -0.32$, $p = 0.024$) and 17.7% (95% CI 12.6% to 23.3%) in fins (Mann-Whitney U Test for fins: $U = 57.5$, $Z = 4.97$, $p = 0.0000$; $R = -0.67$, $p = 0.0000$). Overall, 10.4% (95% CI 3.8% to 16.7%) of tDNA is lost in muscles between the final stage of eggs development and the stage of two-year individuals (Mann-Whitney U Test: $U = 217.5$, $Z = 2.33$, $p = 0.0196$; $R = -0.32$, $p = 0.004$). RTL in muscles and fins of the same individual generally had different values in the stages of larvae and two-year individuals.

4. Discussion and conclusions

In some animals (primates and birds), the length of tDNA and its dynamics are regarded not only as biomarkers of ageing but also biomarkers of experienced stresses (Louzon et al., 2019). For poikilotherms, which include fish, dependence on variable environmental factors has contributed to the development of protective mechanisms that provide the well-known plasticity of these animals (Woodhead, 1998; Petitjean et al., 2019). Could this lead to the appearance of the same tDNA regulation within this class of vertebrates and, hence, to tDNA dynamics? Analysis of the available data on the tDNA age-related dynamics in fish and its sensitivity to stress allows us to answer in the negative. In the same tissue of different fish species and different tissues of the same fish species, the tDNA dynamics may differ (Table).

In peled, during the early life stages, tDNA decreases in two tissues: muscles and fins (Fig. 1), unlike other members of salmonids, although they have a similar life expectancy (Naslund et al., 2015; Pauliny et al., 2015, see Table). Moreover, close species of salmonids (brown trout and Atlantic salmon) showed an opposite correlation of tDNA length with water temperature. At high temperature, tDNA of *S. trutta* decreased (Debes et al., 2016). On the contrary, growth of *S. salar* during the early stages of ontogeny at different temperatures, including high temperature, led to an increase in tDNA (McLennan et al., 2016; 2018). These data indicate species-specific mechanisms for regulating telomere length under stress conditions as well as a general species-specific dynamics of tDNA during ontogeny.

Different dynamics of tDNA can also be the result of stresses having different effects. Severe stress disables protective systems of an organism, whereas moderate stress mobilizes them (Petitjean et al., 2019). For different species, threshold sensitivity to environmental changes may vary, and protective systems may function differently in different tissues. Cod, *Gadus morhua* Linnaeus 1758, showed most tDNA losses in the liver, a metabolically loaded organ, and insignificant losses in the muscles (de Abechuco et al., 2016). *Danio rerio* had short telomeres in the muscles and the gut, which is likely due to degenerative and inflammatory processes (Carneiro et al., 2016). Thus, the regulation of telomere length occurs differently in the same tissues of different species. Both the functional load of the tissue and a degree of the stress effects during the development of an organism may contribute greatly to this process. Perhaps, regulation of telomere length in peled depends on peculiarities of their growth and development during the early life stages.

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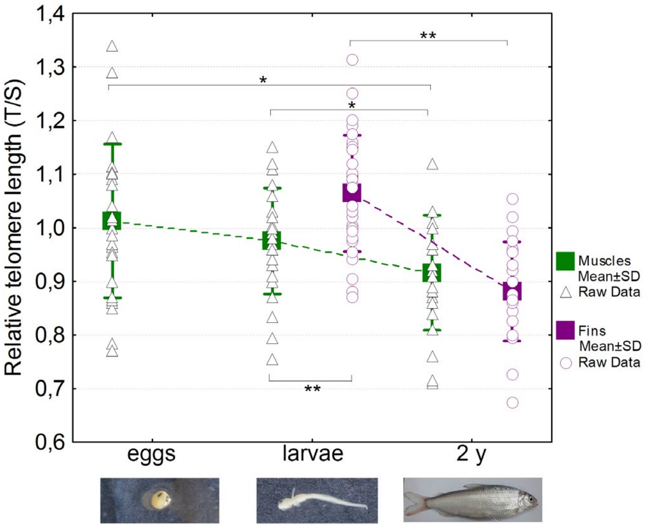

Fig. 1. Age dynamics of tDNA in muscles and fins of peled. It is shown the shortening of telomere length in both tissues. The asterisks denotes a significant difference between the groups (Mann-Whitney U Test): * - p<0.05, ** - p<0.005.

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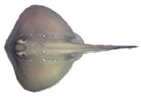
Table. Age telomere length dynamics in different species of fish, their appearance and lifespan

Species, common name	Appearance	ML¹	TL dynamics		Reference
			muscle	fin	
Chondrichthyes (cartilaginous fish)					
Heterodontus portusjacksoni, Port Jackson shark		35 y	↔	↔	Izzo, 2010
Squalus megalops, Piked spurdog		75 y	↔		Izzo, 2010
Urolophus paucimaculatus, Sparsely spotted stingray		12 y	↔		Izzo, 2010
Dentiraja lemprieri, Thornback skate		12 y	↔		Izzo, 2010
Trygonorrhina dumerilii, Southern fiddler ray		15 y	↔		Izzo, 2010
Callorhinchus milii, elephant shark		6 y	↔		Izzo, 2010
Osteichthyes (bony fish)					
Chrysophys aurutus, Snapper		35 y	↓		Izzo, 2010
Cyprinus carpio, Common carp		11 y	↑	↔	Izzo et al., 2014
Lutjanus argentimaculatus, Mangrove red snapper		7 y	↓		Tsui, 2005
Macquaria ambigua, Golden perch		20 y	↔		Izzo, 2010
Menidia menidia, Atlantic silverside		2 y	↔		Gao and Munch, 2015
Neoceratodus forsteri, Australian lungfish		65 y	↔		Izzo, 2010
Nothobranchius furzeri (GRZ), Turquoise killifish		3.5 mo	↔		Hartmann et al., 2009
Nothobranchius furzeri (MZM-0403)		6 mo	↓		Hartmann et al., 2009
Oryzias latipes, Medaka, Japanese rice fish		5 y	↓		Hatakeyama et al., 2008
Platycephalus bassensis, Sand flathead		23 y	↓		Izzo, 2010
Pseudocaranx wrighti, Silver trevally		13 y	↔		Izzo, 2010
Thamnaconus degeni, Degen's (bluefin) leatherjacket		18 y	↓		Izzo, 2010
Trachurus novaezelandiae, Southern yellowtail scad		25 y	↔		Izzo, 2010
Upeneichthys vlamingii, Southern goatfish		10 y	↓		Izzo, 2010
Gadus morhua, Atlantic cod		25 y	↔		de Abechuco et al., 2016
Gambusia holbrooki, Eastern mosquitofish		3 y	↓		Rollings et al., 2014
Danio rerio, Zebra-fish		5.5 y		↓	Henriques et al., 2013

Acipenser baerii, Siberian sturgeon		60 y		↓	Simide et al., 2016
Salmo trutta, Atlantic brown salmon, trout		11 y		↔	Naslund et al., 2015
Oncorhynchus kisutch, Coho salmon		5 y		↔	Pauliny et al., 2015
Coregonus peled, Peled		12 y	↓	↓	This study

[1] – Maximum lifespan, sometimes it depends on the population (for example, the lifespan of *Salmo trutta* can vary from 4 to 11 years (Jonsson et al., 1991)). Arrows describe telomere shortening (↓), maintenance (↔), or increasing (↑) with age. Some data for the table were taken from E.I. de Abechuco et al., 2016 and R. Simide et al., 2016.