Structural and functional adaptations of epilithic lichens of *Umbilicaria* genus in the White Sea coastal conditions

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Abstract

Anatomical and physiological characteristics (width of anatomical layers and the amount of photosynthetic pigments) of two epilithic lichen species *Umbilicaria torrefacta* (Lightf.) Schrader and *U. deusta* (L.) have been studied. The study took place on the supralittoral zone on the coast of the White Sea in two points: Kolezhma village and Keret village in 2014 and 2015. Ecological plasticity of mycobiont which contacts the environment and gives a niche to the photobiont have been revealed, based on the analysis of variance in the study of anatomical structures of two different types of habitats and between different samples of the same species. Coastal conditions provide favorable levels of humidity and light for the *U. torrefacta* and *U. deusta* species. This allows symbiotic organism to maintain a symbiotrophic balance due to the plasticity of the fungal symbiont which contacts the abiotic environment. At the same time these adaptation mechanisms do not include functional changes, such as photosynthetic apparatus of the autotrophic symbiont, conditions for which are set by the fungal organism. *U. deusta* and *U. torrefacta* species only show structural adaptations - the adaptations that follow the path of anatomical structure changes and the relative stability of the physiological parameters. The study shows that anatomical structure of thalli varies more significantly between the two species than within samples of the same species.

Key words: coastal zone, lichens of *Umbilicaria* genus, anatomy, physiology, adaptations

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Introduction

Epilithic lichens are phototrophic components of coastal ecosystem of the White sea. Sea coasts of the Arctic region are characterized by severe conditions, as a result of regional climatic conditions and the influence of the sea dynamical processes. Terrestrial biota, including epilithic lichens that inhabit the coastal rocks and boulders are located in the border area of sea and a coastal land. It is, therefore, exposed to microclimate factors from the two ecosystem elements. Thus, epilithic lichens of sea coasts are divided into two distinct groups depending on the location on the coast and on their adaptations: halophytes and nonhalophytes (Sonina 2014). Nonhalophyte lichens which inhabits rocky substrates in supralittoral area are distinguished by the variety of life forms (ranging from crustose to fruticose) and adaptive potential to the environmental conditions. One of the dominant lichen genus on supralittoral areas of the White Sea coast is *Umbilicaria* genus. *U. torrefacta* (Lightf.) Schraderis a common species for the White Sea coats. Contrastingly, according to our observations *U. deusta* (L.) is significantly less common in lichen cover of the coast. This group of organisms is a complex formed by genetically different objects.

Umbilicaria genus lichen thalli were used as the material for the anatomical and physiological research. There are 12 species of *Umbilicaria* genus in Karelian flora (Fadeeva et al. 2007). The study includes two species: *Umbilicariadeusta* and *U. torrefacta* that belong to *Umbilicariaceae* family. *Umbilicariaceae* Cheval. family is an isolated group of lichenized Ascomycetes with an uncertain systematic position. Most species live on the rocks, mainly in polar and mountain areas of Russia (Davydov 2007). All the species are obligatory epilithic and have umbilicate foliose thallus. Their morphology is characterized by the presence of gomphus (lower cortex structure) which attaches the thallus to the substrate. Phototrophic biont is a green unicellular alga of *Trebouxia* genus (Purvis et al. 1992).

The purpose of this study is to identify the structural and functional adaptations of two lichen species, *Umbilicaria torrefacta* and *U. deusta* to the conditions of the White Sea coast. To evaluate interspecific differences, we used several anatomical and physiological characteristics.

Material and Methods

U. deusta species is a Holarctic mountainous species that grows on the silicate rock outcrops in Hypoarctic area and the mountains of Europe, Asia, North America, Greenland. It is found in the Palearctic, Nearctic, Neotropical and Australasian regions. *U. torrefacta* species is widely spread only within the Holarctic in the Palearctic and Nearctic biogeographical regions (Byazrov 2013). It is an arctic-alpine species spread in the Holarctic (Davydov 2004).

The two species selected for this study have wide environmental ranges: they can be spotted from dry broadleaf subtropical forests to tundra at high latitudes (Byazrov 2013). Due to their broad environmental characteristics, these species must have structural and functional diversity. In our study, we tested this hypothesis. *U. deusta* on the White Sea coast is less common than the *U. torrefacta* species and it prefers rocks at the top of supralittoral area. Such sites are never reached by sea splash and spray. *U. torrefacta* species, however, covers a wider range of coastal habitats. It can be found on rocks within the entire supralittoral. It can be affected by sea water only occasionally.

The study of *U. deusta* and *U. torrefacta* took place in the Republic of Karelia, on the shore of the White Sea in the surroundings of Kolezhma village (Belomorsk district), Pomorsky coast. The area is bordered by the Gulf of Onega and Keret village (Louhi district), located in the Kandalaksha Gulf (Fig. 1). The study was conducted during the period of 2014-2015.

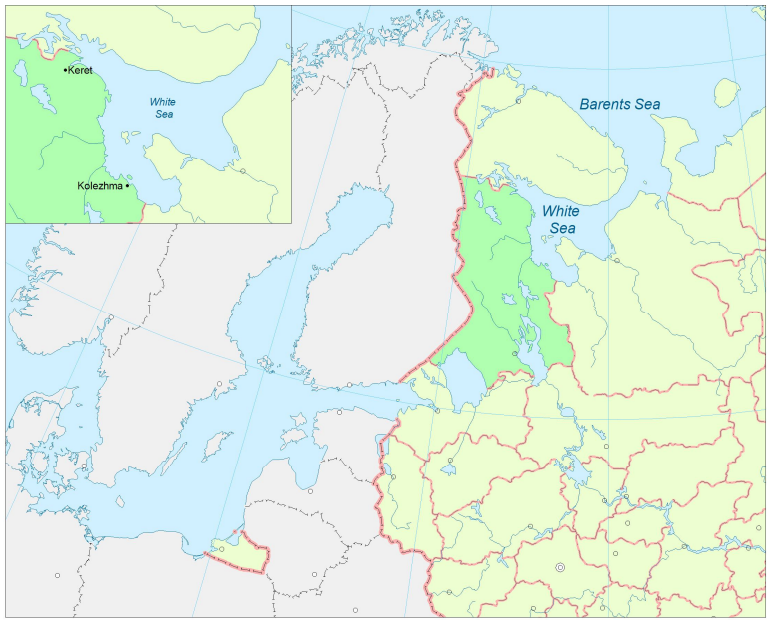

Fig. 1. Study area: Keret – Louhi district, Kolezhma –Belomorsk district, Karelia Republic.

The samples of lichen thalli were taken within the investigated area on the coast along transect lines running from the water line to the soil-plant complex.

Environmental parameters that were estimated for the studied species in their natural habitat were (1) the distance from the water line, (2) the angle and orientation of the substrate surface (determined by a miner`s compass), (3) illumination of the habitat by lightmeter (lightmeter "TKA LUX", Russia). The measured parameters reflect the influence of water factor and illuminating intensity of the habitat.

Samples of *U. torrefacta* thalli were taken from 4 transects in the surroundings of Keret village (average length of transect lines – 48 m: ~ 40 m – zone of littoral, ~ 10 m – supralittoral). The study took place within the Lebyazhya bay in the floodplain of the Keret river. The water in the estuary had a high salinity (24 ‰). Littoral and supralittoral flora is typical for the White Sea coast (Markovskaya et al. 2010). Lichens grow on rocks, formed by granite gneisses with coarse-grained structure, chipped and cracked, and also glacial origin boulders. All selected thalli grew at supralittoral areas. Within each transect, there were 10-20 lichen thalli collected from the plot 1 x 1 m, as one sample.

Another place of sampling was the White Sea coast in the surroundings of Kolezhma village on the Bratov cape. The cape is the output array of granite gneisses [2], which is 30° inclined and goes down into the water, and in the upper horizontal part of the slope there is an early-developed

soil with grasses and heather domination. The substrate surface is coarse, with a large number of chips and cracks. The studied lichen species inhabited two lichen zones: zone 3 - the bottom of the supralittoral, these areas of rocks can be sprinkled with salt water during storms, and zone 4 - the upper supralittoral that water splashes do not reach, where the rock areas adjoin the soil covered by plants (Markovskaya et al. 2010). Altogether, 6 samples of *U. torrefacta* and *U. deusta* thalli were taken here. Samples number 3, 6 and 12 were identified as *U. torrefacta* and also 3 samples of *U. deusta* grew together in zone 4. Three samples of *U. torrefacta* number 4, 7, and 10 were found in zone 3.

Lichen thalli were selected in the places with a high abundance of the studied species (80-100% coverage). We picked thalli of the same size and with similar morphological features (same ontogenetic state).

Altogether, there were 13 samples of lichen thalli collected (each contained 10-20 thalli): 4 samples in the surroundings of Keret village (*U. torrefacta*) and 9 samples in the surroundings of Kolezhma village (3 - *U. deusta*, 6 - *U. torrefacta*).

Anatomical characteristics

The collected species were identified at the laboratory using the standard lichen identification methods (Sonina et al. 2006). Anatomical studies included optical microscopy-based measurements of the thickness of the upper and lower cortex, the algal layer, the medulla and overall thallus thickness. Each layer in each sample was measured 60 times. We used a binocular MSP-10 (LZOS, Russia) and MIKMED-6 (Lomo, Russia) microscopes. Totally, more than 740 slices and 4,000 measurements were made.

Photosynthetic pigments

Determination of photosynthetic pigments concentration was done using an ethanol extract and the methods (Sapozhnikov et al. 1978, Lichtenthaler et Wellburn 1983, Maslova et Popova 1993) using a spectrophotometer SF-2000 UV/Vis Spectrophotometer (Spectr, Russia) at the absorption maxima – 665 and 649 nm for chlorophyll *a* and *b*, accordingly. Determination of carotenoids was carried out at 470 nm with an adjustment for the shift of the absorption spectra according to Maslova et al. (1986). The concentration of pigments was calculated by the following equations, according to Lichtenthaler et Wellburn (1983):

$C_a = 13.95*A_{665} – 6.88*A_{649}$ [μg/ml]
$C_b = 24.96*A_{649} – 7.32*A_{665}$ [μg/ml]
$C_{x+c} = (1000*A_{470} – 2.05* C_a – 114.8* C_b)/245$ [μg/ml]

The concentration of pigment in the extract and its content in the sample was calculated: Co = C * V/ m * 1000
where, Co [Chl *a*, Chl *b*, Car] – is the content of the pigment [mg/g dry (or fresh) weight]; C – is the concentration of pigment [μg/ml]; V – is the volume of extract [ml]; m – is the linkage of plant material [g dry (or fresh) weight].

The pigments were determined with a triple biological replication and nine chemical replicants.

Data processing and statistical analysis

Data processing was done on the basis of ANOVA using Excel (Ivanter et Korosov 2010). We analyzed the distribution of logarithmic values of lichen thalli anatomical parameters. Tables 1 and 2 show the mean values (M) of anatomical layers thickness in lichen thalli and the median (Me) logarithms of the layer thickness. Study of relationships between the parameters of the photosynthetic complex (the concentration of photosynthetic pigments) and the width of thalli anatomical layers of *U. deusta* and *U. torrefacta* was accomplished using correlation and regression analysis.

Results

The study of thalli anatomical structures showed a significant variation in the thickness of algal layers and medulla in *U. torrefacta* samples in the surroundings of Keret village (Table 1, 2; Fig. 2, 3). The algal layer thickness ranged from 25 to 62.5µm, the medulla – 40 to 77.5µm. The thallus width varied from 85 to 172.5µm. The upper and lower cortex formed by the fungal biont varied in a narrow range of values: upper cortex (10 to 15µm), lower cortex (15 to 23µm). Thalli anatomical layers in Kolezhma varied slightly (Table 1, 2; Fig. 2, 3): upper cortex (15 to 25µm), algal layer (50 to 65µm), the medulla – (90 to 105µm), and the lower cortex varied from 15.0 to 27.5µm.

Transect number	UC (µm)	Log UC	AL (µm)	Log AL	MED (µm)	Log MED	LC (µm)	Log LC	TW (µm)	Log TW
	Me	M	Me	M	Me	M	Me	M	Me	M
1	15.0	1.2	37.5	1.6	43.7	1.7	17.5	1.2	112.5	2.1
3	15.0	1.2	62.5	1.8	77.5	1.8	17.5	1.2	172.5	2.2
4	12.5	1.1	52.5	1.7	50.0	1.7	25.0	1.4	128.7	2.1
5	10.0	1.0	25.0	1.4	40.0	1.6	15.0	1.2	95.0	2.0

Table 1. Anatomical structure of *U. torrefacta* lichen thallus samples in the surroundings of Keret village. *Legend*: UC – upper cortex, AL – algal layer, MED – medullae, LC – lower cortex, TW – thallus width, µm – micrometer; M – mean (n=60), Me – median.

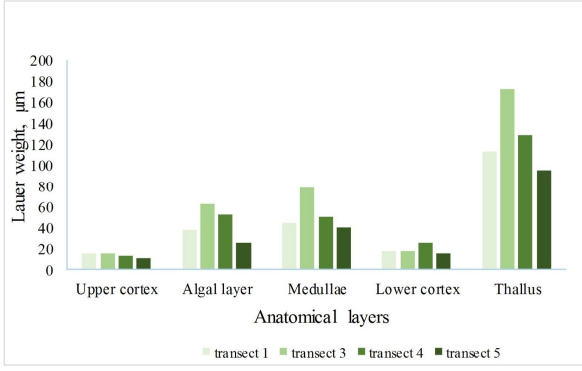

Fig. 2. Anatomic layers in thalli of species *Umbilicaria torrefacta* (Keret).

Species	Sample	Zone	UC (µm)	Log UC	AL (µm)	Log AL	MED (µm)	Log MED	LCL (µm)	Log LC	TW (µm)	Log TW
			Me	M	Me	M	Me	M	Me	M	Me	M
U. trf	3	3	12.5	1.1	60.0	1.8	91.3	2.0	15.0	1.2	183.8	2.3
U. trf	6	3	17.5	1.2	65.0	1.8	103.8	2.0	22.5	1.3	211.3	2.3
U. trf	12	3	15.0	1.1	52.5	1.7	102.5	2.0	22.5	1.3	192.5	2.3
U. trf	4	4	17.5	1.2	62.5	1.8	90.0	2.0	20.0	1.2	190.0	2.3
U. trf	7	4	15.0	1.1	62.5	1.8	92.5	2.0	25.0	1.4	197.5	2.3
U. trf	10	4	2.05	1.4	55.0	1.7	105.0	2.1	27.5	1.4	210.0	2.4
U. dst	5	4	17.5	1.2	67.5	1.8	97.5	2.0	22.5	1.3	203.8	2.3
U. dst	8	4	20.0	1.3	65.0	1.8	93.8	2.0	25.0	1.4	211.3	2.3
U. dst	9	4	10.0	0.8	32.5	1.5	50.0	1.7	15.0	1.2	107.5	2.0

Table 2. Anatomical structure of lichen thalli samples in the surroundings of Kolezhma village. *Legend*: *U. trf – Umbilicaria torrefacta*, *U. dst – Umbilicaria deusta;* UC – upper cortex, AL – algal layer, MED – medullae, LC – lower cortex, TW – thallus width, µm – micrometer; M – mean (*n*=60), Me – median.

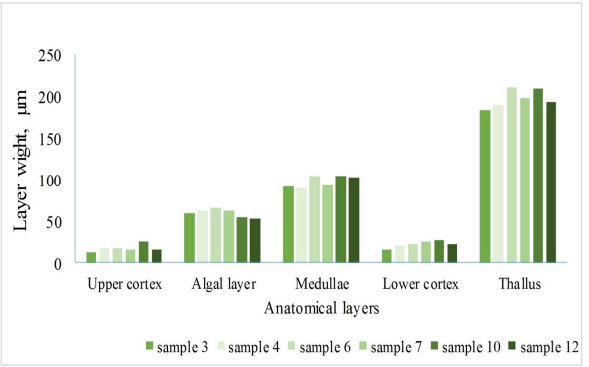

Fig. 3. Anatomic layers in thalli of species *Umbilicaria torrefacta* (Kolezhma).

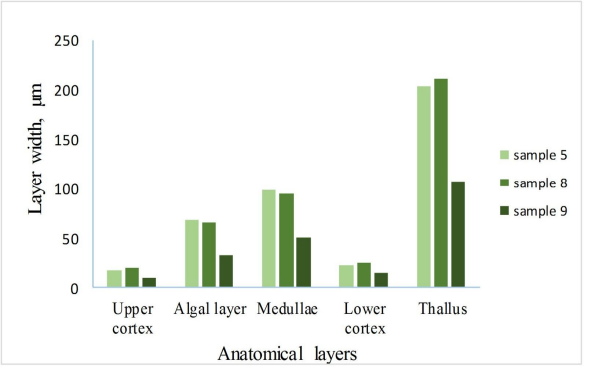

Fig. 4. Anatomic layers in thalli of species *Umbilicaria deusta.*

Analyses*	UC	AL	MED	LC	TW
I	0.00	0.00	0.00	0.00	0.00
II	0.00	0.28	0.04	0.00	0.05
III	0.00	0.00	0.00	0.00	0.00

Table 3. Results of ANOVA of differences between the two samples of lichen species, *U. deusta* and *U. torrefacta* (p values are given).
Notes: * I – comparison of the anatomical layers width of two lichen species *U. deusta* and *U. torrefacta* from the same habitat (Kolezhma village, zone 4.); II – comparison of the anatomical layers width in *U. torrefacta* samples from different habitats (zone 3 and zone 4) around Kolezhma village; III – comparison of the anatomical layers width in *U. torrefacta* samples from different places (Keret village, Kolezhma village).

Thalli of *U. deusta* species were only taken in the surroundings of Kolezhma village in the 4th lichen zone. Samples analysis showed the variation of all the anatomical layers: the upper cortex (10-20μm), the algal layer – (32.5-67.5μm), the medulla (50-97.5μm), the lower cortex (15-25μm), and thallus width (107.5-211.3μm). All parameters vary greatly.

Analysis of variance (ANOVA) revealed significant differences ($p < 0.001$) in all the anatomical layers between the species regardless of the place they grew, *i.e.* in close habitats of zone 4 around Kolezhma or in different habitats – Kolezhma and Keret villages (Table 3). Significant differences between the widths of fungal symbiont thalli anatomical layers of *U. torrefacta* species were revealed in two habitats: zone 3 - the bottom supralittoral zone and zone 4 in the soil-plant complex. The values of the algal layer width of one species on the coast did not differ significantly from other habitats (Table 3 - III).

U. torrefacta species in Keret village showed that the algal layer to thallus width ratio varied from 1: 2.5-3.5. This parameter was even more stable in Kolezhma village coast conditions for *U. torrefacta* species, 1: 3-3.5, and 1: 3 for the *U. deusta* species.

U. torrefacta species in Keret village showed a considerable variation of anatomical layers width. At the same time, chlorophyll *a* stays the main reaction center pigment and chlorophyll *b* is a pigment of the light-harvesting complex (LHC) that shows a wide range of concentration variance (2 times). Calculated parameters vary in a narrow range. The volume of the light-harvesting complex (LHC) varies from 57 to 65% (Table 3).

In Kolezhma village samples of *U. torrefacta*, photosynthetic pigments varied slightly, except for chlorophyll *b* (Table 4). In *U. deusta* samples, chlorophyll *a* and *b* varied considerably, but the carotenoid contents varied slightly (Table 5).

In the studied thalli samples, there were no significant relationships found between the width of algal layer formed by the photosynthetic symbiont and the amount of photosynthetic pigments. *U. torrefacta* samples from the surroundings of Kolezhma revealed significant relationships between thallus width and the amount of chlorophyll ($p = 0.05$), and thallus width and the amount of carotenoids ($p = 0.05$), as evidenced by the strong positive correlation ($r = 0.8$).

Transect number	Chl *a*	Chl *b*	Chl *a+b*	Car	Chl *a/b*	Chl/Car	LHC
1	0.25±0.01	0.11±0.01	0.36±0.02	0.09±0.00	2.46±0.13	4.00±0.07	64.56±2.30
3	0.33±0.02	0.15±0.02	0.48±0.04	0.11±0.01	2.49±0.19	4.37±0.09	64.80±2.95
4	0.17±0.01	0.06±0.00	0.23±0.01	0.06±0.00	2.88±0.08	3.60±0.06	57.02±1.22
5	0.18±0.00	0.07±0.00	0.25±0.00	0.06±0.00	2.65±0.08	3.85±0.04	60.40±1.24

Table 4. Contents of photosynthetic pigments in the thalli of *U. torrefacta* samples collected in the surroundings of Keret village.

Sample	Chl *a*	Chl *b*	Chl *a+b*	Car	Chl *a/b*	Chl/Car	LHC
3	0.22±0.12	0.08±0.01	0.30±0.02	0.08±0.01	2.79±0.06	3.65±0.04	58.36±4.21
4	0.19±0.01	0.07±0.01	0.26±0.02	0.07±0.01	3.22±0.46	3.90±0.54	58.93±4.34
6	0.30±0.01	0.11±.00	0.42±0.01	0.11±0.00	2.70±0.04	3.70±0.05	59.63±0.72
7	0.22±0.01	0.09±0.00	0.31±0.01	0.10±0.00	2.45±0.05	3.23±0.05	64.04±0.91
10	0.31±0.01	0.14±0.01	0.46±0.01	0.11±0.06	2.33±0.20	4.08±0.16	68.79±2.84
11	0.32±0.01	0.14±0.01	0.45±0.02	0.10±0.01	2.36±0.08	4.36±0.10	66.01±1.51
12	0.27±0.01	0.10±0.01	0.36±0.02	0.10±0.01	2.72±0.05	3.81±0.03	59.26±0.74

Table 5. Contents of photosynthetic pigments in the thalli of *U. torrefacta* samples collected in the surroundings of Kolezhma village.

Sample	Chl *a*	Chl *b*	Chl *a+b*	Car	Chl *a/b*	Chl/Car	LHC
5	0.33±0.00	0.14±0.00	0.47±0.01	0.12±0.00	2.43±0.05	3.93±0.10	64.54±0.27
8	0.16±0.00	0.07±0.00	0.23±0.01	0.07±0.00	2.42±0.12	3.08±0.12	65.73±2.33
9	0.16±0.01	0.07±.00	0.23±0.01	0.07±0.00	2.30±0.17	3.32±0.18	69.61±3.38

Table 6. Contents of photosynthetic pigments in the thalli of *U. deusta* samples collected in the surroundings of Kolezhma village.

Place of the sample collection	Lichen species	Parameters	Chl *a*		Chl *b*		Chl *a+b*		Car	
		Y/X	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Keret Village	*U.tor*	AL	0.6	0.4	0.5	0.6	0.6	0.5	0.6	0.4
		TW	0.8	0.08	0.7	0.3	0.6	0.2	0.7	0.3
Kolezhma Village	*U.tor*	AL	0.6	0.2	0.6	0.1	0.5	0.2	0.6	0.2
		TW	0.7	0.07	0.7	0.09	0.8	0.05	0.8	0.03
	U.dst	AL	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
		TW	0.4	0.7	0.4	0.7	0.4	0.7	0.4	0.7

Table 7. Results of correlation and regression analysis of the links between the width of the anatomical layers of lichens and quantitative characteristics of photosynthetic pigments (p-values and correlation (r) values are given).

Discussion

The anatomical structure of heteromeric lichen thalli is characterized by a clear spatial separation of symbionts. Fungal symbiont forms the upper and lower cortex layers which are in contact with the environment. Fungal symbiont also form a medulla - loosely lying fungal hyphae layer located under the algal layer which provides intercellular space for gas exchange. Phototrophic component cells form the algal layer that lies between the upper cortex and the core (Zenova 1999, Tarasova et al. 2012).

In the study *U. deusta* and *U. torrefacta* species showed variation in width of all anatomical structures in both fungal component and algal component. This variability of mycological structures can be explained by the leading role of mycobiont in adaptation to environmental conditions. Mycobiont forms the surface part of the thallus and, thanks to its physical properties, protects the photobiont against adverse environmental factors, such as photoinhibition and the lack of hydration, which are typical for open rocks, where the studied species live. It is well established that mycobiont controls the growth and activity of the photobiont, sometimes creating a nutrient deficiency for him. The specific phenolic compounds that are located on the cell walls of fungal hyphae (lichen acids and other secondary metabolites) can inhibit the growth of the photobiont (Palmqvist et al. 2002), and stimulate the outflow of nutrients to the fungus (Vainstein 1990). Moreover, fungal component forms the layers which form surface structures of thalli that are in contact with the external environment. Complex structure of thalli surface may affect a microenvironment, radiation regime in particular, available for the photobiont. This leads to the fact that some of the water and air reach algae cells through the fungal component structures and fungal components can influence photobiont`s nutrition (Pavlova et Maslov 2008). The phototrophic component of the studied species is formed by single-celled green algae of *Trebouxia* genus. Comparative analysis of the anatomical layer width in the samples of one species (*U. torrefacta*) within Kolezhma showed that algal layer has more or less constant witdth in the thallus structure, while the fungal layers vary significantly when growing in different ecotopes at different distances from the water's edge line (Table 3). This supports the idea that the upper surface structure formed by a mycobiont has a great ecological plasticity and provides a suitable intrathalline microenvironment for the photobiont. The ratio of the photosynthetic layer width to the thallus width remains constant in both studied species in different habitats (an average of 1: 3). In this way, these bionts in symbiotrophic community (the lichen) regulate their metabolism by balancing the anatomical structures. With the increase in the thickness of the thallus (mostly fungal layers) the algal layer thickness increases and vice versa, as evidenced by the stability of the ratio.

ANOVA showed significant differences between all anatomical structures including the algal layer of two *Umbilicaria* species thalli both in different habitats, and in the same ecotope. From the thallus organization point of view, these species have taxonomically different fungal symbionts and have similar species composition of the photobiont – several species of *Treuboxia* genus. This shows that interspecific differences are more significant than intraspecific.

The lack of relationship between the algal layer width and quantitative indicators of photosynthetic pigments suggest that the structural adaptation to environmental conditions is regulated mainly by a the variability of the fungal layers width. A strong relationship ($r = 0.8$) between the width of the thallus and the amount of chlorophyll and carotenoids in *U. torre-*

facta species was revealed. Therefore, participation of the fungal symbiont in the algal biont`s life support might be expected. It is known that dark non-photosynthetic pigments including melanin effectively reduce the photobiont`s stress in conditions of excess illumination (Gessler et al. 2014). They together with secondary metabolites located in the upper cortical layer play the role of screens, protecting the light-harvesting complexes of the algal biont from excess sunshine radiation ([1], Färber et al. 2014). On the one hand, this may be related to the fact that in coastal zones these lichens are in most favorable conditions of humidity and light and the symbiotic organism copes with symbiotrophic balancing due to the plasticity of the fungal symbiont which contacts the abiotic environment.

Wherein the adaptation mechanisms do not include functional adaptations, such as autotrophic biont`s photosynthetic apparatus, because the fungal biont provides conditions for it.

Thereby, the current study shown that supralittoral conditions are a favorable habitat for *U. deusta* and *U. torrefacta*. Adaptation of these species to environmental conditions is provided by varying the anatomical structures of both symbionts. Based on the previously suggested hypothesis about adaptation ways of *Umbilicaria* species (Sonina et Tsunskaya 2014), *U. deusta* and *U. torrefacta* demonstrate a structural adaptation – the adaptation is reflected in anatomical structure variation and a relative stability of the physiological parameters.

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