

Adaptations of epilithic lichens to the microclimate conditions of the White Sea coast

Anzhella V. Sonina*, Anastasya D. Rumjantseva, Anna A. Tsunskaya, Vera I. Androsova

Petrozavodsk State University, Department of Botany and Plant Physiology, Lenin st. 33, Petrozavodsk 185910, Russia

Abstract

Anatomical and functional features of the following three epilithic lichens *Umbilicaria torrefacta*, *Physcia caesia*, *Physcia dubia* were studied. These species have different morphological characteristics of thalli and occupy similar environmental conditions on supralittoral of the White Sea coast. The studied lichens are widespread in the territory of Karelia. *U. torrefacta* is an obligate epilithic species, *Physcia caesia* and *Physcia dubia* colonize both bark of trees and stones. Within the study area, these species were found only on coastal boulders. Photobiont of all studied lichens is unicellular green alga of the genus *Trebouxia* (Purvis et al. 1992). Based on the study, it was found that *Ph. caesia* adapts to the environmental conditions through the variability of photosynthetic pigments level which is confirmed by a strong variation of the chlorophylls a/b ratio and chlorophylls/carotenoids ratio (coefficient of variation, CV > 42%) with the stability of anatomical structures (CV ≤ 11%) – functional adaptation. Lichen *Ph. dubia* adapts through the variability of anatomical layers (upper cortex, algal layer, medullae, lower cortex, thallus thickness) (CV > 22%), and amounts of photosynthetic pigments (CV > 19%) – structural and functional adaptation. For *U. torrefacta*, the structural adaptation to environmental conditions (CV thickness of anatomical layers > 28%, CV amounts of photosynthetic pigments – 7, 8%) was recorded.

Key words: coastal zone, *Umbilicaria torrefacta*, *Physcia caesia*, *Physcia dubia*, physiology, anatomy, adaptations

DOI: 10.5817/CPR2017-2-13

Introduction

Lichens represent the microecosystems composed of one or several fungal bionts (heterotrophs) and one or more phototrophs (algae, cyanobacteria). The phototrophic bionts provide organic matter to heterotrophs

forming the thallus and, due to lichen thallus structure and its physical characteristics, receive environmental protection (Cao et al. 2015).

Received June 20, 2017, accepted November 29, 2017.

*Corresponding author: A. V. Sonina <angella_sonina@mail.ru>

Acknowledgements: The study was supported by the Ministry of Education and Science of the Russian Federation (project № 5.8740.2017/k). We are grateful to the reviewer for the valuable corrections and recommendations, which have improved the quality of our work.

According to our previous studies (Sonina et Tsunskaya 2014, Sonina et Tsunskaya 2016) on lichens of the genus *Umbilicaria*, it was shown that algal biont plays a leading role in the adaptation process of these symbiotic organisms to environmental factors. This detailed study of *Umbilicaria* lichens from different habitats have revealed that in some cases the symbiotrophic organism was better adapted to conditions due to variation of the anatomical structures of the thallus – structural adaptation by the mycobiont. However, it was also obtained that in other cases, the adaptation was reflected in the variation of the amount of photosynthetic pigments – functions of the algal component.

It is also known that in the whole variety of lichen species (about 17 500 - Kirk et al. 2008), which follows to the diversity of the mycobiont, the species diversity of the lichen photobiont is rather lower (about 200 species, half of which are green algae

and half – cyanobacteria) (Tschermak-Woess 1988).

This demonstrates the high adaptive capacity of the phototrophic component in lichenized fungal communities of different types. Results of recent studies by S. Cao and colleagues (Cao et al. 2015) showed that the photosynthetic activity of widely spread algal symbiont *Trebouxia jamesii* is affected by microhabitats conditions. Microhabitats conditions for lichenized algae depend mainly on growth form of thallus which determine proportion and localization of anatomical layers.

The purpose of this study was to identify the contribution of symbionts (mycobiont and photobiont) to the adaptation of epilithic lichens of the genera *Umbilicaria* and *Physcia*, which have different morphological parameters of thalli and grow in the similar conditions on supralittoral of the White Sea coast.

Study area

The study was carried out on the territory of the Republic of Karelia, on the Karelian coast of the White Sea in the surroundings of Keret village (66° 16' 45 " N, 33° 33' 54" E), located in the Loucky district in July-August 2014 and 2016 (Fig. 1). Study area are located within the Lebyazhya

bay in the floodplain of the Keret river. The bay is characterized by tidal dynamics with average magnitude of the tides about 2.0 m. Presence of a halocline determines a numerous important ecological conditions at the area for the formation of ecological niches for marine organisms.

Methods

For anatomical and physiological studies thalli of lichen species *Umbilicaria torrefacta* (Lightf.) (*Umbilicariaceae*) and *Physcia caesia* (Hoffm.) Fűr., *Physcia dubia* (Hoffm.) Lettau (*Physciaceae*) were collected. These species are widely distributed in the territory of Karelia (Fadeeva et al. 2007). *U. torrefacta* - obligate epilithic

lichen while species *Ph. caesia* and *Ph. dubia* can colonize both bark of trees and stones. On the study area, the *Physcia* species were found only on coastal boulders. Photobiont of all study species is a green unicellular alga of the genus *Trebouxia* (Purvis et al. 1992).



Fig. 1. Location of study area: 1 - Lebyazhya bay.

U. torrefacta has dark brown umbilicate, monophyllous thallus, circular to irregular in shape, attached at central point, with characteristic sieve-like perforations along the margins that are often shredded. Lower surface of thallus smooth to coarsely papillate, with trabeculae (plate-like structures) radiating from the umbilicus, rhizomorphs scattered or dense (Purvis et al. 1992). It is arctic-alpine species spread in the Holarctic (Davydov 2004).

Ph. caesia and *Ph. dubia* are characterized by foliose irregularly rosette-shaped thalli with narrow lobes, which are fairly tightly adherent to the substrate by rhizines. Thallus is light gray in color with well-developed soralia on the upper surface. Both species are cosmopolites and nitrophiles (Markovskaya et al. 2010, Purvis et al. 1992).

The above-specified lichen species occur in a wide range of biotopes on the coast

of the White Sea, including rocky sites within supralittoral zone with conditions of periodic splashing with salt water.

All the selected thalli were sampled in the supralittoral zone from surface of boulders (of glacial origin) with a height of 1.2 to 1.8 m which were located 12 to 18 m from the line of the wave's edge. Lichens grew in open conditions without any shading. Totally 16 sets of lichens were collected (each set included about 20 thalli): 4 sets of *U. torrefacta*, 6 sets of *Ph. caesia* and 6 sets of *Ph. dubia*. Lichen thalli were collected in 0.25 x 0.25 m sized areas with a high abundance of studied species (80–100% coverage). Collected thalli had similar size and similar morphological features (one ontogenetic state).

For study of anatomical characteristics of thallus and content of photosynthetic pigments, the standard methods of optical microscopy were used (see Sonina et Tsun-

skaya 2016). Anatomical features of thalli were studied using light microscope "Axio Scope A1" (Carl Zeiss, Germany). Totally, more than 1000 anatomical slices of thalli and 3500 measurements were made.

Determination of photosynthetic pigments concentration was done using an ethanol extracts. Extracts were measured by spectrophotometer SF-2000 (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. The concentration of pigments was calculated using the equations of Lichtenthaler et Wellburn (1983). The content of photosynthetic pigments was determined with a triple biological replication and nine chemical replicats.

Data processing and statistical analysis

Data processing was done on the basis of ANOVA using Excel according to Ivanter et Korosov (2010). We analyzed the distribution of logarithmic values of lichen thalli anatomical parameters (upper cortex, algal layer, medullae, lower cortex, thallus thickness), layer thicknesses in particular. Tables 1 and 2 show the values of the median (Me) of width of anatomical layers lichen thalli and logarithms of the mean

value of the width layers. Study of the relationships between the chlorophyll-related parameters and the width of thalli anatomical layers was accomplished using a correlation and regression analysis. Level of parameters variation was estimated by using of coefficient of variation which was calculated as $CV = \sigma/M * 100 \%$, where σ – standard deviation, M – arithmetic mean (Ivanter et Korosov 2010).

Results

Results of anatomical study of three species showed that in the samples of *Physcia caesia* all layers thickness varied slightly and variation coefficient did not exceed 11% (see Table 1). The thickness of all anatomical layers of thalli of *Physcia dubia* and *Umbilicaria torrefacta*, varied in a wider range than in *Ph. caesia* and the coefficient of variation was higher than 20% (Table 1). Analysis of variance (ANOVA) of anatomical layers revealed significant differences between all anatomical layers of species of different genera (see II and III, Table 2). The differences between the medulla, algal layer and lower cortex were recorded for lichens of genus *Physcia* (see Table 2)

Samples of *U. torrefacta* had significantly thinner thalli than *Physcia* (see Table 2). Thallus thickness of *U. torrefacta* ranged from 95.0 to 172.5 μm , while the values of thallus thickness of *Physcia* spe-

cies varied from 190.0 to 302.5 μm (*Ph. dubia*) and 256.0–276.0 μm (*Ph. caesia*). Thickness of inner layers (algal layer, medulla) of *U. torrefacta* reached two times lower values than in *Physcia* thalli (see Fig. 2). The differences were registered for the ratio of thallus thickness to the algal layer thickness. For thalli of *U. torrefacta* this ratio was 2.5 (3): 1, for thalli of both *Physcia* species – 1.5 (1.8): 1. This ratio reflects the proportion of algal layer in the lichen thallus which was lower in thalli of *U. torrefacta* than in the *Physcia* thalli. Algal cells in the thallus of *U. torrefacta* form a dense layer with clearly distinguishable boundaries (see Fig. 3). Meanwhile, location of aggregated algal cells in the *Physcia* thalli forms small discrete patches around which air cavities are observed (see Fig. 4, 5). Such features of algal layer make it volumetric and heteromorphic (algae cells with cavities).

| Species | Sam-ple | UC | Log | AL | Log | MED | Log | LC | Log | TT | Log |
|--------------|---------|------|-----|-------|-----|-------|-----|------|-----|-------|-----|
| | | (µm) | UC | (µm) | AL | (µm) | MED | (µm) | LC | (µm) | TT |
| | | Me | M | Me | M | Me | M | Me | M | Me | M |
| <i>Ph.c</i> | 4 | 24.0 | 1.4 | 184.0 | 2.2 | 40.0 | 1.6 | 20.0 | 1.2 | 256.0 | 2.4 |
| <i>Ph.c</i> | 7 | 24.0 | 1.3 | 184.0 | 2.3 | 40.0 | 1.6 | 20.0 | 1.2 | 276.0 | 2.4 |
| <i>Ph.c</i> | 9 | 44.0 | 1.3 | 136.0 | 2.2 | 44.0 | 1.6 | 20.0 | 1.3 | 224.0 | 2.4 |
| <i>Ph.c</i> | 12 | 32.0 | 1.4 | 160.0 | 2.2 | 40.0 | 1.7 | 20.0 | 1.2 | 264.0 | 2.3 |
| <i>Ph.c</i> | 8 | 28.0 | 1.4 | 152.0 | 2.2 | 48.0 | 1.7 | 16.0 | 1.2 | 256.0 | 2.4 |
| <i>Ph.c</i> | 6 | 40.0 | 1.4 | 116.0 | 2.2 | 24.0 | 1.6 | 16.0 | 1.2 | 196.0 | 2.4 |
| CV(%) | | 7.0 | | 4.0 | | 11.0 | | 9.0 | | 6.0 | |
| <i>Ph.d</i> | 3 | 25.0 | 1.5 | 160.0 | 2.3 | 50.0 | 1.7 | 22.5 | 1.4 | 302.5 | 2.5 |
| <i>Ph.d</i> | 5 | 17.5 | 1.3 | 60.0 | 1.9 | 77.5 | 1.9 | 10.0 | 1.0 | 190.0 | 2.3 |
| <i>Ph.d</i> | 14 | 17.5 | 1.3 | 107.5 | 2.1 | 82.5 | 1.9 | 10.0 | 1.1 | 235.0 | 2.4 |
| <i>Ph.d</i> | 17 | 21.3 | 1.3 | 105.0 | 2.0 | 108.7 | 2.1 | 12.5 | 1.1 | 260.0 | 2.5 |
| <i>Ph.d</i> | 2 | 15.0 | 1.2 | 85.0 | 2.0 | 147.5 | 2.2 | 10.0 | 1.0 | 267.5 | 2.4 |
| <i>Ph.d</i> | 1 | 21.3 | 1.2 | 122.5 | 2.0 | 110.0 | 2.1 | 5.0 | 0.9 | 265.0 | 2.4 |
| <i>Ph.d</i> | 11 | 17.5 | 2.3 | 132.5 | 2.1 | 95.0 | 1.9 | 10.0 | 0.9 | 265.0 | 2.4 |
| CV(%) | | 22.0 | | 43.0 | | 38.0 | | 30.0 | | 38.0 | |
| <i>U.tor</i> | 1 | 15.0 | 1.2 | 37.5 | 1.6 | 43.7 | 1.7 | 17.5 | 1.2 | 112.5 | 2.1 |
| <i>U.tor</i> | 3 | 15.0 | 1.2 | 62.5 | 1.8 | 77.5 | 1.8 | 17.5 | 1.2 | 172.5 | 2.2 |
| <i>U.tor</i> | 4 | 12.5 | 1.1 | 52.5 | 1.7 | 50.0 | 1.7 | 25.0 | 1.4 | 128.7 | 2.1 |
| <i>U.tor</i> | 5 | 10.0 | 1.0 | 25.0 | 1.4 | 40.0 | 1.6 | 15.0 | 1.2 | 95.0 | 2.0 |
| CV(%) | | 37.0 | | 38.0 | | 31.0 | | 41.0 | | 28.0 | |

Table 1. Anatomical structure of *Physcia caesia* and *Physcia dubia* lichen thallus on the coast of the White Sea. Notes: Sample – each sample included about 20 thalli; *Ph.c* – *Physcia caesia*, *Ph.d* – *Physcia dubia*, *U.tor* – *Umbilicaria torrefacta*, UC – upper cortex, AL – algal layer, MED – medullae, LC – lower cortex, TT – thallus thickness, µm – micrometer; M – mean (n=60), Me – median.

| Analysis* | UC | AL | MED | LC | TT |
|-----------|---------|---------|---------|---------|---------|
| I | 0.69 | 0.00*** | 0.00*** | 0.00*** | 0.75 |
| II | 0.00*** | 0.00*** | 0.00*** | 0.00*** | 0.00*** |
| III | 0.00*** | 0.00*** | 0.00*** | 0.00*** | 0.00*** |

Table 2. Results of ANOVA differences between the samples of three lichen species (*Physcia dubia*, *Physcia caesia*, *Umbilicaria torrefacta*) (p-values are given). Notes: * I – comparison of the anatomical layers width of two lichen species *Physcia caesia* and *Physcia dubia*; II – *Physcia caesia* and *Umbilicaria torrefacta*; III – *Physcia dubia* and *Umbilicaria torrefacta*, UC – upper cortex, AL – algal layer, MED – medullae, LC – lower cortex, TT – thallus; *** - p < 0,001.

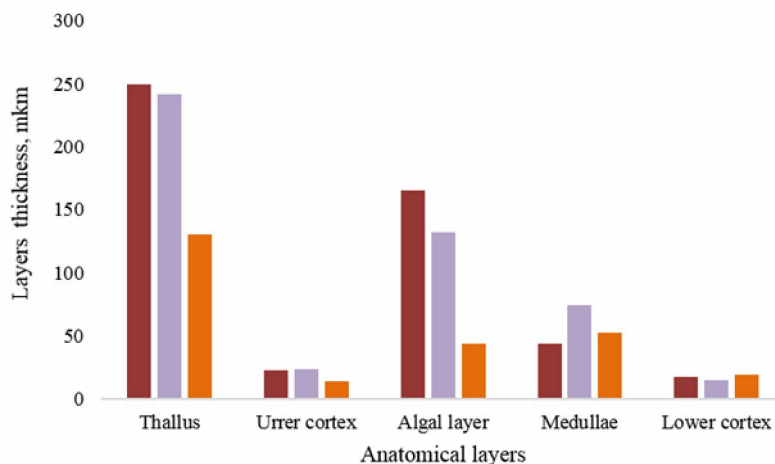


Fig. 2. Mean values of anatomical layers width of three lichen species (1 column – *Physcia caesia*, 2 column – *Physcia dubia*, 3 column – *Umbilicaria torrefacta*).

| Sample | Chl <i>a</i> ± σ | Chl <i>b</i> ± σ | Car ± σ | Chl <i>a+b</i> ± σ | Chl <i>a/b</i> ± σ | Chl / Car ± σ |
|--------|------------------|------------------|-----------|--------------------|--------------------|---------------|
| 4 | 0.22±0.02 | 0.12±0.03 | 0.08±0.02 | 0.34±0.05 | 1.78±0.20 | 4.65±0.90 |
| 6 | 0.05±0.01 | 0.06±0.02 | 0.01±0.00 | 0.11±0.03 | 1.09±0.29 | 9.31±6.19 |
| 7 | 0.11±0.04 | 0.10±0.04 | 0.02±0.01 | 0.21±0.07 | 1.21±0.31 | 9.32±3.74 |
| 8 | 0.11±0.04 | 0.09±0.06 | 0.03±0.01 | 0.18±0.02 | 1.51±0.53 | 15.15±22.27 |
| 9 | 0.14±0.03 | 0.10±0.02 | 0.02±0.01 | 0.24±0.02 | 1.39±0.46 | 15.08±6.83 |
| 10 | 0.07±0.02 | 0.03±0.00 | 0.02±0.00 | 0.11±0.02 | 2.22±0.29 | 4.35±0.56 |
| 12 | 0.11±0.05 | 0.05±0.02 | 0.05±0.02 | 0.16±0.07 | 1.96±0.21 | 2.96±0.37 |
| CV (%) | 47 | 41 | 74 | 42 | 26 | 58 |

Table 3. Contents of photosynthetic pigments (mg·g⁻¹ dry weight) in the thalli of *Physcia caesia*.

Analysis of the content of photosynthetic pigments revealed a high level of variation in chlorophylls and carotenoids in samples of three studied lichen species (CV > 30%) (see Table 3, 4, 5). In the species *Ph. caesia*, the content of carotenoids varied to a higher extent (CV = 74%), and, consequently, the ratio of chlorophylls to carotenoids followed such high variation (CV = 58%) (see Table 3).

The species *Ph. dubia* had a smaller variation (CV = 20%) of the chlorophyll *a/b* ratio which ranged from 1.6 to 2.5 (see Table 4).

The low variation of estimated parameters (chlorophyll *a/b* ratio, ratio of chloro-

phylls to carotenoids) was recorded for thalli of *U. torrefacta*. The ratio remained more constant values due to a complex change in pigment content, *i.e.* increase of chlorophyll was associated with an increase of content of chlorophyll *b* and carotenoids (see Table 5).

Significant differences in the content of photosynthetic pigments and ratios between the studied lichen species (see Table 6) were found in ANOVA. No significant correlations were recorded between the amounts of pigments, the thickness of the algal layer and the thallus thickness (see Table 7).

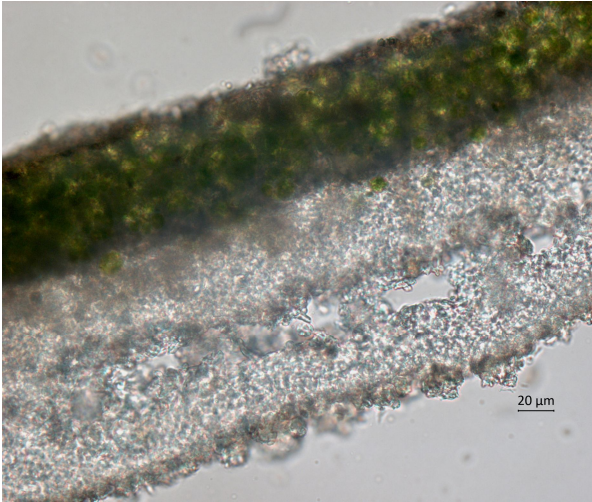


Fig. 3. Cross section of the thallus *Umbilicaria torrefacta*.

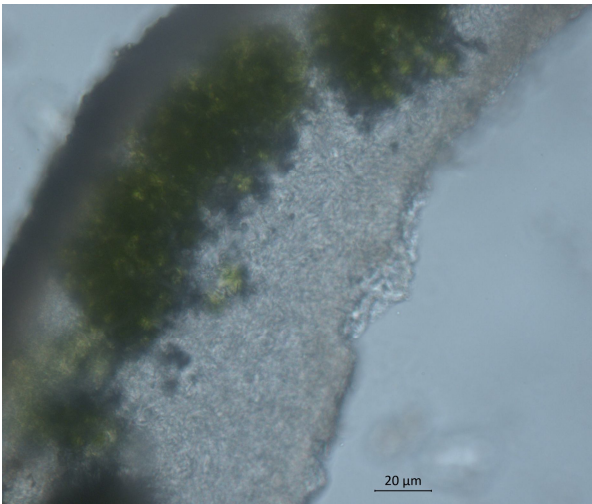


Fig. 4. Cross section of the thallus *Physcia dubia*.

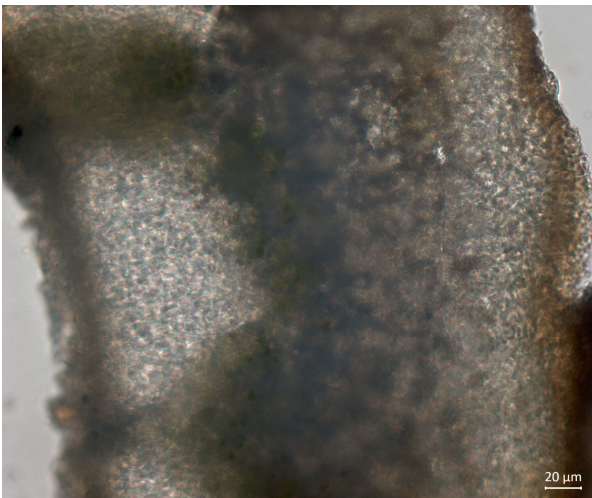


Fig. 5. Cross section of the thallus *Physcia caesia*.

| Sample | Chl <i>a</i> ± σ | Chl <i>b</i> ± σ | Car ± σ | Chl <i>a+b</i> ± σ | Chl <i>a/b</i> ± σ | Chl / Car ± σ |
|--------|------------------|------------------|-----------|--------------------|--------------------|---------------|
| 1 | 0.23±0.01 | 0.12±0.01 | 0.35±0.02 | 0.07±0.01 | 1.99±0.06 | 5.29±0.34 |
| 2 | 0.31±0.05 | 0.22±0.07 | 0.53±0.12 | 0.07±0.00 | 1.70±0.24 | 7.19±1.30 |
| 3 | 0.25±0.01 | 0.16±0.03 | 0.41±0.04 | 0.05±0.01 | 1.63±0.23 | 3.66±5.40 |
| 5 | 0.14±0.02 | 0.08±0.03 | 0.21±0.04 | 0.05±0.01 | 1.85±0.37 | 4.03±0.89 |
| 11 | 0.17±0.03 | 0.07±0.02 | 0.24±0.04 | 0.06±0.01 | 2.55±0.17 | 4.30±0.35 |
| 14 | 0.37±0.05 | 0.18±0.03 | 0.55±0.07 | 0.11±0.01 | 2.04±0.04 | 4.92±0.07 |
| 17 | 0.27±0.07 | 0.13±0.04 | 0.40±0.12 | 0.09±0.02 | 2.10±0.14 | 4.62±0.34 |
| CV (%) | 32 | 39 | 31 | 34 | 19 | 30 |

Table 4. Contents of photosynthetic pigments (mg·g⁻¹ dry weight) in the thalli of *Physcia dubia*.

| Sample | Chl <i>a</i> ± σ | Chl <i>b</i> ± σ | Chl <i>a+b</i> ± σ | Car ± σ | Chl <i>a/b</i> ± σ | Chl / Car ± σ |
|--------|------------------|------------------|--------------------|-----------|--------------------|---------------|
| 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 |
| 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 |
| 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 |
| 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 |
| CV (%) | 32 | 42 | 35 | 31 | 7 | 8 |

Table 5. Contents of photosynthetic pigments (mg·g⁻¹ dry weight) in the thalli of *Umbilicaria torrefacta*.

| Analysis* | Chl <i>a</i> | Chl <i>b</i> | Car | Chl <i>a/b</i> | Chl / Car |
|-----------|--------------|--------------|---------|----------------|-----------|
| I | 0.00*** | 0.00*** | 0.00*** | 0.00*** | 0.002** |
| II | 0.00*** | 0.00*** | 0.00*** | 0.00*** | 0.00*** |
| III | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

Table 6. Results of ANOVA differences between the samples of three lichen species (*Physcia dubia*, *Physcia caesia*, *Umbilicaria torrefacta*) according to total content of chlorophylls (*p*-values are given). Notes: *I – *Physcia caesia* and *Physcia dubia*; II – *Physcia caesia* and *Umbilicaria torrefacta*; III – *Physcia dubia* and *Umbilicaria torrefacta*; *** - $p < 0,001$, ** - $p < 0,01$.

| Lichen species | Parameters | Chl <i>a</i> | | Chl <i>b</i> | | Car | |
|----------------------|------------|--------------|----------|--------------|----------|----------|----------|
| | | <i>r</i> | <i>p</i> | <i>r</i> | <i>p</i> | <i>r</i> | <i>p</i> |
| <i>U. torrefacta</i> | AL | 0.6 | 0.4 | 0.5 | 0.6 | 0.6 | 0.4 |
| | TT | 0.8 | 0.08 | 0.7 | 0.3 | 0.7 | 0.3 |
| <i>Ph. caesia</i> | AL | 0.00 | 0.9 | 0.03 | 0.7 | 0.00 | 0.9 |
| | TT | 0.03 | 0.7 | 0.2 | 0.4 | 0.00 | 0.9 |
| <i>Ph. dubia</i> | AL | 0.01 | 0.8 | 0.00 | 0.9 | 0.03 | 0.7 |
| | TT | 0.1 | 0.5 | 0.13 | 0.4 | 0.03 | 0.7 |

Table 7. Results of correlation and regression analysis of the links between the thickness of the anatomical layers of lichens and quantitative characteristics of photosynthetic pigments (*p* - values and correlation (*r*) values are given). Notes: AL – algal layer, TT – thallus.

Discussion

The studied lichen genera species have a different morphological structure and belong to the plagiotropic biomorph type but to different classes: *Umbilicaria sp.* belongs to the class of umbilical thalli, umbilical-lobed group, *Physcia sp.* - to foliose thalli class, dissected-lobed rhizoidal group (Golubkova 1983). Both genera have a heteromeric thallus structure which is characterized by a thick algal layer (Purvis et al. 1992). Nevertheless, there is a significant difference between the anatomical structures of the genera. In *Umbilicaria*, the algal layer is clearly formed as a narrow band. In *Physcia*, however, the algal layer is discrete and fungal hyphae occur between clusters of algal cells. Such anatomy organization provides studied *Physcia* species by increasing of the algal layer thickness compared to *Umbilicaria sp.* On the one hand, this structural feature makes it possible to keep the thallus moist due to increased amount of fungal hyphae. It also contributes to improving of gas exchange (Slonov et al. 2009). In fact, increased moisturizing of the thallus and facilitated carbon dioxide influx into a thallus due to air cavities provides the ability to maintain high level of photosynthetic activity (Lange et Tenhunen 1981). It should be noted that the mycobiotic layers in *Ph. caesia* samples that contact with the environment, *i.e.* the upper and lower cortex layers, are structurally more stable, their thickness varies only in a narrow range. (CV 7 and 9%, correspondingly). Medulla layer of species thallus is more variable (CV is 11%) While thickness of algal layer has less variable values (CV is 4 %) (*see* Table 1).

Moreover, in previous studies (Androsova et al. 2015, Sonina et Tsunskaya 2015), the ratio of thallus thickness to the algal layer thickness is more or less constant and reaches 4(3): 1. In this study the ratio in both *Physcia* species is 1.5 (1.8): 1, indicating a larger share of the algal layer in *Physcia sp.* thallus than in

Umbilicaria sp. (Tsunskaya et Sonina 2015, Sonina et Tsunskaya 2016) or *Cladonia sp.* (Androsova et al. 2015). Although the algal layer thickness of *Physcia sp.* is significantly higher than in *Umbilicaria sp.* (*see* Table 2), the amount of photosynthetic pigments is not related to the algal layer and thallus thickness. Probably, the increase in the algal layer thickness is the result of a more loose density of the algal cells and the inclusion of the fungal biont in this layer.

When comparing photosynthetic pigments content in the studied samples (CV > 30%), calculated per thallus dry weight, a high level of chlorophylls and carotenoids variation was found. In *U. torrefacta* samples, the calculated amount of chlorophylls and chlorophylls to carotenoids ratio vary slightly (CV = 7%, 8%), which indicates the pigment apparatus stability. For the samples of two *Physcia* species the calculated values vary over a wide range (Tables 3, 4). This may indicate the instability of habitat conditions, which are determined by proximity of the sea coast (strong winds, periodic splashing by salt water) and the pigment apparatus responses to them with the relative anatomical structures stability in these species (Table 2). Lichens' photosynthetic activity is largely determined by the environmental conditions: humidity level, temperature, light intensity (Nash 1996).

Accordingly, it is established that *Ph. caesia* showed stable values of both algal and fungal biont's structures in the thallus. On the White Sea coast under the influence of the sea dynamic conditions a significant variation in the quantitative values of the pigment apparatus was revealed. It means that the instability of the conditions influences the physiological indicators such as photosynthetic apparatus, a functional indicator of the symbiotic organism. High variability of pigments indicates a high level of functional variability of the photobi-

ont, which allows the symbiotic organism to be stable in a wide range of conditions (Sonina 2014).

Ph. dubia species showed significant variations in both structural (the anatomical layers of both bionts) and functional parameters (quantitative values of photosynthetic pigments and estimated characteristics) in this study.

For *U. torrefacta*, the estimated parameters of the pigment apparatus varied slightly with a significant variation in the anatomical layers thickness and the amount of photosynthetic pigments, which indicates its stability under given environmental conditions. Studies on *Umbilicaria* genus within the White Sea coast (localities Keret and Kolezhma) and terrestrial communities (Petrozavodsk) (Sonina et Tsunskaya 2016, Sonina et Tsunskaya 2015) also indicate a greater variation of the anatomical structures in the thalli and relative stability of physiological parameters (number of photosensitive pigments). As a result of the studies of *U. torrefacta* from different habitats it was established that in some cases the symbiotic organism is adapted to environmental conditions thanks to variation of the anatomical structures of the thallus. The variation of anatomical structures (structural adaptation) is mainly due

to the mycobiont (changes in thickness of cortex and medulla layers). In other cases, however, the adaptation might be due to variation of the amount of photosynthetic pigments - functions of the algal component (Sonina et Tsunskaya 2015).

Based on the study, it was established that *Ph. caesia* adapts to environmental conditions due to the variability of photosynthetic pigments with the stability of anatomical structures. Such behavior is typical for a functional type of adaptation. *Ph. dubia* adapts by substantial variation both in the anatomical layers characteristics and the amount of photosynthetic pigments. Therefore, *Ph. dubia* shows a structural-functional adaptation. *U. torrefacta* is characterized by structural adaptation to environmental conditions as found earlier (Sonina et Tsunskaya 2016).

In conclusion, studied species of epilithic lichens showed different types of adaptation to similar environmental conditions on supralittoral zone of the White Sea coast. It was shown in our study that both photo- and mycobionts in the symbiotic association contribute to the adaptability to habitat conditions. The problem of the relationship between lichen adaptive strategies and environmental conditions, however, still remains unresolved.

References

- ANDROSOVA, V. I., MARKOVSKAYA, E. F. and SEMIONOVA, E. V. (2015): Photosynthetic pigments of lichens of the genus *Cladonia* in rocky forest communities of the mountain Olovgora (Arkhangelsk region). *Achievements of Modern Natural Sciences*, 2: 120-125. (In Russian).
- CAO, SH., ZHANG, J., ZHENG, H., LIU, CH. and ZHOU, Q. (2015): Photosynthetic performance in Antarctic lichens with different growth forms reflect the diversity of lichenized algal adaptation to microhabitats. *Polish Polar Research*, 36 (2): 175-188, doi: 10.1515/popore-2015-0012.
- DAVYDOV, E. A. (2004): Additions to the lichen biota of Altai Mountains (Siberia). I. *Turczaninowia*, 7(4): 47-59. (In Russian).
- FADEEVA, M. A., GOLUBKOVA, N. S., VITIKAINEN, O. and AHTI, T. (2007): Conspectus of lichens and lichenicolous fungi of the republic of Karelia. Petrozavodsk, Karelian Research Centre RAS, 2007, 192 p. (In Russian).
- GOLUBKOVA, N. S. (1983): Analysis of lichen flora of Mongolia. Leningrad: Nauka, 248 p. (In Russian).

- IVANTER, E. V., KOROSOV, A. V. (2010): Elementary biometrics. Petrozavodsk: Petrozavodsk State University, 104 p. (In Russian).
- KIRK, P. M., CANNON, P. F., MINTER, D. W. and STALPERS, J. A. (2008): Dictionary of the fungi. 10. Wallingford Oxon UK Press: CABI, 771 p.
- LANGE, O. L., TENHUNEN, J. D. (1981): Moisture content and CO₂ exchange of lichens. II. Depression of net photosynthesis in *Ramalina maciformis* at high water content is caused by increased thallus carbon dioxide diffusion resistance. *Oecologia* (Berlin), 51: 426-429.
- MARKOVSKAYA, E. F., SERGIENKO, L. A., SHKLYAREVICH, G. A., SONINA, A. V., STARODUBTSEVA, A. A. and SMOLKOVA, O. V. (2010): Natural complex of the coasts of the White Sea. Petrozavodsk: Karelian Research Centre RAS, 85 p. (In Russian).
- NASH, T.N. III. (1996): Lichen biology. Cambridge University Press, pp. 88-135.
- PURVIS, O. W., COPPINS, B. J., HAWKSWORTH, D. L., JAMES, P. W. and MOORE, D. M. (1992): The Lichen flora of Great Britain and Ireland. London: Natural History Museum Publications in association with the British Lichen Society. 710 p.
- SLONOV, L. KH., SLONOV, T. L. and KHANOV, Z. M. (2009): Ecological and physiological features of lichens of the mountain system of the Central part of the North Caucasus. Nalchik: Elbrus. 155 p. (In Russian).
- SONINA, A. V. (2014): Epilithic lichens in ecosystems of Northwestern of Russia: biodiversity, ecology. Petrozavodsk, 47 p. (In Russian).
- SONINA, A. V., STEPANOVA, V. I. and TARASOVA, V. N. (2006): Lichens. Handbook. Part I: Morphology. Anatomy. Systematics. Petrozavodsk: Petrozavodsk State University, 216 p. (In Russian).
- SONINA, A. V., TSUNSKAYA, A. A. (2014): Structural and functional adaptation of the lichens of genus *Umbilicaria* in rocky habitats of South Karelia. *Principles of Ecology*, 4: 48-62, doi: 10.15393/j1.art.2015.4244 (In Russian).
- SONINA, A. V., TSUNSKAYA, A. A. (2016): Structural and functional adaptation of epilithic lichens of *Umbilicaria* genus in the White Sea coastal conditions. *Czech Polar Reports*, 6(2): 169-179, doi: 10.5817/CPR2016-2-15.
- TSCHERMAK-WOESS, E. (1988): The algal partner. In: M. Galun (ed.): *CRC Handbook of Lichenology*, 1. CRC Press Boca Raton, Florida, pp. 39-92.