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PLANT PHYSIOLOGY

Photosynthetic Capacity of *Fucus vesiculosus* Linnaeus, 1753 (Phaeophyta: Fucales) in the Barents Sea during the Tidal Cycle

I. V. Ryzhik[a, b, *], A. A. Kosobryukhov[c], E. F. Markovskaya[d], and M. V. Makarov[a]

[a] *Murmansk Marine Biological Institute, Russian Academy of Sciences, Murmansk, 183010 Russia*
[b] *Murmansk Arctic State University, Murmansk, 183038 Russia*
[c] *Institute of Fundamental Problems of Biology, Russian Academy of Sciences, Pushchino, Moscow oblast, 142290 Russia*
[d] *Petrozavodsk State University, Petrozavodsk, Republic of Karelia, 185910 Russia*
**e-mail: alaria@yandex.ru*

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Abstract—During the tidal cycle, *Fucus vesiculosus* L. lost moisture (up to 30% of wet weight) and was characterized by a sinusoidal pattern in photosynthetic activity. Three peaks in the photosynthesis capacity were observed at the beginning and middle of low tide and at the beginning of high tide. There were no structural changes in the photosynthetic apparatus. When analyzing the curves of CO_2 gas exchange, the processes of photosynthesis in the algae exposed to the air was limited by the activity of the light and dark phases of photosynthesis. The increase in the content of lipid peroxidation products, catalase activity, and accumulation of proline in *F. vesiculosus* thalli indicated the presence of reversible oxidative stress during low tide.

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INTRODUCTION

The growth of algae in the littoral zone is closely related to tidal cycles, which affect abrupt changes in the living conditions four times a day. At low tide, the aquatic environment changes to the air, the temperature of the environment, lighting, salinity, etc., change as well. At this time, the moisture content in the macroalgae thallus may decrease (Kamnev, 1989; Bisson and Kirst, 1995; Schagerl and Moostl, 2011), as may the rate of photosynthesis and respiratory gas exchange rates (Quadir et al., 1979; Dring and Brown, 1982; Andreev et al., 2012). The adaptation of algae to periodic drying is mainly associated with the accumulation of substances that retain moisture (Wiltens et al., 1978; Quadir et al., 1979; Kamnev, 1989; Davison and Pearson, 1996; Kuznetsov et al., 2006), and with the changes in the activity of physiological processes at the level of the light phase of photosynthesis (Andreev et al., 2012).

Fucus species are widely distributed throughout the world. On the Murmansk coast, the upper littoral is the main habitat zone of *F. vesiculosus* Linnaeus, 1753 (Phaeophyta: Fucales); in other regions, this species can grow both in the littoral and in the sublittoral zone (Zaneveld, 1937; Russell et al., 1998; Gylle et al., 2009, 2011; Malavenda, 2014). It is assumed that competition with other species is one of the reasons for the absence of *F. vesiculosus* at greater depths in the Barents Sea. Earlier, during the experimental rearing of *F. vesiculosus* at different depths, the physiological activity of cells decreased. The number of epiphytes on the thalli increased as the depth increased, and, as a result, the algae died (Makarov et al., 2010). *F. vesiculosus* possibly belongs to the species that need periodic drying for functional activity, like *Pelvetia canaliculata,* another upper littoral species, which dies in the absence of periodical drying (Thomas, 2002).

This study aims to analyze the physiological state of *F. vesiculosus* during the tidal cycle in natural conditions, as well as to identify the mechanisms of its adaptation to periodic drying.

MATERIALS AND METHODS

This study was carried out in situ in the littoral zone of Zelenetskaya Bay (69°07′ N, 36°04′ E) in July–August 2013–2014 at the Dalnezelenetskaya Seasonal Biological Station, Murmansk Marine Biological Institute (MMBI), Russian Academy of Sciences.

The bladder wrack *Fucus vesiculosus* of the same age (4–5 dichotomous branches) growing in the upper littoral zone was studied. During the period of the experiments, the duration of drying (low tide) was six hours in the zone of *F. vesiculosus* growth.

Thalli of *Fucus* algae are highly branched, and they grow in thickets and are characterized by a projective cover of up to 100%. During low tide, an algae layer of up to 20-cm thick forms on the littoral. In this case, individual parts of thalli or whole thalli may appear on the surface and dry out to a large extent, or they may

remain within a thicket, where they are not subjected to intensive drying.

The apical portions of thalli were used to study the photosynthetic capacity processes. The analysis was carried out in vivo during the daytime tidal cycle (illumination intensity 650–800 μmol E/(m^2 s), air temperature of 20–25°C, and water temperatures of 7–8°C). The thalli, which were under water for more than 6 h, were examined first; then, as the water receded at low tide, the thalli, which were found on the surface of the algae thickets and experienced intense drying, were examined every 30–60 min. After the onset of the tide, when the algae were again submerged in water, thalli were analyzed every 10–15 min for 2 h. The sampling frequency was determined by the capabilities of the device and the rate of primary processing of the samples. In the experiment aimed to determine the effect of the moisture content in the thalli on the photosynthetic capacity (A_{max}), samples were taken both from the surface of the layer of algae (dried) and from the middle of the thicket (wet).

The photosynthetic capacity A_{max} was determined using a portable infrared gas analyzer LCPro+ (ADC BioScientific Ltd., UK). The apical part of the thallus was placed in the assimilation chamber of the gas analyzer. After stationary values were set, the rate of CO_2 gas exchange was determined under atmospheric CO_2 conditions; ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) had a higher affinity to this rate. Carbon dioxide relationships of the rate of photosynthesis were determined taking into account the change in the concentration of CO_2 in the air supplied to the assimilation chamber of the gas analyzer (0–1600 μmol CO_2/(m^2 s)) at saturating light intensity. The CO_2 concentrations supplied to the assimilation chamber were set using a gas analyzer microprocessor and were changed sequentially (50, 100, 200, 400, 800, 1200, and 1600 μmol CO_2/(m^2 s)). The curves of CO_2 gas exchange were analyzed according to the accepted model (Farquhar et al., 1980) with modifications (Caemmerer and Farquhar, 1982; Harley and Sharkey, 1991) using the Photosyn Assistant Ver. 1.1.2 (Parsons and Ogston, 1999). In accordance with the equations provided by the authors cited, the model allowed us to determine the maximum carboxylation rate ($V_{c\,max}$), the light saturated electron transport rate (J_{max}), the triose phosphate utilization, and a number of other parameters.

The content of photosynthetic pigments was determined by spectrophotometry (spectrophotometer JENWAY 6305 UV/VIS). Carotenoids (β-carotene, violaxanthin, and fucoxanthin) were preliminarily separated by paper chromatography, and chlorophylls *a* and *c* ($c_1 + c_2$) were determined in solution. The qualitative and quantitative composition of pigments was analyzed using modified techniques (*Pigmenty...*, 1964; Lee, 1978; Maslova et al., 1986).

The moisture content in the thalli was calculated from the ratio of the wet and dry weight of the thallus cuts ($N = 20$). The cut weight was determined on a balance (VLTE-210, Russia) at a 0.001-g accuracy: wet weight, after removing droplet-liquid moisture from the cut surface with filter paper; dry weight, after drying in a drying oven ($T = 105$°C) for 24 h.

The catalase activity (CA), the lipid peroxidation rate (LPO), and the concentration of the proline amino acid were determined during several periods of low tide. The apical vegetative part of the thallus of up to 0.5-cm long was used for analysis.

The LPO was assessed by the accumulation of thiobarbituric acid reactive substances (TBARS) (Esterbauer and Cheesman, 1990; Olenichenko et al., 2008). The following procedure was applied: 100 mg of algae was homogenized in 1.2–1.5 mL of distilled water in a porcelain mortar; 1.2–1.5 mL of 10% trichloroacetic acid was added to the resulting homogenate. The resulting solution was centrifuged at 8000 rpm for 15 min. Then, 0.5 mL of a 0.67% thiobarbituric acid (TBA) solution was added to 0.5 mL of the supernatant. The resulting solution was kept in a boiling water bath for 10 min, then cooled down to room temperature, and diluted to a final volume of 2 mL. The measurements were performed at a wavelength of 540 nm.

The catalase activity was determined using a modified spectrophotometric method (Korolyuk et al., 1988), based on the ability of hydrogen peroxide to form a stable colored complex with molybdenum salts. A 100-mg algae sample was ground in phosphate buffer under cold, then centrifuged at 8000 rpm for 15 min. Hydrogen peroxide (2 mL) was added to 0.1 mL of the supernatant; the mixture was incubated for 10 min at 18°C. In order to terminate the reaction, 1 mL of 4% ammonium molybdate was added to the mixture. The measurements were carried out using a spectrophotometer at a wavelength of 410 nm.

The content of free proline in algal cells was determined using the reaction with ninhydrin (Bates et al., 1973). A 500-mg sample was homogenized in a 3% aqueous solution of sulfosalicylic acid and centrifuged at 8000 rpm for 15 min. Then, 2 mL of the extract, 2 mL of acidic ninhydrin, and 2 mL of glacial acetic acid were added to the tubes. The mixture was incubated in a water bath for 1 h, and the reaction was terminated in an ice bath. After cooling, 4 mL of toluene was added to the test tubes, and the mixture was shaken vigorously for 15–20 s. The upper colored toluene layer was separated from the aqueous phase and heated up to 18°C; the measurements were carried out at a wavelength of 520 nm. The proline concentration was determined using a calibration curve and calculated using the Bates formula (Bates et al., 1973). The measurements were carried out on a JENWAY 6305 UV/VIS spectrophotometer.

Three biological and three analytical replicates were applied for each measurement. The Statistica 6.0

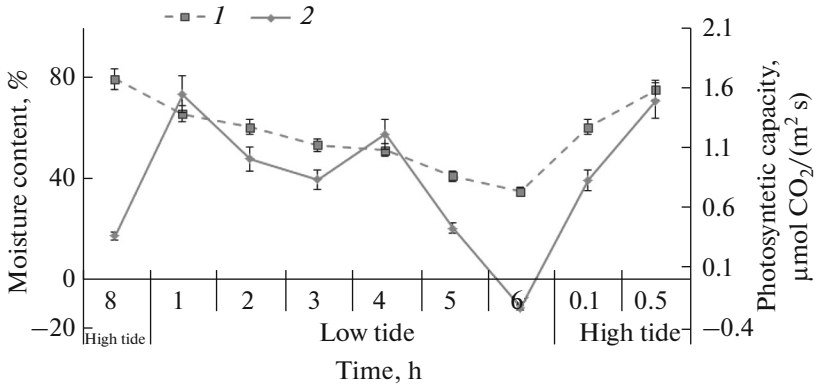

Fig. 1. Moisture content (*1*) and the photosynthetic capacity (*2*) of *Fucus vesiculosus* thalli during the tidal cycle.

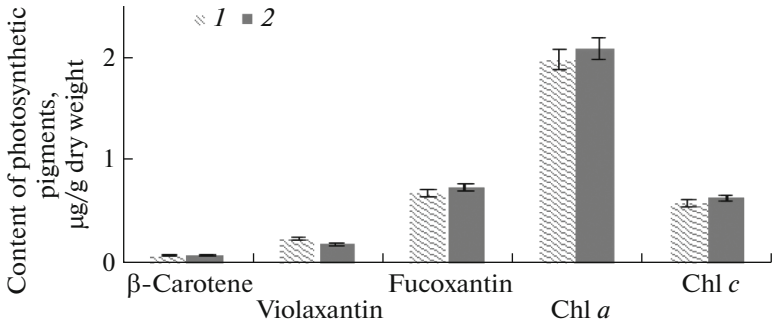

Fig. 2. Content of photosynthetic pigments in the cells of *Fucus vesiculosus* during (*1*) high tide and (*2*) low tide.

and MS Excel 2007 programs were used for statistical data processing. The reliability of the results was assessed using Student's *t*-test at $p = 0.95$. The graphs show the mean values and the confidence interval.

RESULTS

During high tide, when the algae were submerged, the moisture content in the thalli of *F. vesiculosus* was ~80%. During low tide, depending on the duration of drying, cloudiness, wind speed, air temperature, and air humidity, the moisture content in the thalli decreased down to 40%. At the onset of the next high tide, the moisture content was restored to its initial value within 30 min, regardless of the degree of dehumidification (Fig. 1).

During the tidal cycle (end of high tide–beginning of high tide), A_{max} of *F. vesiculosus* had the form of a three-peaked curve with two peaks at low tide and one peak at the beginning of high tide (Fig. 1). During the entire tidal cycle, no significant changes were found in the content of photosynthetic pigments, the ratio of chlorophylls and carotenoids (Fig. 2, Table 1), or the size of the light-harvesting complex (xanthosome), estimated by the ratio of Chl *a* and the sum of Chl *c* + fucoxanthin (Makarov, 2012).

In order to search for the dependence of A_{max} on the moisture content in the thallus, we studied the plants that were at low tide both on the surface and in the middle of algae thickets; accordingly, they were characterized by different degrees of drying. During low tide, the moisture content of thalli on the surface decreased down to 40%, while it did not change in the

Table 1. Ratio of chlorophylls and carotenoids, as well as the relative sizes of xanthosomes in *Fucus vesiculosus* during high and low tide

Ratio	High tide	Low tide
Chl *a*/carotenoids	1.92 ± 0.18	2.02 ± 0.19
Chl *a*/Chl *c* + fucoxantine	4.03 ± 0.35	3.98 ± 0.37

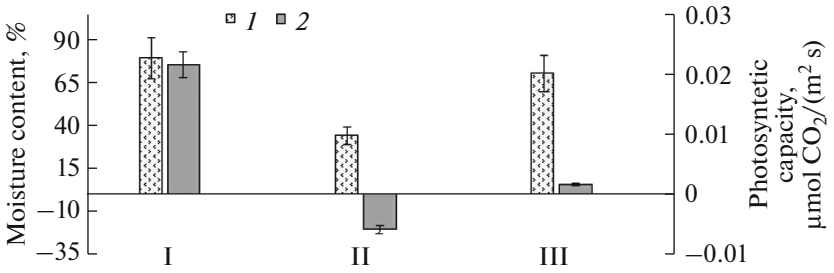

Fig. 3. (*1*) Moisture content and (*2*) photosynthetic capacity of *Fucus vesiculosus*, depending on the location of plants at low tide. I, high tide, plants in water; II, low tide for 5 hours, plants on the surface of the algae thicket; III, low tide for 5 hours, plants in the middle of the thicket.

algae sampled from inside the thickets. The differences in the moisture content were insignificant between the plants from inside the thickets and the plants submerged in water. During this period, the A_{max} of plants decreased regardless of their degree of drying: down to negative values in thalli from the surface (respiration prevailed), and down to low but positive values in thalli located inside the thickets (Fig. 3).

Comparative analysis of the carbon dioxide curves showed similar maximum possible A_{max} values in algae that were kept for a long time both at low tide (drained) and at high tide (covered with water) (Table 2). However, the value of this indicator turned out to be significantly higher than the real ones, when negative gas exchange was observed at low tide, and A_{max} was three times lower at high tide. The ratios of the light and dark phases of photosynthesis ($J_{max}/V_{c\,max}$) were approximately the same in the algae exposed for a long time to the air (during low tide) and covered by water (more than five hours during high tide), constituting 2.4 and 2.5, respectively. Such similarity of A_{max} was preconditioned by the same contribution of the ratio of the activity of the light and dark phases of photosynthesis.

A sharp change in the environmental conditions during low tide, causing changes in the moisture content and A_{max} in *F. vesiculosus*, suggested the presence of oxidative stress in algal cells. The content of TBARS in tissues, indicating the presence of LPO processes, showed a significant, almost threefold, increase in these compounds in the first two hours of drying. However, their content had decreased already after 3 h to the initial level, which was maintained until the onset of the tide (Fig. 4).

These data indicated the presence of oxidative stress in the first hours of the low tide and disruption of membrane structures. Due to the activity of the antioxidant and repair systems, a recovery process was observed after the second hour of drying. The decrease in the content of reactive oxygen species (ROS) was facilitated by the enzyme catalase, which was active in the plants during the entire period of low tide, with the maximum observed at the 4th hour (Fig. 5).

Observations of catalase activity during several tidal cycles showed that the type of curve was the same in all cases. Some shifts in the peak of enzyme activity in one direction or another depended on the weather conditions (temperature, cloudiness, wind speed, and humidity); in particular, periods of a decrease and increase in enzyme activity occurred earlier on hotter days.

Monitoring of the proline content in the tissues of *F. vesiculosus* over several tidal cycles evidenced that the concentration of this amino acid decreased during

Table 2. Parameters of approximation of carbon dioxide curves of CO_2 gas exchange of *Fucus vesiculosus*, calculated using the Farquhar model

Parameter, μmol CO_2/(m^2 s)	Conditions*			
	1	2	3	4
Maximum CO_2 absorption capacity	2.2 ± 0.28	4.07 ± 0.11	4.67 ± 0.94	1.78 ± 0.46
CO_2 emission rate in darkness	0.23 ± 0.03	0.24 ± 0.04	0.49 ± 0.08	0.67 ± 0.16
Maximum carboxylation rate of Rubisco	0.81 ± 0.1	4.65 ± 0.35	3.57 ± 0.95	3.07 ± 0.74
Carboxylation efficiency, μmol CO_2/(m^2 s Pa)	0.022 ± 0.012	0.032 ± 0.016	0.050 ± 0.013	0.064 ± 0.013
Electron transport rate at light saturation	2.1 ± 0.4	13.1 ± 1.1	16.6 ± 1.5	7.73 ± 2.6
Triose phosphate utilization rate	0.93 ± 0.12	1.19 ± 0.11	1.46 ± 0.14	0.80 ± 0.20
Carbon dioxide compensation point	177 ± 5	204 ± 4	114 ± 12	217 ± 14

*1, 5 hours without water; 2, 10 min in water, 10-cm depth; 3, 30 min in water, 30–40-cm depth; 4, 10 hours in water, 40-cm depth.

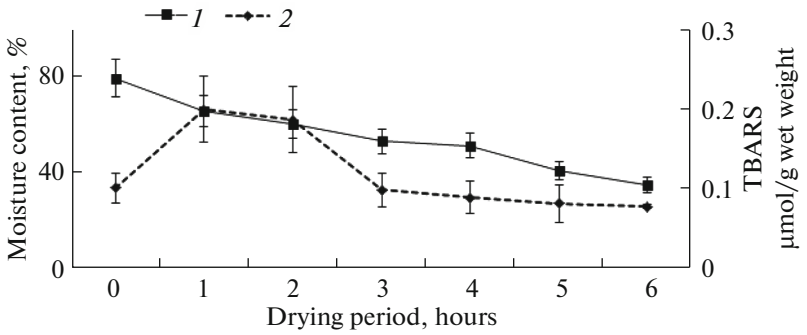

Fig. 4. (*1*) Moisture content and (*2*) TBARS in thalli of *Fucus vesiculosus* during low tide.

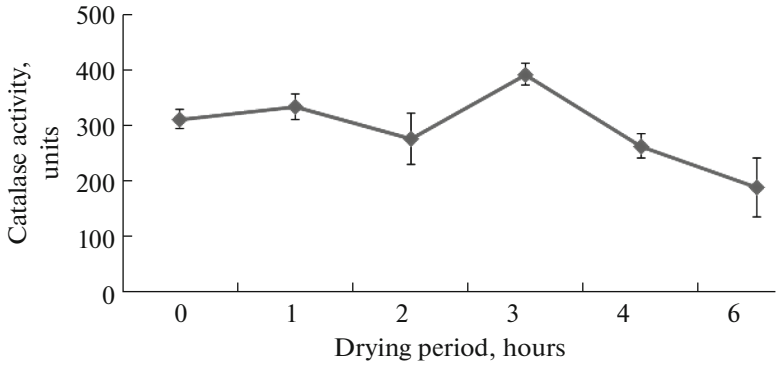

Fig. 5. Catalase activity in the cells of *Fucus vesiculosus* during low tide.

the first hours of low tide, then it increased sharply after 3–4 hours of drying, and then the concentration decreased again (Fig. 6).

DISCUSSION

During the tidal cycle, the upper littoral zone dries for 8 hours and the lower littoral zone dries for 2–3 hours, on the coast of the Barents Sea, near the Biological Station MMBI (Zelenetskaya Bay). *F. vesiculosus* is a unique species, which can grow in the upper littoral and may descend into the sublittoral due to its high adaptive capabilities.

The photosynthetic activity of this species during the tidal cycle was characterized by a three-peak curve, with two maxima at low tide and one at the beginning of high tide. At the end of low tide (6 h of drying), the A_{max} decreased down to negative values of gas exchange. The A_{max} values at the beginning of the

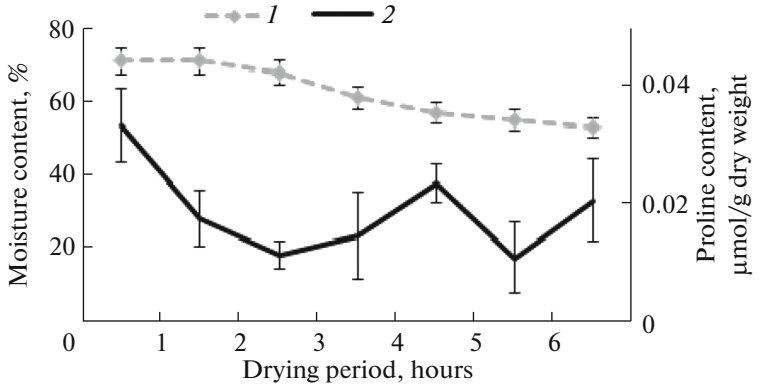

Fig. 6. Content of (*1*) moisture and (*2*) proline in thalli of *Fucus vesiculosus* during low tide.

high tide were significantly higher than at the end. Negative values of gas exchange indicated a significant inhibition of the processes of photosynthesis during the drying period.

During the tidal cycle, changes in the content and ratio of photosynthetic pigments, as well as in the size of the light-harvesting complex, were not observed. These data indicated that changes in A_{max} occurred due to changes in the rate of light reactions and were associated with functional rather than structural rearrangements of the photosynthetic apparatus.

The rate of electron transport, the maximum rate and efficiency of carboxylation, and the rate of dark-phase CO_2 emission in *F. vesiculosus* were 3–4 times higher during high tide than during low tide, based on calculation of the data obtained. No differences were found during the periods of high and low tide for indicators such as the triose phosphate utilization rate and the carbon dioxide compensation point. The A_{max} values were almost twofold higher during the transition to the aquatic environment at the beginning of the high tide. This transition was accompanied by a rapid increase in the maximum carboxylation rate and electron transport rate; after 30 min, other processes were also activated (e.g., both the triose phosphate utilization rate and the dark-phase respiration rate increased). These data indicated that other carboxylation mechanisms were launched with the transition to the aquatic environment, which were not recorded by the method used for determining A_{max}.

We used a method that took into account the absorption of only atmospheric carbon in the form of CO_2, which was carboxylated with the participation of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). However, the content of CO_2 in the aquatic environment is low and the main source of carbon for algae is bicarbonate, which is converted into accessible form using carboxylase. The possibility of switching the mechanisms of carboxylation and the ability of littoral algae to use air instead of bicarbonate for photosynthesis as a source of inorganic carbon was discovered in the middle of the 20th century by R.G.S. Bidwell, the pioneer in these studies (Bidwell, 1958). Some studies indicate a decrease in photosynthesis of littoral algae during low tide (Bidwell and Craigie, 1963; Williams and Dethier, 2005), which may be related to the study of particularly long-term exposition of algae to the air. Our work revealed an increase in the A_{max} of littoral algae in the first phase of low tide, under short-term drying, which confirmed the results of similar studies (Quadir et al., 1979; Gao et al., 1999). In particular, this increase is achieved by the ability of *F. vesiculosus* to accumulate carbon in tissues, similarly to the Crassulaceae plants characterized by Crassulacean acid metabolism (CAM), thereby performing the processes of photosynthesis for some time without an external carbon source (Kawamitsu and Boyer, 1999).

It can be assumed that the resistance of this species to drying is determined by its ability to use atmospheric CO_2. However, in most works studying the adaptation of *Fucus* species to drying, the changes in the moisture content in thalli were analyzed. Thus, it is known that *F. vesiculosus* is able to withstand prolonged drying and quickly restores the lost moisture, when plants are able to lose up to 91% of water (Kanwisher, 1957) and stay in the air for up to 32 hours without loss of viability (Kawamitsu et al., 2000; Andreev et al., 2012). Our study demonstrates that *F. vesiculosus* can withstand a humid environment for about one month and quickly recovers its photosynthetic activity when released into water. In the White Sea, it was also reported that the littoral *Fucus* species lose moisture more slowly than the sublittoral ones (Andreev et al., 2012).

Several mechanisms have been described that prevent algae dehydration during low tide, namely, the release of polysaccharide substances, such as fucoidan, onto the thallus surface (Lobban et al., 1985), the accumulation of substances with osmotic properties in cells, such as hydrin-like proteins (Wiltens et al., 1978; Quadir et al., 1979; Li et al., 1998), and changes in ion concentrations inside cells (Bisson and Kirst, 1995). However, studies carried out on various algae species showed that the height of their growth in the littoral zone does not depend on the mechanisms regulating the rate of moisture loss by the thallus (Dorgelo, 1976; Schonbeck and Norton, 1979; Ji and Tanaka, 2002). This may mean that all of the above mechanisms primarily provide the conditions for maintaining carbon dioxide metabolism in the aquatic environment and during drying.

In algae exposed to the air for a long time at low tide, the functional indicators of photosynthetic activity, calculated using the model, were lower than in thalli exposed to the aquatic environment. At the same time, an increase in dark-phase respiration, a high rate and efficiency of the carboxylation process, a high activity of electron transport, and even an increase in the rate of the carbon dioxide compensation point were noted when the algae were submerged for a long time.

During the transition of algae to the aquatic environment at the beginning of high tide, the A_{max} increased almost twofold. This process was accompanied by an increase in the rate of electron transport in the electron transport chain (ETC) of chloroplasts and, hence, in the rate of regeneration of the CO_2 acceptor, ribulose bisphosphate. The rate of electron transport increased by 6–8 times for the first 30 minutes. The maximum rate of carboxylation (Rubisco activity) also increased almost sixfold, which was comparable with an increase in the rate of electron transport. However, a significant increase in the rate of these reactions did not lead to a similar increase in A_{max}. At the very beginning of high tide, the $J_{max}/V_{c\,max}$

value in plants that were immersed in water for 30 min increased up to 4.6, which indicated a possible limitation of A_{max} by the Rubisco activity. As a result, at the beginning of high tide, although the Rubisco activity increased compared with that at low tide, it did not carry into effect a corresponding increase in A_{max} due to the transition to another carbon source (bicarbonate).

The dynamics of photosynthetic activity of the light and dark phases of photosynthesis in *F. vesiculosus* evidence the reversible changes in the performance of the photosynthetic apparatus (PA) during low tide, which could be caused by the increase in illumination and temperature and the developing oxidative stress.

A_{max} in algae increases in the first hours of low tide, when plants are exposed to high illumination, which increases fivefold or more, since more than 80% of photosynthetically active radiation (PAR) does not penetrate deeper than the very surface 1-m water layer in the coastal zone of the Barents Sea (Makarov et al., 2010). However, the A_{max} of various species of littoral algae in the first hours may both increase and decrease significantly; according to earlier studies, it is unlikely that this effect is associated solely with an increase in the illumination intensity (Johnson et al., 1974; Wiltens et al., 1978; Quadir et al., 1979; Oquist and Fork, 1982; Hanelt, 1998; Ganlin et al., 2008).

The change in A_{max} may be associated with an increase in the rate of electron transport and an increase in the ROS content, as well as with the subsequent activation of protective reactions at the photochemical stage of photosynthesis (increased thermal dissipation, fluorescence, etc.) (Collén and Davison, 1999; Yoshinobu et al., 2000; Heber et al., 2007; Kolupaev, 2007). The increase in ROS is evidenced by our data on the accumulation of LPO products during the initial period of drying. The subsequent decrease in LPO products is associated with the activation of antioxidant systems, their active functioning can also ensure maintenance of the second peak of photosynthetic activity. An increase in the catalase content and/or an increase in the activity of this enzyme during the first peak is explained by the accumulation of ROS, and a further decrease in its activity is associated both with a decrease in ROS concentration (Radyukina, 2015) and with the activation of other antioxidant protective systems. We also hypothesize that free proline may also be involved in maintaining physiological activity and protecting against oxidative stress. The dynamics of the proline content shows a significant accumulation after 3–4 hours of drying, which corresponds to the middle of low tide. It has been noted previously that proline performs many functions in plant cells, including acting as a signaling molecule for activating the body systems responsible for plant restoration after stress (Bates et al., 1973; Szabados and Savouré, 2010). Some studies evidence its antioxidant capacity for reducing the concentration of ROS and activating alternative pathways for ROS detoxification (Matysik et al., 2002). It is quite possible that it participates in the detoxification of ROS, which are formed as a result of photosynthetic activity in fucoid cells in the initial period of dehydration; it may also participate in the activation of catalase synthesis.

A decrease in A_{max} in *F. vesiculosus* to negative values during long-term exposure of thalli in the air may indicate either the limited possibilities of fixing atmospheric CO_2 or the limited potential of antioxidant systems that ensure the activity of the photosynthetic apparatus. The first hypothesis is supported by our data on the possibility of rapid recovery of PA in algae after the onset of high tide and on the retention of its activity during prolonged dehydration of plants, as well as by previously published data (Bidwell and Craigie, 1963; Quadir et al., 1979; Williams and Dethier, 2005; Schagerl and Moostl, 2011).

Hydrolability, i.e., the ability to lose a significant amount of moisture during low tide and its rapid recovery at high tide, is one of the mechanisms of resistance of *F. vesiculosus* to drying. In addition, adaptation to habitat conditions is apparently associated with the activation of protective antioxidant systems and carboxylation mechanisms. Their efficiency and duration of performance seem to correlate with the average duration of the drying period at low tide in the local growing conditions of the species (Flores-Molina et al., 2014). At the same time, 3–4 hours of drying, which are the period of the presence of algae of this species in the air at quadrature tides, is a transitional period when functional systems are rearranged; i.e., the photosynthetic processes slow down and protective mechanisms are activated. Apparently, proline also participates in the formation of protective mechanisms.

The long-term periodical presence of littoral algae in the air during low tide has a positive effect. Many marine organisms, both animals and plants, cannot withstand such prolonged drying. Although the habitat conditions for *Fucus* algae here are far from optimal, growing in the littoral zone gives them an additional competitive advantage and protecting them against epiphytes and herbivorous animals.

Our study evidences that the adaptation of macroalgae inhabiting the littoral zone with periodic drying is associated with the hydrolability of the algae, with the activation of protective antioxidant systems and of the facultative carboxylation mechanisms. Apparently, the duration of the effective operation of all protective mechanisms correlates with the average duration of the drying period at low tide in the growth zone of the species and preconditions for its additional competitive advantage.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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