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METABOLITE CONTENT AND ENERGY VALUE OF THE BROWN ALGA *ASCOPHYLLUM NODOSUM* (L.) LE JOLIS UNDER CONDITIONS OF THE BARENTS SEA

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The brown alga *Ascophyllum nodosum* (L.) Le Jolis is a valuable producer of bioactive compounds and a key component of the Barents Sea ecosystem. Analyzing algal biomass and determining its energy value are relevant for assessing the status of the species in the ecosystem and its resource potential. For a better understanding of the changes occurring in *A. nodosum* during the commercial summer–autumn harvesting period, it is important to investigate the allocation of metabolites within the thallus and the contribution of different structures to total biomass. In this study, biochemical parameters (total proteins, lipids, carbohydrates, polyphenols, chlorophyll *a* and *c*, total carotenoids, and fucoxanthin) were determined by standard methods. Both *in situ* biomass and laboratory-processed biomass were measured; based on these data, the energy content and the energy equivalent of biomass were calculated. For *A. nodosum* sampling, two Barents Sea bays were selected: Zavalishin Bay and Korabelnaya Bay. Those are located close to each other but differ in hydrological conditions. In both bays, *A. nodosum* forms dense intertidal mats. It was found that biomass peaked in June in both bays, with minimal differences between sites and a mean value of 25 kg·m^{-2}. However, the energy equivalent of biomass at this time differed: in samples from Zavalishin Bay, this parameter was 1.4 times higher, while ash content was 1.4 times lower. Also, *A. nodosum* from Zavalishin Bay featured higher content of polyphenols and fucoxanthin. We examined the distribution of bioactive compounds among functionally differentiated thallus zones (receptacles, apical tips, and the remaining thallus), as well as in relation to the phase of reproduction (fertile *vs.* sterile thalli), and abiotic habitat conditions (a set of factors included salinity, temperature, and wave exposure). We revealed patterns of metabolite distribution in *A. nodosum* from the Barents Sea under the effect of three factors: the thallus zone, phase of reproduction, and habitat. The thallus zone noticeably affected the allocation of fucoxanthin, proteins, lipids, carbohydrates, chlorophyll *c*, chlorophyll *a*, and total carotenoids. The habitat of the alga had a significant effect on the content of polyphenols, proteins, and fucoxanthin, and also on the level of carbohydrates and lipids. The phase of reproduction noticeably affected the content of proteins, polyphenols, chlorophyll *c*, and lipids.

Keywords: *Ascophyllum nodosum*, biomass, energy value of biomass, protein, carbohydrates, lipids, pigments, polyphenols

The brown algae (Phaeophyceae) are one of the most productive groups of marine macrophytes and play a vital role in coastal ecosystems. Their high productivity significantly contributes to the cycling of matter and energy in coastal ecosystems, providing the basis for the development of many marine communities. Furthermore, the brown algae are a promising target for industrial use as a source of biomass, biologically active substances, and other products.

In this context, *Ascophyllum nodosum* (L.) Le Jolis is of particular interest: an alga included in the list of aquatic bioresources subject to commercial use by the Order of the Government of the Russian Federation dated 18.11.2017 No. 2569-r [2026]. Recent studies revealed its high metabolic activity and ability to synthesize both primary metabolites (proteins, lipids, and carbohydrates) and secondary ones (*inter alia* polyphenols and fucoxanthin) [Pereira et al., 2020]. However, a thallus of the brown alga is morphologically and functionally heterogeneous and consists of zones that perform several physiological functions. Spatial allocation of metabolites within the thallus boosts the overall efficiency of the organism functioning: resources are directed to the areas where they are most needed. Despite accumulated data on *A. nodosum* chemical composition [Daurtseva, 2018; Obluchinskaya, 2024; Obluchinskaya et al., 2024; Pereira et al., 2020], the distribution of biologically active compounds across functionally differentiated thallus zones – receptacles (responsible for reproduction), apical tips (zones of active growth), and the remaining thallus (performing a supporting function, and also photosynthesis and storage of substances) – remains poorly understood.

Information on the energy value of thallus zones is also scarce, while such data are required for proper production calculations, food and feed value assessment, and trophic relationships modeling [Gorbatenko, 2018].

Arctic populations, including those from the Barents Sea, are especially poorly studied in this context, despite their commercial potential.

Investigating shifts in the content of metabolites (polyphenols and pigments), related to phases of reproduction in macrophytes, is fundamental for revealing factors that regulate the productivity of marine algal communities during vegetation cycles. The phytochemical composition of the raw algal material is highly variable due to both internal factors (developmental stages and reproductive phases) and external conditions (habitat characteristics and seasonality of harvesting). The brown algae, *A. nodosum* in particular, are sensitive to changes in environmental factors, especially in hydrodynamics. Surf, or wave exposure, affects algal biochemistry, morphology, and stability, and this effect is often more significant than that of temperature or salinity.

The practical value of this study is related to the potential for optimizing the industrial use of *A. nodosum*. Analyzing the age characteristics of the alga is particularly important, as plants older than 4–5 years, which bear the bulk of the reproductive burden, are of primary industrial interest [Shoshina, 1998; Shoshina, Kapkov, 2014]. The length of such individuals is comparable to the distance at which algae are cut during industrial harvesting (approximately 30 cm from the base) [Case Studies, 1987].

Thus, results of a comprehensive survey of *A. nodosum* open prospects for the development of biotechnological production and the efficient use of marine resources.

The aim of this study is to comparatively analyze the chemical composition of functionally differentiated thallus zones of *Ascophyllum nodosum* (receptacles, apical tips, and thallus without apical zone), and to examine biomass distribution and its energy value using samples from Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea).

MATERIAL AND METHODS

The work was focused on the brown alga *A. nodosum* inhabiting two nearby Barens Sea bays which differ in hydrological conditions: Zavalishin Bay and Korabelnaya Bay. According to our data, within littoral zones surveyed, the alga forms independent thickets with a projective coverage of 80–100%, and its thalli reach their maximum length. In other areas of Teriberskaya Bay, this species occurs in separate groups within littoral *Fucus* communities; its length typically reaches 30 cm, and its biomass is 0.5 kg·m^{-2}.

Zavalishin Bay extends into the southern coast of the eastern outer part of Teriberskaya Bay and features a rocky shore dominated by rounded boulders. The degree of surf was assessed in terms of a combination of factors: openness of the water area, shore exposure to prevailing winds, and height of breaking waves. The littoral zone is relatively open to wave action. However, unlike areas of completely open Barents Sea coast, which are subject to storm surges with large accelerations, this site is characterized by lower intensity of surf processes due to the location and configuration of the bay. This allows to classify the area as a moderate surf zone (Table 1). Depths in the middle part of the bay reach 15 m. The mean tidal range is approximately 4 m, which facilitates regular water renewal and maintains a dynamic hydrological regime. In Korabelnaya Bay, located in the inner part of Teriberskaya Bay, the brown alga was sampled on the shoreward side of a small island located near the main sandy beach. This area is relatively well protected from the direct effect of the open sea, and this results in weak surf (see Table 1). Depths in the central Korabelnaya Bay are approximately 7–8 m, and this also mediates reduced wave action on the littoral zone.

Table 1. Abiotic characteristics of the brown alga sampling sites

Sampling time	Sampling site	Salinity, ‰	Temperature, °C	Wave exposure (surf)
September 2023	Zavalishin Bay	20.2 ± 0.2	+11.8 ± 0.1	Moderate
	Korabelnaya Bay	33.8 ± 0.1	+11.8 ± 0.2	Weak
June 2024	Zavalishin Bay	8.1 ± 0.1	+6.9 ± 0.1	Moderate
	Korabelnaya Bay	13.0 ± 0.1	+6.9 ± 0.1	Weak
July 2024	Zavalishin Bay	27.2 ± 0.2	+12.0 ± 0.2	Moderate
	Korabelnaya Bay	32.1 ± 0.2	+10.0 ± 0.1	Weak

Temperature and salinity were measured at the time of sampling. According to our data, in Zavalishin Bay, salinity was lower than in Korabelnaya Bay, whereas water temperature did not differ significantly during the period of work (Table 1).

The material was sampled at the beginning of the reproduction cycle (September 2023), at its peak (June 2024), and at its end (July 2024) in accordance with methodology of hydrobotanical survey [Izuchenie ekosistem, 2005]. The alga was sampled during low tide. Salinity was measured with a portable saltwater refractometer (RHS-10ATC, China), and temperature, with a mercury thermometer (TL-4, Russia). Surf in the littoral zone was assessed visually according to a scale of Guryanova *et al.* [Izuchenie ekosistem, 2005].

Within *A. nodosum* belt, sites of 0.25 m^2 (50 × 50 cm) were surveyed. All attached plants within every site were mown down. Biomass (wet plant mass, *in situ*, kg·m^{-2}) was determined immediately after cutting by weighing (WH-A08 scale) with an accuracy of 0.005 kg. Green plant parts

rapidly lose moisture after cutting, and weighing carried out at different, albeit close, times gives dissimilar results. Therefore, we compared biomass of the just-cut alga with the laboratory-processed biomass, *i. e.*, the sum of individual biomasses of thalli cleared of epiphytes and delivered to a laboratory. In addition to the individual biomass and laboratory-processed biomass ($kg \cdot m^{-2}$), after the alga was delivered to the laboratory, we determined the number of individuals to calculate the population density ($ind. \cdot m^{-2}$). Next, receptacles and apical tips were separated from thalli, and each part was weighed individually on a laboratory scale VLTE-210 (Gosmetr, Russia) with an accuracy of 0.001 g to determine the percentage (%) of biomass contribution of each part to the total biomass. Then, the samples were frozen and stored at −18 °C (Derby F30B chest freezer) for subsequent chemical analysis.

Production characteristics were assessed based on wet and dry-weight biomass of the alga during summer and autumn, its energy equivalent, and the biochemical composition of functionally differentiated thallus zones.

The mean sample for biochemical analysis was collected by the quartering method (GOST 12536-79, international technical standard).

Pigment extraction was performed with 70% acetone involving a modified method described previously [Connan, 2015; Daurtseva, 2018]. Pigment content in extracts was determined spectrophotometrically. Spectra were obtained on a Nicolet Evolution 500 spectrophotometer (Spectronic Unicam) in quadruplicate. The content of chlorophyll *a* and *c*, fucoxanthin, and total carotenoids was determined according to the literature [Connan, 2015; Vilg et al., 2015; Wang et al., 2018].

Total lipid content was assessed after complete extraction of lipid fractions with extractants of different polarity, followed by gravimetric determination of the total fraction [Metody fiziologo-biokhimicheskogo issledovaniya, 1975].

For protein determination, the Lowry method was applied using Folin's reagent after pigments were removed [Lowry et al., 1951; Metody fiziologo-biokhimicheskogo issledovaniya, 1975; Promyslovye, 1998].

The content of total neutral carbohydrates was analyzed using the phenol-sulfuric acid method [DuBois et al., 1956].

Total polyphenol content was determined spectrophotometrically at 750 nm with Folin–Ciocalteu reagent by standard techniques [Ford et al., 2019; Van Alstyne, 1995]. Phloroglucinol (Sigma-Aldrich, Germany) was used as a standard. Polyphenol content was expressed as the equivalent of phloroglucinol in $mg \cdot g^{-1}$ of the algal absolutely dry weight (hereinafter d. w.).

The method for determining total ash is based on assessing the ash mass in the alga after combustion of organic matter in a sample [GOST 26185-84, 2018].

The energy value of the alga ($kcal \cdot g^{-1}$) was calculated by a formula involving the generally accepted values of the specific energy value of proteins (P), carbohydrates (C), and lipids (L) [Metody opredeleniya produktsii, 1968]: (5.65 P + 4.10 C + 9.45 L) / 100.

The energy equivalent of biomass was quantified based on the obtained data on biomass and energy value, with moisture content taken into account ($kcal \cdot m^{-2}$).

All measurements were performed in triplicate. The results are expressed as $mg \cdot g^{-1}$ d. w.

Statistical analysis involved Statistica and IBM SPSS Statistics software. MS Office Excel was used for calculations and plotting. For processing of all the data, descriptive statistics was applied. Compliance

with normal distribution was tested using the Shapiro–Wilk W test. For samples with signs of normal distribution, one-way analysis of variance (ANOVA) was carried out. When detecting a statistically significant effect of a factor, pairwise comparisons were performed applying Tukey's HSD test. In cases of data normality violations, nonparametric tests were used: the Wilcoxon signed-rank test, for paired (related) measurements; the Kruskal–Wallis test, for unrelated groups (it was followed by the Mann-Whitney U test for pairwise comparisons). To assess the effect of several factors, such as habitat, thallus zone, and algal reproductive stage, on metabolite distribution, a multivariate analysis of variance (MANOVA) was carried out. Differences were considered statistically significant at $p < 0.05$.

RESULTS

The results of *A. nodosum* biomass determination in Zavalishin Bay and Korabelnaya Bay (the Barents Sea) are presented in Table 2. In Zavalishin Bay, *in situ* biomass was 1.04–1.08 times higher than laboratory-processed one ($p = 0.03$, Wilcoxon signed-rank test), and in Korabelnaya Bay, it was 1.06–1.15 times higher ($p = 0.01$, Wilcoxon signed-rank test). In the littoral zone, the alga features various levels of moisture, but the dynamics of the calculated dry-weight biomass did not differ from the dynamics of wet biomass.

Table 2. Results of determination of *Ascophyllum nodosum* biomass in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea)

Parameter	Zavalishin Bay			Korabelnaya Bay		
	September 2023	June 2024	July 2024	September 2023	June 2024	July 2024
Wet biomass (*in situ*), kg·m^{-2}	15.91 ↓ ± 0.58	25.03 ↑ ± 0.24	23.28 ± 0.80	14.88 ± 0.47	25.96 ↑ ± 0.69	14.13 ↓ ± 0.23
Wet biomass (laboratory-processed), kg·m^{-2}	14.78 ↓ ± 0.53	23.77 ↑ ± 0.45	21.76 ± 0.75	13.91 ± 0.45	23.04 ↑ ± 0.69	13.27 ↓ ± 0.20
Dry-weight biomass, kg·m^{-2}	4.86 ↓ ± 0.17	13.53 ↑ ± 0.26	8.56 ± 0.29	8.29 ± 0.26	12.87 ↑ ± 0.39	4.55 ↓ ± 0.70
Population density (abundance), ind.·m^{-2}	8,288 ↑ ± 166	4,486 ± 209	4,150 ↓ ± 165	2,673 ± 96	2,877 ↑ ± 47	1,046 ↓ ± 14
Mean moisture content, %	67.13 ↑ ± 0.55	54.07 ↓ ± 0.82	60.66 ± 0.52	67.36 ± 0.70	78.58 ↑ ± 0.74	65.68 ↓ ± 0.56

Note: ↓ are the minimum values in the row; ↑ are the maximum values in the row.

In the littoral zone of Zavalishin Bay, the wet biomass of *A. nodosum* ranged 15.91 to 25.03 kg·m^{-2}; the maximum value was recorded in June. The peak wet biomass of the alga sampled in Korabelnaya Bay, 25.96 kg·m^{-2}, was also registered in June. The value in July was the lowest noted, 14.13 kg·m^{-2}. Interestingly, in Korabelnaya Bay, the pattern of fluctuations in population density coincides with the biomass dynamics, while in Zavalishin Bay, the maximum population density was observed in September, when biomass is low. The lowest dry-weight biomass was revealed in Zavalishin Bay in September (4.86 kg·m^{-2}) and in Korabelnaya Bay in July (4.55 kg·m^{-2}). In both areas, the dry-weight biomass of samples was the highest in June, when algae are in the phase of maximum receptacle development.

The alga from Zavalishin Bay was characterized by a higher population density throughout the entire observation period. It peaked in September: 8,288 ind.·m^{-2}. For samples from Korabelnaya Bay, the value was significantly lower: 1,046–2,877 ind.·m^{-2}.

To determine the ratio of functionally differentiated thallus zones (apical tips and receptacles relative to the remaining thallus) of *A. nodosum* from Zavalishin Bay and Korabelnaya Bay, we sampled plants older than 4 years. After dividing the thallus, the weight of each zone was assessed, and the mean percentage ratio of its vegetative and generative zones was quantified. The results of determination of the allocation spectrum are presented in Fig. 1.

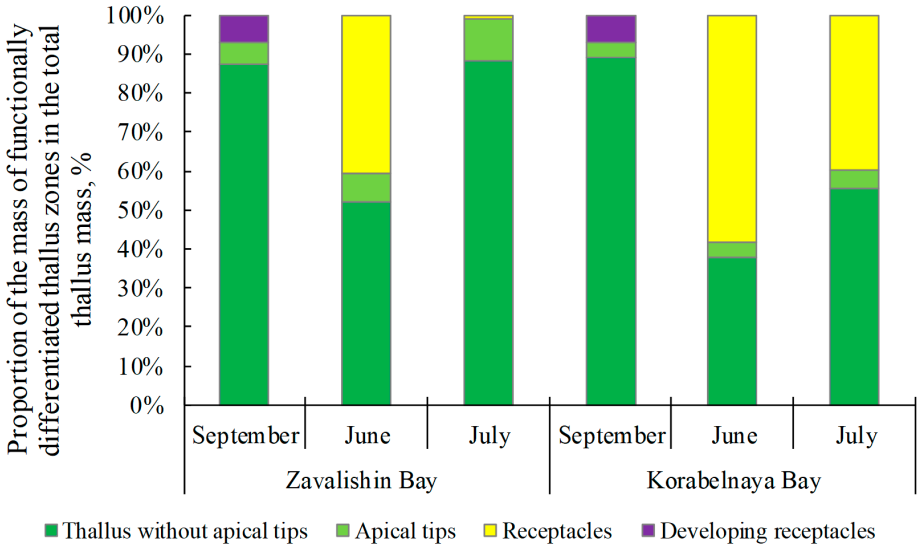


Fig. 1. Allocation spectrum of the biomass dynamics for *Ascophyllum nodosum* vegetative-generative thallus in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea)

Determination of the allocation spectrum of biomass for *A. nodosum* vegetative-generative thallus shows that the thallus zone accounts for 37–89% of the total biomass; the apical zone, for 3–7%; and the generative zone, for 7–58%. In June, the generative zone was represented by mature receptacles and contributed much to the total thalli biomass: the values were 41% of the total thalli mass for the alga from Zavalishin Bay and 58% for those from Korabelnaya Bay.

Table 3 presents data on the content of primary metabolites – proteins, lipids, and carbohydrates – in functionally differentiated thallus zones of *A. nodosum*. These values were used to calculate the energy value (energy capacity) of each zone in kcal·g^{-1}.

The protein content in the samples ranged from 20.55 to 79.41 mg·g^{-1} d. w. On average, the alga from Zavalishin Bay featured higher values, with particularly high protein content in September across all thallus zones: 60.73–79.41 mg·g^{-1} d. w. Receptacles contained more protein in September than in June and July.

The total lipid content ranged from 5.19 to 31.30 mg·g^{-1} d. w. in different thallus zones. Receptacles, on average, contained more lipids than other thallus zones, with particularly large and statistically significant differences ($p = 0.01$, Tukey's HSD test) in Zavalishin Bay in June (2.5–4 times) and in Korabelnaya Bay in July (2.8–4 times). When comparing apical tips and thallus without apical zone, it was established that apical tips contained 1.4 times more lipids ($p = 0.001$, Tukey's HSD test).

Carbohydrates prevailed in the samples studied (see Table 3). Their amounts were higher in thallus without apical zone (487.7–773.9 mg·g^{-1} d. w.) than in other zones (354.4–618.5 mg·g^{-1} d. w.). In September and June, apical tips had less carbohydrates than receptacles; in July, the opposite was observed.

Table 3. Content of proteins, lipids, and carbohydrates, and energy value of functionally differentiated thallus zones of *Ascophyllum nodosum* in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea)

Parameter	Functionally differentiated thallus zone	Zavalishin Bay			Korabelnaya Bay		
		September 2023	June 2024	July 2024	September 2023	June 2024	July 2024
Proteins, mg·g^{-1} d. w.	Receptacles	79.41 ↑ ± 0.93	45.64 ↓ ± 0.17	53.48 ± 0.01	55.95 ↑ ± 0.01	44.75 ± 0.02	35.60 ↓ ± 0.06
	Apical tips	60.73 ↑ ± 0.35	40.77 ↓ ± 0.14	46.28 ± 0.05	23.33 ↓ ± 0.02	41.44 ↑ ± 0.12	24.93 ± 0.88
	Thalli without apical tips (stumps)	76.39 ↑ ± 0.39	29.03 ↓ ± 0.26	49.59 ± 0.03	21.81 ± 0.05	21.95 ↑ ± 0.08	20.55 ↓ ± 0.44
Lipids, mg·g^{-1} d. w.	Receptacles	15.82 ↓ ± 0.02	24.66 ↑ ± 0.13	16.58 ± 0.03	8.59 ↓ ± 0.03	20.62 ± 0.06	31.30 ↑ ± 0.21
	Apical tips	15.90 ↑ ± 0.01	10.35 ↓ ± 0.06	15.26 ± 0.01	8.35 ↓ ± 0.02	8.39 ↓ ± 0.02	10.99 ↑ ± 0.05
	Thalli without apical tips (stumps)	13.21 ↑ ± 0.01	8.09 ↓ ± 0.07	11.91 ± 0.01	5.37 ± 0.01	5.19 ↓ ± 0.09	7.81 ↑ ± 0.07
Carbohydrates, mg·g^{-1} d. w.	Receptacles	618.51 ↑ ± 0.28	504.42 ± 0.70	354.46 ↓ ± 0.35	526.5 ↑ ± 0.25	434.3 ± 0.47	486.1 ↓ ± 0.90
	Apical tips	521.93 ± 0.42	434.2 ↓ ± 0.67	552.15 ↑ ± 0.35	403.17 ± 0.10	389.1 ↓ ± 0.07	565.9 ↑ ± 0.62
	Thalli without apical tips (stumps)	623.86 ± 0.76	773.9 ↑ ± 0.81	557.34 ↓ ± 0.15	487.7 ↓ ± 0.25	530.72 ± 0.83	591.5 ↑ ± 0.32
Energy value, kcal·g^{-1} d. w.	Receptacles	3.13 ↑ ± 0.03	2.56 ± 0.05	1.91 ↓ ± 0.06	2.56 ↑ ± 0.04	2.23 ↓ ± 0.02	2.49 ± 0.05
	Apical tips	2.63 ↑ ± 0.03	2.11 ↓ ± 0.02	2.67 ↑ ± 0.01	1.86 ↓ ± 0.04	1.91 ± 0.01	2.56 ↑ ± 0.01
	Thalli without apical tips (stumps)	3.11 ± 0.05	3.41 ↑ ± 0.01	2.68 ↓ ± 0.01	2.17 ↓ ± 0.02	2.35 ± 0.02	2.62 ↑ ± 0.01

Note: ↓ are the minimum values in the row; ↑ are the maximum values in the row.

Ranges of *A. nodosum* energy values, calculated based on the content of proteins, lipids, and carbohydrates in different thallus zones, were as follows: 1.91–3.13 kcal·g^{-1} for receptacles, 1.86–2.67 kcal·g^{-1} for apical tips, and 2.17–3.41 kcal·g^{-1} for thalli.

To calculate the energy equivalent of dry-weight biomass, we analyzed the ratios of different thallus zones (see Fig. 1) in the most representative *A. nodosum* specimens, which make up the bulk of the population biomass (Table 4, Fig. 2). When determining the production characteristics of the alga, we took into account the total ash content as well (Table 4).

Ash content in the alga from Zavalishin Bay ranged within 15.40–17.49%, and in samples from Korabelnaya Bay, the values ranged within 17.62–21.06% ($p = 0.05$, Kruskal–Wallis test).

Table 4. Energy equivalent of biomass and ash content of whole thalli of *Ascophyllum nodosum* in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea)

Parameter	Zavalishin Bay			Korabelnaya Bay		
	September 2023	June 2024	July 2024	September 2023	June 2024	July 2024
Energy equivalent of dry-weight biomass, kcal·m^{-2}	71.77 ↓ ± 0.23	281.06 ↑ ± 0.24	186.29 ± 0.54	83.85 ± 0.37	175.22 ↑ ± 0.54	81.17 ↓ ± 0.46
Ash, %	17.38 ± 0.02	15.4 ↓ ± 0.01	17.49 ↑ ± 0.02	17.62 ↓ ± 0.03	21.06 ↑ ± 0.01	20.88 ± 0.02

Note: ↓ are the minimum values in the row; ↑ are the maximum values in the row.

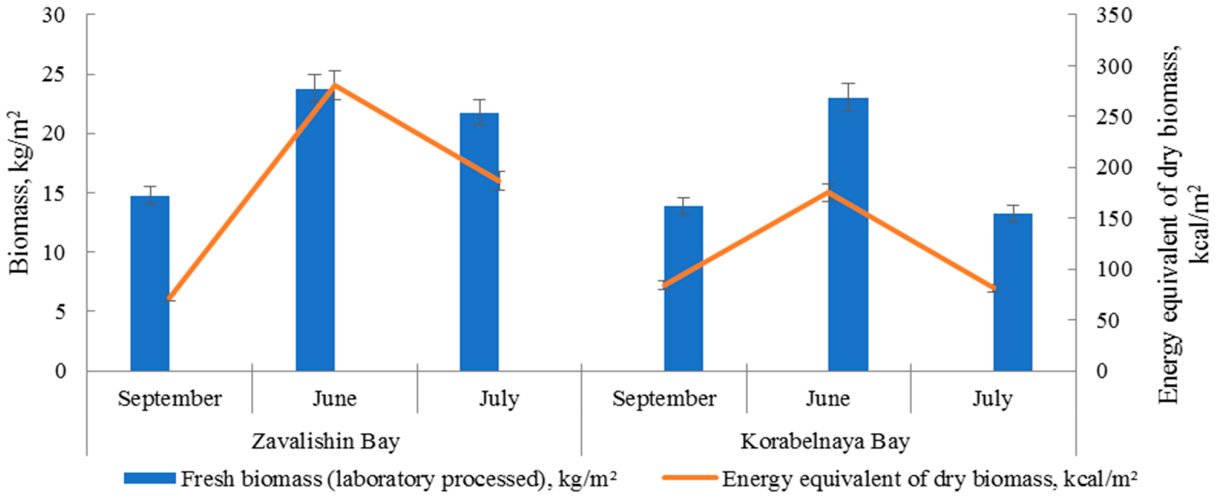


Fig. 2. Dynamics of biomass and energy equivalent of biomass for *Ascophyllum nodosum* in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea)

During the survey, we recorded differences in accumulation of several secondary metabolites (polyphenols and pigments) between thallus zones. The range of polyphenol content (Fig. 3) in different zones was from 15.1 to 55.8 mg·g^{-1} d. w. No distribution patterns were revealed for polyphenols in different thallus zones; however, *A. nodosum* from Zavalishin Bay tended to feature higher polyphenol content than the alga from Korabelnaya Bay. It was especially noticeable in September: polyphenol content was, on average, 2.4 times higher ($p = 0.02$, Kruskal–Wallis test).

To analyze the pigment composition of the brown alga, we determined the content of chlorophyll *a* and *c*, total carotenoids, and separately fucoxanthin (Table 5).

In *A. nodosum*, chlorophyll *a* content ranged within 0.24–1.85 mg·g^{-1} d. w.; chlorophyll *c*, 0.03–0.40 mg·g^{-1} d. w.; carotenoids, 0.32–0.76 mg·g^{-1} d. w.; and fucoxanthin, 0.26–0.64 mg·g^{-1} d. w. Mature receptacles contained significantly more chlorophyll *c* and fucoxanthin than other parts of the alga. Chlorophyll *a* content was the highest in receptacle primordia and in developing apical tips. The value for total carotenoids was lower in the thallus than in apical tips and receptacles. On average, the alga from Zavalishin Bay contained 1.3 times more fucoxanthin than the plant from Korabelnaya Bay ($p = 0.012$, Mann–Whitney *U* test).

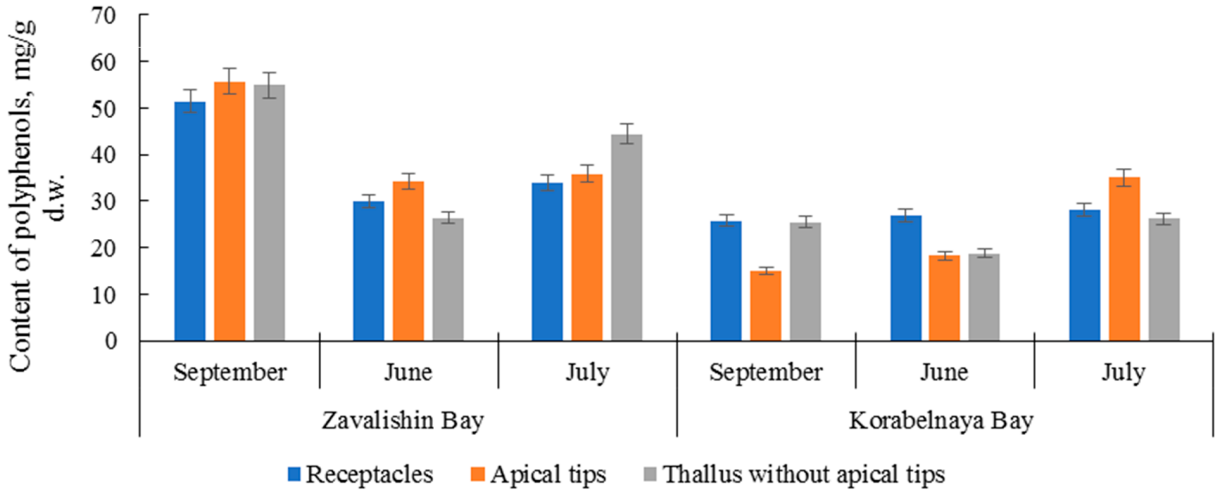


Fig. 3. Content of total polyphenols in functionally differentiated thallus zones of *Ascophyllum nodosum* in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea), mg·g^{-1} dry weight

Table 5. Content of photosynthetic pigments in functionally differentiated thallus zones of *Ascophyllum nodosum* in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea)

Pigment	Functionally differentiated thallus zone	Zavalishin Bay			Korabelnaya Bay		
		September 2023	June 2024	July 2024	September 2023	June 2024	July 2024
Chlorophyll *a*, mg·g^{-1} d. w.	Receptacles	1.08 ↑ ± 0.04	0.97 ± 0.05	0.24 ↓ ± 0.02	0.72 ± 0.01	1.25 ↑ ± 0.04	0.32 ↓ ± 0.03
	Apical tips	0.82 ↓ ± 0.00	1.76 ↑ ± 0.03	1.02 ± 0.02	1.25 ± 0.01	1.85 ↑ ± 0.04	1.17 ↓ ± 0.01
	Thalli without apical tips	0.81 ± 0.01	0.88 ↑ ± 0.23	1.20 ↓ ± 0.00	0.69 ↓ ± 0.00	1.23 ↑ ± 0.01	1.08 ± 0.07
Chlorophyll *c*, mg·g^{-1} d. w.	Receptacles	0.05 ↓ ± 0.00	0.40 ↑ ± 0.08	0.12 ± 0.01	0.06 ↓ ± 0.00	0.22 ↑ ± 0.05	0.17 ± 0.03
	Apical tips	0.04 ↓ ± 0.02	0.08 ± 0.03	0.09 ↑ ± 0.00	0.05 ↓ ± 0.00	0.05 ↓ ± 0.01	0.10 ↑ ± 0.03
	Thalli without apical tips	0.03 ↓ ± 0.01	0.04 ± 0.01	0.06 ↑ ± 0.01	0.04 ↓ ± 0.00	0.04 ↓ ± 0.01	0.05 ↑ ± 0.01
Total carotenoids, mg·g^{-1} d. w.	Receptacles	0.70 ↑ ± 0.02	0.67 ± 0.09	0.39 ↓ ± 0.01	0.36 ± 0.01	0.59 ↑ ± 0.04	0.32 ↓ ± 0.07
	Apical tips	0.52 ± 0.02	0.76 ↑ ± 0.12	0.38 ↓ ± 0.01	0.57 ± 0.00	0.73 ↑ ± 0.15	0.46 ↓ ± 0.05
	Thalli without apical tips	0.47 ↑ ± 0.01	0.39 ± 0.06	0.34 ↓ ± 0.01	0.34 ↓ ± 0.01	0.49 ↑ ± 0.01	0.36 ± 0.03
Fucoxanthin, mg·g^{-1} d. w.	Receptacles	0.64 ↑ ± 0.00	0.64 ↑ ± 0.10	0.63 ± 0.01	0.32 ↓ ± 0.02	0.48 ↑ ± 0.06	0.39 ± 0.04
	Apical tips	0.49 ± 0.03	0.51 ↑ ± 0.01	0.46 ↓ ± 0.01	0.37 ↓ ± 0.02	0.41 ↑ ± 0.07	0.39 ± 0.02
	Thalli without apical tips	0.40 ↑ ± 0.02	0.29 ↓ ± 0.02	0.37 ± 0.01	0.26 ↓ ± 0.02	0.30 ± 0.02	0.31 ↑ ± 0.05

Note: ↓ are the minimum values in the row; ↑ are the maximum values in the row.

To assess the effect of three factors on the distribution of metabolites in *A. nodosum* thalli, we carried out a multivariate analysis of variance (MANOVA) (see Supplements 1–4: https://marine-biology.ru/mbj/article/view/525). The factor of habitat (two Barents Sea bays, Zavalishin Bay and Korabelnaya Bay) was used as a comprehensive rank indicator of abiotic conditions (salinity and surf).

As revealed, the factor of thallus zone had a significant effect (21.95–61.96%) on the distribution of all studied metabolites, except for polyphenols. The reproductive phase affected much the content of proteins (58.42%), polyphenols (44.89%), chlorophyll *c* (25.67%), and lipids (16.90%). As a comprehensive abiotic factor, habitat was statistically significant for the content of polyphenols (84.11%), proteins (78.12%), and fucoxanthin (59.52%). Also, it had a noticeable effect on the distribution of carbohydrates (26.02%) and lipids (25.70%).

The analysis of interactions between the factors revealed the presence of a combined effect of thallus zone and reproductive phase on levels of lipids (43.88%), proteins (28.76%), carbohydrates (27.40%), and chlorophyll *c* (26.00%). The conjoint effect of thallus zone and habitat was statistically significant for fucoxanthin (28.93%) and proteins (26.44%). The effect of reproductive phase and habitat was noticeable for polyphenols (55.31%), proteins (51.09%), and lipids (21.83%). Finally, the interaction of all three factors had a statistically significant effect on polyphenol content only (29.88%).

DISCUSSION

The content of metabolites in the brown algae and their reserves in the littoral zone are known to vary depending on environmental conditions and physiological characteristics of the species [Bogolitsyn et al., 2023; Chernova, 2015]. For each population of the species, the period of maximum accumulation of biologically active metabolites and the period of maximum energy capacity (when biomass has a high energy potential) may not match [Biomass Conversion Processes, 1985].

Our data for *A. nodosum* from Zavalishin Bay and Korabelnaya Bay (the Barents Sea) provide evidence for the fact that the peak of biomass coincides with the peak of the energy equivalent of dry-weight biomass and does not coincide with the peak of polyphenol and pigment accumulation in the alga. Therefore, the site and time of sampling should be chosen based on the intended use of biomass.

According to the literature, the brown alga *A. nodosum* forms dense thickets with high biomass in the littoral zone of the North Atlantic, and also off southern coasts of the Barents and Kara seas. In the littoral zone of the eastern Kola Bay, on rocky placers of semi-open shores, its biomass reaches 69 kg·m^{-2}, and in sheltered areas, 42 kg·m^{-2}. On open boulder coasts, the value is lower: about 60 kg·m^{-2}. In the White Sea, biomass varies from 27.6 to 43.2 kg·m^{-2}, and in Kandalaksha Bay, from 24 to 34 kg·m^{-2}. In Onega Bay, values can reach 52–60 kg·m^{-2}, but more often do not exceed 30–35 kg·m^{-2}. In the northern Kola Bay (the Barents Sea), the biomass is lower, up to 4.2 kg·m^{-2}, while the total reserves are estimated at 371.4 tons (wet mass), or 74 tons (dry mass) [Podkorytova, Roshchina, 2021]. Analysis of N. Evseeva [2015] covered determination of the dynamics of *A. nodosum* biomass May to September in the littoral zone west of the Kola Bay. The minimum value was recorded in September (5.5 kg·m^{-2}), and the maximum one, in June (25 kg·m^{-2}).

Notably, in 2024, *A. nodosum* biomass was much higher than in previous years of research. In 2022, the biomass in the species belt in Korabelnaya Bay and Zavalishin Bay averaged 14.9 kg·m^{-2}; in 2023, the mean value in Zavalishin Bay was 16.5 kg·m^{-2}, and in Korabelnaya Bay, 11.9 kg·m^{-2} (according to information from S. Kolbeeva). A significant rise in biomass recorded in 2024 is likely to be associated with higher temperatures in June and July compared to those of the same months in 2022 and 2023. In 2025, the values were 21.5 kg·m^{-2} in Zavalishin Bay and 25.2 kg·m^{-2} in Korabelnaya Bay. According to summarized climate and oceanographic data, both in 2023 and 2024, temperatures in June and especially July exceeded long-term norms by 1–2 °C, and this is consistent with the general warming trend in the Arctic Atlantic.

As shown previously, in the Barents Sea, *A. nodosum* biomass peaks in June and July; after receptacle shedding, the biomass significantly decreases (by 15–50%) [Evseeva, 2015; Kapkov, Shoshina, 2021; Shoshina, Kapkov, 2014]. This is mediated by the fact that the proportion of all receptacles to the total thallus mass in *A. nodosum* averages 10–30% [Evseeva, 2023; Kuznetzov, 1960]. However, this parameter can vary greatly depending on habitat, maturity stage of receptacles, and plant's age. The peak biomass in early summer is likely the result of both intensive vegetative growth and the maximum development of the generative zone. The latter one is represented by mature receptacles, proportion of which in June reaches 40% in Zavalishin Bay and 58% in Korabelnaya Bay. Spatial variability in the proportion of receptacle mass in July (1% in Zavalishin Bay and 39% in Korabelnaya Bay) indicates the effect of local environmental factors on the reproductive phase of the brown alga. In September, the proportion of receptacle primordia decreases to 7% in both bays; this is associated with the initial stage of generative structure formation before the next reproductive cycle.

The assessment of *A. nodosum* biomass in Korabelnaya Bay and Zavalishin Bay in this study revealed a similar pattern of changes: maximum biomass values were observed during the fertile period corresponding to summer months. At the same time, in Zavalishin Bay, the biomass was characterized by a higher energy equivalent and lower ash content, thus indicating local variability in the species production parameters, *inter alia* under conjoint effect of abiotic factors (surf, salinity, and temperature).

An assessment of the energy value of thallus zones of *A. nodosum* from the two bays revealed both common trends and differences due to local conditions. Based on data in Tables 3 and 4, it can be concluded that the directions of changes in biomass and the energy equivalent of dry-weight biomass coincide (see Fig. 2).

The content of proteins, lipids, and carbohydrates in functionally differentiated thallus zones varied depending on site and time of *A. nodosum* sampling.

Our research revealed that thallus without apical zone contains 1.3 times more carbohydrates than other functional zones across all periods. In June and July, the total sugar content in apical tips is lower than in receptacles. In September, there are more carbohydrates in apical tips than in receptacle primordia. An increase in total carbohydrates in apical tips closer to autumn correlates with data on the distribution of mannitol (one of the main carbohydrates in the brown algae) in different parts of *Fucus vesiculosus* thallus, as reported by M. Klindukh [2018].

Shifts in carbohydrate content in algae can be determined by the species, its reproductive stage, and habitat [Obluchinskaya, 2024]. Multivariate analysis revealed that carbohydrate content was affected by the thallus zone, habitat, and the interaction of two factors: the thallus zone and reproductive stage.

We observed that mature receptacles contain less carbohydrates than receptacle primordia; the same pattern is noted for protein content in receptacles.

The brown algae typically contain 3–15% of protein d. w. [O' Brien et al., 2022]. These algae can serve as a protein source that requires neither arable land nor fresh water for cultivation. However, their protein content is variable and depends on the species, habitat parameters, season, and stage of thallus development [Bogolitsyn et al., 2023].

Data on higher protein content in the alga from Zavalishin Bay, where surf is more intense than in Korabelnaya Bay, are consistent with the results on determining the total protein content in *Laminaria saccharina* (= *Saccharina latissima*), the variability of which depended on water mobility [Promyslovye, 1998]. According to the literature, on average, protein content is higher in plants growing under surf conditions than in sheltered areas.

In June, *A. nodosum* receptacles contained more protein than other thallus parts. These data are comparable with the results presented in the work of E. Obluchinskaya [2020]. As shown in this study, in terms of free amino acid content, *F. vesiculosus* receptacles are not inferior to its apical tips.

According to data on the zone-specific distribution of metabolites in *F. vesiculosus* thallus, its central zone is the primary photoassimilation tissue, while apical tips are the acceptor zone, where active biosynthetic processes occur. Proteins prevalent in the central zone of the thallus are associated mostly with photosynthesis and carbohydrate metabolism. Proteins prevalent in apical tips are associated with nucleic acid metabolism, biosynthesis of protein macromolecules, and cellular respiration [Lemesheva et al., 2019].

Fucales are characterized by apical growth. It occurs through the division of the apical meristem: cells in the apical zone of the thallus (trunk and branches) which has the view of a triangular truncated pyramid. The apical meristem contains a central apical cell or cells located in the apical tip, which is surrounded by a group of actively dividing meristematic cells [Kamnev, 2023].

There are published data on a correlation between seawater salinity and the content of individual amino acids both in different parts of *F. vesiculosus* thallus and in young alga. The presence of such correlation may indicate the involvement of these amino acids in osmoregulation in the brown algae [Obluchinskaya, 2020].

In general, samples from Zavalishin Bay had higher protein and lipid content than samples from Korabelnaya Bay, except for July. This seems to result from differences in the timing of receptacle shedding driven by temperature differences in these two bays in July (Table 2).

Within one plant, the growing parts of the thallus are the most energy-rich ones: the energy value of thinned and more branched parts of an alga at the initial stage of its development is higher than that of the more mature, thickened thallus [Alexandrov, 2001]. In Zavalishin Bay and Korabelnaya Bay, the highest energy value was characteristic of *A. nodosum* apical tips in July (2.56–2.67 kcal·g^{-1} d. w.) and receptacles in September (2.56–3.13 kcal·g^{-1} d. w.) (see Table 3).

Lipids are typically extracted from algal biomass as a lipid-pigment complex [Parshina, 2022]. The pigment complex of *A. nodosum* includes chlorophyll *a* and *c*, fucoxanthin, auroxanthin, neoxanthin, violaxanthin, antheraxanthin, lutein, zeaxanthin, and β-carotene. However, their content in *A. nodosum* is lower than in other brown algae (*F. vesiculosus* and *Fucus distichus*) [Daurtseva, Obluchinskaya, 2019; Ignatova et al., 2021]. Seasonal dynamics and pigment distribution within the thallus

were analyzed in the brown algae of the genus *Saccharina* [Gerasimenko et al., 2015]. As shown, the pattern of changes in the content of lipids and photosynthetic pigments in different thallus zones was species-specific and depended on the season and sampling site. A study of *F. vesiculosus* pigments showed that their content in vegetative tissues of adult plants is the highest in the basal thallus zones and the lowest in apical tips [Tarakhovskaya, Maslov, 2010]. This is due to different levels of irradiance of apical and basal thallus zones: Fucales typically form dense thickets, with apical tips and receptacles on the surface.

The content of photosynthetic pigments can depend not only on irradiance but also on processes occurring within a plant itself: accumulation or consumption of reserve substances, growth, reproduction, *etc.* Those can alter the area-to-mass ratio, *i. e.*, the basis for calculating pigment content [Makarov, 2010].

According to [Ryabushko et al., 2017], elevated fucoxanthin levels in the brown algae of the genus *Cystoseira* indicate the key role of this carotenoid in the adaptation of the algal photosynthetic apparatus to anthropogenic effects.

This study revealed that there is more fucoxanthin and chlorophyll *c* in receptacles than in vegetative thallus zones. This is consistent with the fact that *A. nodosum* receptacles facilitate both gamete formation and pigment accumulation, and this appears to be related to their physiological activity and performance of protective functions.

When comparing polyphenol content in different thallus zones of *A. nodosum* from two bays of the Barents Sea, we did not find a common trend. This is also consistent with results of previous studies of polyphenols in several species of the brown algae from various habitats [Tkach, Obluchinskaya, 2017]. Some authors have shown that polyphenol content is low throughout the reproductive phase (April to June), and the maximum is reached during the period of receptacle shedding [Kyung-Tae, 2012; Obluchinskaya, Zakharova, 2020]. Seasonal changes in polyphenol accumulation vary across marine areas. In general, it can be noted that the mean content of polyphenols is higher in the alga from Zavalishin Bay than in the alga from Korabelnaya Bay.

Biomass, energy value, and ash content are important factors to consider when evaluating an alga as a promising raw material for various industries. Together, its biomass and abundance allow us to assess the population structure and its role in the biocenosis. In the brown algae, the rapid biomass accumulation means a high rate of CO_2 absorption from the environment during photosynthesis (this contributes to carbon sequestration), and also the formation of significant raw material potential for biogas production. High ash content indicates mineral richness (iodine, potassium, calcium, and magnesium). This is beneficial for food industry, pharmaceuticals, fertilizer, and feed production; however, this reduces combustion efficiency when biomass is used in bioenergy [Biomass Conversion Processes, 1985]. Low energy value makes the brown algae a dietary product. At the same time, they are less profitable as fuel, although their advantage is rapid growth without competition for arable land. Their main product is not energy, but biologically active metabolites (polysaccharides, polyphenols, fucoxanthin, *etc.*).

Thus, the metabolite content of *A. nodosum* is determined by a comprehensive interaction of endogenous factors (those are related to the reproductive phase and the thallus zone) and abiotic factors (those reflect environmental conditions). This must be taken into account when assessing the resource potential of algae and optimizing their industrial use.

The challenge of analyzing the effect of factors on the biochemistry of the brown algae lies in the difficulty of identifying the key environmental parameters that determine their physiological state and chemical composition. As established for *A. nodosum* [Khailov et al., 1992], surf (wave exposure) affects biochemical parameters more than water temperature and salinity. The effect of differences in salinity in the studied bays is low, as its values are within an optimal range for the species, whereas temperature dynamics during summer (in July) can affect the timing of receptacle shedding. Moreover, surf is a key factor determining thallus morphology and protein content, oxygen and nutrient availability, and the degree of mechanical stress; this directly affects metabolite accumulation in an alga.

Conclusions:

1. Analysis of *Ascophyllum nodosum* biomass in two water areas of the Barents Sea revealed a common pattern: its values were the highest during the fertile period (a mean of 25 $kg \cdot m^{-2}$) corresponding to summer months. However, in Zavalishin Bay, the biomass of this brown alga was characterized by a higher energy equivalent (by 1.4 times) and lower ash content (by 1.4 times) compared to the biomass in Korabelnaya Bay. This indicates local variability in the species physiological parameters.
2. An assessment of different thallus zones of *A. nodosum* in Zavalishin Bay and Korabelnaya Bay (Teriberskaya Bay of the Barents Sea) revealed that the highest energy value was characteristic for apical tips during the reproduction phase (fertile thalli) (July, 2.67 and 2.56 $kcal \cdot g^{-1}$, respectively) and receptacles in the late vegetative period (sterile thalli) (September, (3.13 and 2.56 $kcal \cdot g^{-1}$).
3. The potential of individual thallus zones as sources of biologically active metabolites is determined by the specialized distribution of compounds. Thus, the highest content of lipids and fucoxanthin was recorded in mature receptacles; protein, in receptacle primordia and mature receptacles in summer; carbohydrates, in the middle thallus zone in July (for Korabelnaya Bay) and in June (for Zavalishin Bay); polyphenols, in the apical zone of the thallus in September (for Zavalishin Bay) and in July (for Korabelnaya Bay); chlorophyll *a* and carotenoids, in apical tips in June; and chlorophyll *c*, in receptacles in June.
4. Patterns of metabolite distribution in *A. nodosum* from the Barents Sea were established under the effect of three factors: thallus zone, developmental phase, and habitat. The thallus zone had a statistically significant effect on the allocation of fucoxanthin, proteins, lipids, carbohydrates, chlorophyll *a*, chlorophyll *c*, and total carotenoids. Habitat affected much the content of polyphenols, proteins, and fucoxanthin, as well as levels of carbohydrates and lipids. Algal reproductive phase significantly affected the content of proteins, polyphenols, chlorophyll *c*, and lipids.

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СОДЕРЖАНИЕ МЕТАБОЛИТОВ И ЭНЕРГЕТИЧЕСКАЯ ЦЕННОСТЬ БУРОЙ ВОДОРОСЛИ *ASCOPHYLLUM NODOSUM* (L.) LE JOLIS В УСЛОВИЯХ БАРЕНЦЕВА МОРЯ

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Бурая водоросль *Ascophyllum nodosum* (L.) Le Jolis является ценным продуцентом биологически активных веществ, а также важным звеном в экосистеме Баренцева моря. Изучение биомассы водорослей и определение её энергетической ценности актуальны для оценки общего состояния вида в экосистеме и его ресурсного потенциала. Для лучшего понимания изменений, происходящих в *A. nodosum* в промысловый летне-осенний период, важно проанализировать аллокацию метаболитов по таллому и вклад различных структур в общую биомассу. В ходе работы биохимические показатели (общий белок, липиды, углеводы, полифенолы, хлорофилл *a* и *c*, сумма каротиноидов и фукоксантин) исследованы по общепринятым методикам. Определена натурная и камеральная биомасса, на основе полученных данных рассчитана энергетическая ценность и энергетический эквивалент биомассы. Для сбора *A. nodosum* выбраны две губы Баренцева моря, расположенные близко друг к другу, но различающиеся по гидрологическим условиям, — губа Завалишина и губа Корабельная, где аскофиллум формирует плотные заросли на литорали. Пик биомассы в обеих губах выявлен в июне, различия в значениях минимальны, среднее для двух мест — 25 кг·м$^{-2}$. Энергетический эквивалент в этот период не одинаков: в образцах из губы Завалишина показатель выше в 1,4 раза, чем в образцах из губы Корабельная, а показатель зольности ниже в 1,4 раза. Также в водорослях из губы Завалишина отмечено большее содержание полифенолов и фукоксантина. Рассмотрено распределение биологически активных

соединений по функционально дифференцированным зонам таллома (рецептакулам, апексам и остальному таллому), а также в зависимости от фазы размножения (фертильные либо стерильные водоросли) и от абиотических условий местообитания (проанализирован комплекс факторов — солёность, температура и прибойность, или волновой режим). Установлены закономерности распределения метаболитов в *A. nodosum* Баренцева моря под воздействием трёх факторов: зоны таллома, фазы развития и местообитания. Зона таллома оказывала значительное влияние на аллокацию фукоксантина, белков, липидов, углеводов, хлорофилла *c*, хлорофилла *a* и суммы каротиноидов. Местообитание существенно воздействовало на содержание полифенолов, белков и фукоксантина, а также на уровень углеводов и липидов. Фаза размножения водорослей оказала значительное влияние на содержание белков, полифенолов, хлорофилла *c* и липидов.

Ключевые слова: *Ascophyllum nodosum*, биомасса, энергетическая ценность биомассы, белок, углеводы, липиды, пигменты, полифенолы