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RESTORATION OF THE *CHARA ACULEOLATE* KÜTZING PHYTOCENOSIS IN THE TENDROVSKY BAY (BLACK SEA)

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D. D. Koroliesova

Black Sea Biosphere Reserve, Golaya Pristan, Russian Federation
E-mail: *chernyakova.darya@gmail.com*

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For the *Chara aculeolata* Kützing phytocenosis in the Tendrovsky Bay of the Black Sea, long-term dynamics of growth areas and biomass of macrophytes was analyzed. Its partial degradation was observed since 1993. In 1993–2010, the area of the phytocenosis decreased from 100 to 6.3 km^2. In 2010–2021, elements of regenerative succession were registered. A gradual slow expansion of growth areas and an increase in algae biomass were noted over the 10-year monitoring, and a sudden significant recovery was recorded in 2021. According to the data of 2021, the *C. aculeolata* phytocenosis was distributed over an area of 36 km^2, and the biomass of the dominant species reached 1,800 g·m^{-2}. Possible reasons for the observed changes are discussed.

Keywords: Charophyta, macrophytobenthos, regenerative succession, long-term dynamics, recolonization

Charophytes are recorded from a variety of water bodies. Those algae are most typical for bottom vegetation of freshwater oligotrophic lakes [Pełechaty et al., 2019], as well as sea bays and lagoons of partially saline seas of Eurasia [Kovtun et al., 2011]. Their dense beds determine the conditions for the functioning of coastal ecosystems, form the habitat for many species of hydrobionts [Beilby et al., 2022; Sooksawat et al., 2017] and serve as an important food resource for waterbird species [Schmieder et al., 2006].

The first mentions of charophytes from the Black Sea date back to the early XX century [Pauli, 1927; Zernov, 1908]. Communities of charophyte algae were widely distributed in the northern Black Sea [Milchakova, Aleksandrov, 1999; Morozova-Vodyanitskaya, 1959; Palamar-Mordvintseva, 1998; Sadogursky, 2009]. Their development was maximum in the Karkinitsky [Morozova-Vodyanitskaya, 1959; Sadogursky, 2009], Tendrovsky, Yagorlytsky, and Dzharylgachsky bays [Cherniakov, 1995; Pogrebnyak, 1965; Tkachenko, Maslov, 2002], where their total stock was estimated at 1,176.8 thousand tones. More than 40% of this volume accounted for the Tendrovsky Bay, where *Lamprothamnium papulosum* (Wallroth) J. Groves, 1916 and *Chara aculeolata* Kützing, 1832 dominated [Pogrebnyak, 1965].

About 30 years ago, ubiquitous reduction in growth areas and decrease in the productivity of phytocenoses of charophytes were registered; in the Tendrovsky Bay, these algae degraded almost completely. After 1993, *C. aculeolata* was revealed in this bay in small areas, and it did not form characteristic phytocenoses [Cherniakov, 1995; Korolesova, 2017; Tkachenko, Maslov, 2002].

In 2010, we recorded a slight restoration of the *C. aculeolata* phytocenosis. Therefore, the aim of the research was to estimate the dynamics of restoration succession, current state, and boundaries of the phytocenosis in the shallow area of the Tendrovsky Bay.

MATERIAL AND METHODS

The Tendrovsky Bay is located in the northwestern Black Sea. It is a semi-enclosed shallow water body, naturally divided into eastern and western parts. As Charophyta communities were not noted in the western, deeper bay part, this paper presents data for the eastern one. Its total area is 365 km^2, and the mean depth is 1.5 m. Silty and silty-sandy sediments dominate there [Cherniakov, 1995]. The mean salinity of surface waters is 13.5‰. Their maximum temperature is observed in August and ranges within +20…+32.3 °C. In the macrophytobenthos, two types of Charophyta communities are described – *L. papulosum* and *C. aculeolata* [Korolesova, 2017; Pogrebnyak, 1965].

To study the restoration dynamics of the *C. aculeolata* community throughout the eastern Tendrovsky Bay, a square network of stations with a step of 2 km was used. The material was macrophytes sampled at network stations annually in the summer season in 2010–2021. We used a standard geobotanical technique [Kalugina-Gutnik, 1975] and laid a frame of 25 × 25 cm in triplicate at each station. Qualitative sampling was carried out with a scraper with a working width of 30 cm or manually. For bottom phytocenoses, we determined a projective cover of abundant species and their biomass (g·m^{-2} wet weight).

Samples of macrophytes were washed in seawater and fixed with a 4% formalin solution or frozen at a temperature of −18 °C. Some of the algae were herbarized [Gollerbakh, Krasavina, 1983; Minicheva et al., 2014].

Macrophytes were determined down to a species level according to monographic summaries [Gollerbakh, Krasavina, 1983; Vinogradova, 1974; Zinova, 1967], and nomenclatural changes were given in accordance with AlgaeBase (https://www.algaebase.org/). *C. aculeolata* taxonomic status is presented according to the report of Charophyta regional flora [Borisova, Tkachenko, 2008], since the taxonomic position of the species remains not fully clarified, and published sources contain different names – *Chara intermedia* A. Braun, 1859 (syn. *Chara papillosa* Kützing, 1834) and *Chara baltica* (Hartman) Bruzelius, 1824 [Romanov et al., 2020]. The phytocenoses are named in accordance with the classification of the Black Sea bottom vegetation [Kalugina-Gutnik, 1975].

The growth area of macrophytes was calculated using the Quantum Gis software (3.28.5).

RESULTS AND DISCUSSION

The *C. aculeolata* phytocenosis belongs to monocenoses, since the biomass of the dominant species makes up more than 90% of the total biomass. In the community, 10 species of macrophytes were identified: *C. aculeolata*, *L. papulosum*, *Chaetomorpha linum* (O. F. Müller) Kützing, 1845, *Lophosiphonia obscura* (C. Agardh) Falkenberg, 1897, *Callithamnion granulatum* (Ducluzeau) C. Agardh, 1828, *Chondria capillaris* (Hudson) M. J. Wynne, 1991, *Chondria dasyphylla* (Woodward) C. Agardh, 1817, *Laurencia obtusa* (Hudson) J. V. Lamouroux, 1813, *Polysiphonia opaca* (C. Agardh) Moris & De Notaris, 1839, and *Stuckenia pectinata* (Linnaeus) Börner, 1912. The following species were characterized by the highest occurrence: red algae (Rhodophyta), *Ch. capillaris* and *L. obscura* (63 and 50%, respectively); Charophyta, *L. papulosum* (38%); and higher aquatic plants (Angiospermatophyta), *S. pectinata* (25%).

In 2010–2020, the *C. aculeolata* phytocenosis was registered on average at 6% of stations, and the area it occupied varied from 4 to 8 km^2, with a mean of 6.3 km^2. In 2021, the phytocenosis was recorded at 13 stations out of 27 studied (its occurrence was 48%); its area reached 36 km^2, or 10% of the total monitoring area (Fig. 1). The *C. aculeolata* community was represented by dense, almost closed beds with a projective cover of 90–100%; it was distributed along the Tendrovska Spit and to the northwest of Smaleny Island. By 2021, the growth area was about 40% of that of the 1960s and almost doubled the area of the mid-1990s.

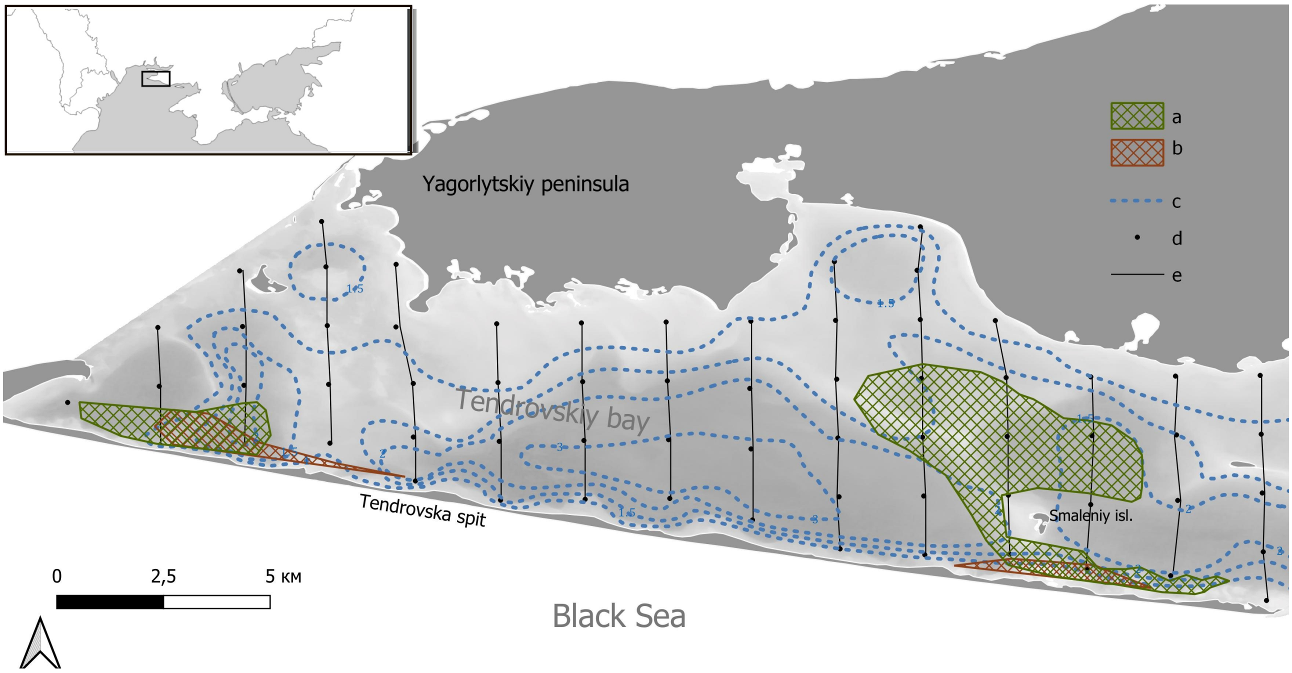

Fig. 1. Map of the *Chara aculeolata* phytocenosis distribution and monitoring stations scheme in the eastern Tendrovsky Bay: a, phytocenosis area in 2021; b, phytocenosis area in 2010–2020; c, isobaths; d, monitoring network stations; e, transects

In 2010–2016, the mean biomass of the *C. aculeolata* phytocenosis was (485.28 ± 221.17) g·m^{-2}. In 2021, it reached 1,926 g·m^{-2}, with the dominant species accounting for more than 90% of the community biomass (1,800 g·m^{-2}). In total, the values of the phytocenosis biomass became comparable with those of the 1960s, exceeding the values characteristic of the last decade by more than 4 times. To date, the phytocenosis restoration is observed within previously known growth boundaries (after 25 years of its partial degradation) [Pogrebnyak, 1965].

At this stage, it is impossible to identify reliably the causes of these changes. The restoration of Charophyta communities after partial or complete degradation is described in the literature for the Baltic Sea bays [Torn, Martin, 2003] and European fresh water bodies [Pełechaty et al., 2019; Sand-Jensen et al., 2017; Simons et al., 1994].

Most researchers believe that Charophyta restoration is directly driven by a decrease in the level of exposure to adverse environmental factors – anthropogenic load, eutrophication, *etc.* [Kovtun et al., 2011; Torn, Martin, 2003]. For the northwestern Black Sea, the restoration of communities of charophytes is also associated with their long-term cycles [Cherniakov, 1995].

The decrease in the level of eutrophication in the Tendrovsky Bay occurred long before the registration of the first elements of the restoration succession of the *C. aculeolata* phytocenosis there [Korolesova, 2017; Zaika et al., 2004]. In our opinion, *C. aculeolata* recolonization may be related to the effect of abiotic and biotic factors, including the cyclical development of Charophyta communities.

Conclusion. Based on the research carried out, elements of restorative succession and recolonization of the *Chara aculeolata* phytocenosis in the eastern Tendrovsky Bay in 2010–2021 were identified. By 2021, the biomass of the community and the area it occupied turned out to be comparable with those of the 1960s and exceeded the values recorded in the mid-1990s.

To identify the causes of the *C. aculeolata* recolonization, further investigation of a complex of biotic and abiotic factors affecting the composition and structure of Charophyta communities in the Tendrovsky Bay is required.

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ВОССТАНОВЛЕНИЕ ФИТОЦЕНОЗА *CHARA ACULEOLATA* KÜTZING В ТЕНДРОВСКОМ ЗАЛИВЕ (ЧЁРНОЕ МОРЕ)

Д. Д. Королесова

Черноморский биосферный заповедник, Голая Пристань, Российская Федерация
E-mail: *chernyakova.darya@gmail.com*

Проанализирована долгосрочная динамика площадей произрастания и биомассы макрофитов фитоценоза *Chara aculeolata* Kützing в Тендровском заливе Чёрного моря. Частичную его деградацию отмечали с 1993 г. За период с 1993 по 2010 г. площадь произрастания фитоценоза сократилась с 100 до 6,3 км^2. В 2010–2021 гг. зарегистрированы элементы восстановительной сукцессии. Зафиксированы постепенное медленное расширение площадей произрастания и увеличение биомассы водорослей в течение 10 лет мониторинга и внезапное значительное восстановление в 2021 г. По данным 2021 г., исследуемый фитоценоз распространён на площади 36 км^2, биомасса доминирующего вида достигла 1800 г·м$^{-2}$. В работе обсуждаются возможные причины наблюдаемых изменений.

Ключевые слова: Charophyta, макрофитобентос, восстановительная сукцессия, многолетняя динамика, реколонизация