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COMPETITIVE ADVANTAGES OF THE DIATOM *SKELETONEMA COSTATUM* CLEVE, 1873 IN THE BLACK SEA IN THE WINTER–SPRING PERIOD

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Individual physiological features of the *Skeletonema costatum* vegetation under low light intensity and low temperature are described; these peculiarities allow the species to prevail in the Black Sea phytoplankton in winter and early spring. This marine diatom is characterized by high growth efficiency under light-limiting conditions ($0.13 \text{ day}^{-1} \cdot (\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{-1}$) which indicates an increase in the specific growth rate of the alga with a rise in light intensity by $1 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Moreover, the species is characterized by low values of the light intensity saturating the growth – $12 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at $+5 \text{ }^\circ\text{C}$ and $18 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at $+10 \text{ }^\circ\text{C}$. At $+5 \dots +10 \text{ }^\circ\text{C}$, *S. costatum* growth rate is about 2 times higher than that of other representatives of the Black Sea phytoplankton in the winter–spring period. This diatom shows increased sensitivity to high light intensity: at $+10 \text{ }^\circ\text{C}$, photoinhibition of microalgae growth is observed under light intensity above $120 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

Keywords: diatoms, *Skeletonema costatum*, light intensity, temperature

The diatom *Skeletonema costatum* Cleve, 1873 is one of the prevailing representatives of the Black Sea phytoplankton in the winter–spring period when, according to field observations, its bloom occurs in coastal areas. A study of the species diversity of microalgae in Crimean coastal waters carried out by M. Senicheva in 1983–2006 showed as follows: in years with colder winter (temperature below $+8 \text{ }^\circ\text{C}$) with intense convective mixing of water, *S. costatum* contribution to the total phytoplankton biomass can reach 95–98 %. The species development peaks in early spring (February–March); during these months, the temperature minimum ($+6 \dots +8 \text{ }^\circ\text{C}$) is recorded, as well as the maximum concentration of mineral salts. In years with warmer winter ($+8 \dots +12 \text{ }^\circ\text{C}$) and less intense convective mixing of water, the species diversity of algae increases significantly, but *S. costatum* remains one of the prevailing species (Senicheva, 2008). According to Yu. Bryantseva (2008), in January and February 2004–2006, *S. costatum* contribution to the total phytoplankton abundance in the Sevastopol Bay varied within 89–94 %.

Apparently, *S. costatum* prevalence under low light intensity and low temperature is due to certain competitive advantages of this diatom over other phytoplankton representatives: those allow the species to prevail in sea during winter and early spring. The results of our own complex experimental

studies [their methodological aspects are presented in (Akimov & Solomonova, 2019 ; Shoman & Akimov, 2012, 2015)] allowed to identify several individual physiological features of the species during cultivation under low light intensity and low temperature:

1. *S. costatum* is characterized by high growth efficiency (α) under light-limiting conditions – $0.13 \text{ day}^{-1} \cdot (\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{-1}$. This parameter is not temperature-dependent within a range of $+8 \dots +20 \text{ }^\circ\text{C}$. The described value reflects an increase in algal specific growth rate under light limitation with a rise in the light intensity by $1 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. According to the results of one of the recent reviews (Edwards et al., 2015), the growth efficiency of different phytoplankton representatives under light limitation varies within $0.001\text{--}0.1 \text{ day}^{-1} \cdot (\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{-1}$; at the same time, the prevailing ratio of the α values in diatoms covers a range of $0.015\text{--}0.03 \text{ day}^{-1} \cdot (\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{-1}$. Considering that, the value of *S. costatum* growth efficiency is comparable with the maximums recorded in microalgae in total.
2. *S. costatum* has lower values of the light intensity saturating the growth (I_k) than other diatom species. Thus, at a temperature of $+5 \text{ }^\circ\text{C}$, the I_k value for *S. costatum* was $12 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and at $+10 \text{ }^\circ\text{C}$, it was $18 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. At $+15 \text{ }^\circ\text{C}$, the light dependence of the growth rate reached the plateau under the light intensity of $24 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. For comparison: for *Phaeodactylum tricornutum* Bohlin, 1897 and *Nitzschia* sp. No. 3, the I_k values under similar growth conditions at $+10 \text{ }^\circ\text{C}$ were 40 and $33 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively (Shoman & Akimov, 2012). According to literature data, the saturation of the growth rate for diatoms at the optimal temperature ($+18 \dots +22 \text{ }^\circ\text{C}$) is recorded at an average level of $84 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Richardson et al., 1983). Having data on approximately a twofold decrease in the I_k value at $+10 \text{ }^\circ\text{C}$, we can conclude that it decreases to $40 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The minimum values of photosynthetically active radiation incident on the sea surface in January–February are $4\text{--}5 \text{ E} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$. Due to a large extent of the upper quasi-homogeneous layer (about 30 m) during late winter, the mean light intensity there does not exceed $2 \text{ E} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ($\approx 25 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) (Finenko et al., 2018). Thereby, in January–February, phytoplankton exists under conditions of a temperature minimum, low light intensity, and extended upper quasi-homogeneous layer.
3. *S. costatum* is characterized by a high growth rate at low temperatures. Specifically, at $+5 \dots +10 \text{ }^\circ\text{C}$, its growth rate is approximately twice as high as that of other representatives of the diatom complex of the winter–spring succession in the Black Sea phytoplankton. So, the experiments showed as follows: within the specified temperature range, other growth conditions being equal, *S. costatum* specific growth rate is $0.9\text{--}1.5 \text{ day}^{-1}$, while in *Chaetoceros curvisetus* Cleve, 1889, *Cylindrotheca closterium* (Ehrenberg) Reimann & J. C. Lewin, 1964, *Thalassiosira parva* Proschkina-Lavrenko, 1955, and *Ditylum brightwellii* (T. West) Grunow, 1885, this value is $0.3\text{--}0.8 \text{ day}^{-1}$ (Akimov & Solomonova, 2019).
4. *S. costatum* shows an increased sensitivity to high light intensity. Under the conditions of a laboratory experiment at a temperature of $+15 \text{ }^\circ\text{C}$, light inhibition of algal growth begins to manifest itself at a light intensity above $140 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and at $+10 \text{ }^\circ\text{C}$, above $120 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. As known, *S. costatum* development peaks in early spring (Bryantseva, 2008). In April, a shift in growth conditions (an increase in photosynthetically active radiation, rise in temperature, and beginning of a temperature water stratification) results in a change in the species composition of the phytoplankton community and a significant increase in its diversity. During the winter–spring succession in the Black Sea phytoplankton in years with warmer spring, cold-loving small-celled diatom species are replaced in April–May by more thermophilic ones – *Chaetoceros curvisetus*, *Chaetoceros affinis* Lauder, 1864,

Pseudo-nitzschia delicatissima (Cleve) Heiden, 1928, *Proboscia alata* (Brightwell) Sundström, 1986, and *Dactyliosolen fragilissimus* (Bergon) Hasle, 1996. At the same time, in years with colder spring, *S. costatum* can prevail in plankton until late May (Senicheva, 2008). Thus, the combination of light intensity conditions and temperature conditions observed in the Black Sea in April is unfavorable for *S. costatum*: it results in a significant decrease in the algal growth rate and, apparently, is one of the reasons for the replacement of *S. costatum* by other algae species in mid-spring.

Conclusion. Main competitive advantages of *Skeletonema costatum* during vegetation under low light intensity and low temperature are high growth efficiency ($0.13 \text{ day}^{-1} \cdot (\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{-1}$), low values of the light intensity saturating the growth ($12 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at $+5 \text{ }^\circ\text{C}$ and $18 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at $+10 \text{ }^\circ\text{C}$), and high specific growth rate at low temperature ($0.9\text{--}1.5 \text{ day}^{-1}$ at $+5\text{--}+10 \text{ }^\circ\text{C}$). Along with low competition, this creates the most favorable conditions for *S. costatum* development in the Black Sea in winter and early spring.

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**КОНКУРЕНТНЫЕ ПРЕИМУЩЕСТВА ДИАТОМОВОЙ ВОДОРΟΣЛИ
SKELETONEMA COSTATUM CLEVE, 1873
В ЧЁРНОМ МОРЕ В ЗИМНЕ-ВЕСЕННИЙ ПЕРИОД**

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Описаны индивидуальные физиологические особенности вегетации морской диатомовой микроводоросли *Skeletonema costatum* в условиях низкой освещённости и низкой температуры, позволяющие ей занимать доминирующую позицию в фитопланктоне Чёрного моря в зимний и ранневесенний период. Показано, что для *S. costatum* характерна высокая эффективность роста в условиях светового лимитирования ($0,13 \text{ сут}^{-1} \cdot (\text{мкЭ} \cdot \text{м}^{-2} \cdot \text{с}^{-1})^{-1}$), отражающая увеличение удельной скорости роста водорослей при повышении интенсивности света на $1 \text{ мкЭ} \cdot \text{м}^{-2} \cdot \text{с}^{-1}$, а также низкие значения насыщающей рост интенсивности света ($12 \text{ мкЭ} \cdot \text{м}^{-2} \cdot \text{с}^{-1}$ при температуре $+5 \text{ }^\circ\text{C}$ и $18 \text{ мкЭ} \cdot \text{м}^{-2} \cdot \text{с}^{-1}$ при $+10 \text{ }^\circ\text{C}$). При $+5 \dots +10 \text{ }^\circ\text{C}$ скорость роста *S. costatum* примерно в 2 раза выше, чем у других представителей фитопланктона Чёрного моря в зимне-весенний период. Для *S. costatum* характерна повышенная чувствительность к свету высокой интенсивности: при $+10 \text{ }^\circ\text{C}$ фотоингибирование роста микроводоросли отмечено при интенсивности света выше $120 \text{ мкЭ} \cdot \text{м}^{-2} \cdot \text{с}^{-1}$.

Ключевые слова: диатомовые водоросли, *Skeletonema costatum*, интенсивность света, температура