PATTERNS OF CONTOUR ALGAL COMMUNITIES’ FUNCTIONING IN AQUATIC ECOSYSTEMS OF THE DNIEPER BASIN (UKRAINE) UNDER DIFFERENT ALTERNATIVE STABLE REGIMES

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The paper presents the concept of contour algal communities functioning in aquatic ecosystems of the Dnieper basin under different alternative stable regimes. The major factors are distinguished, which can trigger the shift of the water bodies under study from clear water regime to high turbidity regime: climate change, changes in nutrient conditions and water-level drawdown. In particular, higher water temperature, increase in phosphorus content, a decline in N:P-ratio cause planktonic Cyanobacteria blooms, which intercept solar radiation and suppress photosynthesis of contour algal communities. The water-level drawdown brings about the reduction of the water volume, increase in the nutrient concentration, acceleration of the water column’s warming in spring and intensive phytoplankton growth, decreasing the Secchi-disk transparency. In response to the complex effect of these changes contour algal communities activate the mechanisms aimed at maintaining the community’s dynamic equilibrium under the unfavorable conditions of high turbidity. These mechanisms include changes in the ratio of phyta with a decrease in the diatoms’ share and increase in the shares of green and blue-green algae; gaining the competitive advantage by diatoms from Rhopalodiaceae family with nitrogen-fixing endosymbionts; enlargement in the share of shade-tolerant species and species with high saprobity index. These transformations in the structure of contour algal communities may be of practical value and can be used as reliable biological indicators of regional and global environmental changes.

Key words: contour algal communities, alternative stable states, climate change, nitrogen-to-phosphorus ratio.

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У роботі представлена концепція функціонування контурних водоростевих угруповань у водних екосистемах Дніпра за різних альтернативних стабільних режимів. Визначено основні чинники, які можуть спричинити переход до «режиму прозорої води» з «режиму високої каламутності»: кліматичні зміни, зміни біогенного режиму, зниження рівня води. Зокрема, підвищення температури води, зростання вмісту фосфору, зменшення N:P-співвідношення призводить до «цвітіння» води планктонними Cyanobacteria, які екранують товщу води та пригнічують фотосинтез контурних водоростевих угруповань. Зниження рівня води прискорює прогрівання товщі води навесні, зумовлює зростання концентрації біогенных елементів та інтенсифікацію розвитку фітопланктону з відповідним зниженням прозорості води. У відповідь на комплексну дію цих змін контурні водоростеві угруповання активують механізми, спрямовані на підтримання динамічної рівноваги в умовах високої каламутності. Ці механізми включають: зміну співвідношення виділ їжі зменшенням частки діатомових водоростей і збільшенням – зелених і синьозелених; отримання конкурентної переваги діатомовими водоростями з родини Rhopalodiaceae з азотфіксуючими ендосимбіонтами; зростання частки тіньовитриявалих видів і видів з високим індексом сапробності. Такі трансформації в структурі контурних водоростевих угруповань можуть бути використані як репрезентативні біологічні індикатори регіональних і глобальних змін навколишнього середовища.

Ключові слова: контурні водоростеві угруповання, альтернативні стабільні стани, кліматичні зміни, співвідношення азоту і фосфору.

Introduction
Contour algal communities, i.e. algal communities living at the interface of two phases, are an important component of aquatic ecosystems' biodiversity and are marked by high sensitivity to external impacts (Gosselain et al., 2005; Karosienė & Kasperovičienė, 2012; Zaytsev, 2015).

Among numerous fundamental issues related to studying contour algal communities a valuable place is held by the concept of alternative stable regimes (Scheffer et al., 1992, 1993; Hansson, 1992; Havens et al., 2001; Scheffer & Carpenter, 2003; Scheffer & Van Nes, 2007; Vadeboncora et al., 2008; Protasov, 2014; Hilt, 2015). According to this concept, an aquatic ecosystem can stay in one of two alternative regimes: high turbidity regime (when the total primary production is mainly formed by phytoplankton) and clear water regime (when it is mainly formed by contour communities – higher aquatic plants, benthic, epiphytic algae).

High turbidity regime is considered to be more stable than clear water regime, and an aquatic ecosystem’s shift from one regime to another depends on nutrient content and phytoplankton abundance affecting the optic characteristics of water.

Different alternative stable regimes may coexist even within a single lake, if it is marked by a large water area, spatial heterogeneity or varying nutrients inflow from the catchment to different parts of the lake. Such aquatic ecosystems often comprise a mosaic of patches with different alternative regimes, which remain unchanged for a long time until an extreme event (e.g., human impact) triggers a shift in the pattern (Scheffer et al., 2001b; Scheffer & Carpenter, 2003; Janssen et al., 2014). The process, when aquatic ecosystem shifts from high turbidity phase to clear water phase is called contourization, and the reverse process – decontourization (Protasov, 2014).

The alternative stable state theory was originally developed for Dutch lakes (Scheffer et al., 1992, 1993), and is usually applied to natural water bodies. However, as regards large natural-artificial aquatic ecosystems, such as lowland reservoirs, the issue of regime shift is still understudied.

In the view of the above, the aim of this research is to develop the concept of contour algal communities’ functioning in aquatic ecosystems of the Dnieper basin under different alternative stable regimes.

Material and methods
The paper is based upon the field studies conducted in various aquatic ecosystems within the Dnieper basin from 2008 to 2021: the cascade of the Dnieper reservoirs and the
Cooling Pond of the Chornobyl Nuclear Power Plant. The research was carried out within the framework of the state research project “Support of development of high-priority areas of research (KPKVK 6541230)”.


Algal samples were analyzed under the light microscope MBB-1A with the ocular lens 7×, and the objectives ×40, ×90 (immersion) and under the light microscope Axio Imager A1 at the Research Equipment Center of the Institute of Hydrobiology of the NAS of Ukraine. Epiphytic algae biomass was calculated per unit of higher aquatic plants surface (Semenyuk et al., 2020).

The data on inorganic nitrogen and phosphorus content in Kyiv Water Reservoir and Kaniv Water Reservoir are a courtesy of Mariia Linchuk, Junior Researcher.

The algal taxonomic nomenclature is given in accordance with the international electronic catalogue AlgaeBase (Guiry & Guiry, 2023).

**Results and discussion**

Relation between Secchi-disk transparency and contour algal communities in the context of the alternative stable regimes theory

The box plots summarizing the epiphytic algae biomass values according to the ranges of Secchi-disk transparency in the Dnieper reservoirs show that both the average and the maximal biomasses get higher with the Secchi-disk transparency increasing (Fig. 1). According to Hansson (1988) low transparency suppresses primary production of contour algal communities, even when other resources (such as nutrients) are sufficient and available for algae.

The upper right point on the plot (Fig. 1) may be considered as corresponding to clear water regime, and the lower left point – to high turbidity regime.

According to our previous data, a strong positive relation was detected between Secchi-disk transparency and epiphytic algae gross primary production ($R^2 = 0.73$) and between Secchi-disk transparency and A/R-ratio ($R^2 = 0.81$) (Semenyuk & Shcherbak, 2016). With the water transparency being minimal (0.50–0.75 m), the gross primary production made up 0.06–0.21 (0.13±0.07) mg O₂·10 cm⁻².

![Fig. 1. The box plots summarizing the contour algal communities’ biomass values on *Phragmites australis* (Cav.) Trin. ex Steud. according to the Secchi-disk transparency ranges in the cascade of the Dnieper reservoir: points – average values, boxes – standard errors, whiskers – fluctuation ranges](image-url)
of plant surface \cdot \text{day}, and \text{A/R-ratio} = 0.03-0.11 (0.07\pm0.02) \cdot \text{day}. With Secchi-disk transparency increasing to 1.60-1.70 \text{m}, the gross primary production reached 1.31-1.54 (1.42\pm0.11) \text{mg O}_2 10 \text{cm}^{-2} \cdot \text{day}, and \text{A/R-ratio} = 0.94-1.67 (1.28\pm0.08) \cdot \text{day}.

Such positive relation between Secchi-disk transparency and contour algal communities’ development agree with findings of other researchers (Hansson, 1992; Greenwood & Rosemond, 2005; Oliveria et al., 2010; Cano et al., 2012).

\textbf{Analysis of the main factors triggering regime shifts}

Aquatic ecosystems can shift abruptly from one alternative stable regime to another. Such shift is usually triggered by stochastic events, for example, extreme climatic conditions. However, gradual changes of environmental conditions such as human-induced eutrophication and global warming may have little apparent effect on the regime of ecosystems, but still they alter the “stability domain” of the current regime. Consequently, it becomes more probable that the ecosystem will shift to another alternative regime in response to natural or human-induced fluctuations (Scheffer et al., 2001a).

The long-term field data analysis makes it possible to distinguish the major factors which can trigger aquatic ecosystems’ shift from one alternative regime to another. These are climate change, changes in nutrient conditions and large-scale hydrotechnical operations.

\textbf{Climate change.} The evidence of the current climate change both at a regional and global scale becomes more and more numerous each year (Hartman et al., 2013). An important question unresolved so far is how the warmer climate will affect the probability that shallow lakes will fall into high turbidity regime (Scheffer & Van Nes, 2007).

In the view of the above we have considered the year-on-year dynamics of the water temperature in Kyiv Water Reservoir’s shallow areas and biomass of epiphytic algae on emergent plants (Fig. 2).

According to our previous studies (Semenyuk & Shcherbak, 2016), the optimal temperature range for contour algal communities’ vegetation in summer is 22–24 °C (shown in Fig. 2 by two dashed lines). It is noteworthy that the peaks of contour algal communities’ biomass were observed in years when the water temperature was within the optimal range (2013, 2015). Meanwhile, in years when the water temperature exceeded the optimal range (for example, in 2012, 2014, 2016), the total algal biomass decreased, with the share of diatoms reducing and the share of green algae increasing. This is because green algae gain competitive edge at warmer water temperatures than diatoms.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{Fig2.jpg}
\caption{Year-on-year dynamics of contour algal communities’ biomass (B) on emergent plants in and the average water temperature (t) in the lowland reservoir shallow areas in summer (two dashed lines indicate the optimal temperature range for epiphytic algae in summer – 22–24 °C (Semenyuk & Shcherbak, 2016))}
\end{figure}
In our opinion the reduction of epiphytic algae biomass in years with increased water temperature can be explained by two reasons:

1) Higher temperature negatively affects diatoms – the main component of epiphytic algal communities.

2) Higher temperature affects epiphytic algae indirectly – via phytoplankton. For example, when water temperature increases to 25–26 °C, Cyanobacteria dominate phytoplankton, and algal blooms may occur (Shcherbak, 2019). Consequently, water transparency decreases, and epiphytic algae cannot get sufficient amount of solar radiation.

Thus in the years with the average water temperature in summer 22–24 °C the ecosystem of the reservoir was in clear water regime, and when the water temperature exceeded this range, the ecosystem shifted to high turbidity regime. Cyanobacterial blooms are the main mechanism causing such changes.

It is noteworthy that different (sometimes opposite) theories exist as regards the relation between climate change and alternative stable regimes. For example, Scheffer et al. (2001a, b) show that the probability of clear water phases in spring increased with higher lake water temperature, and decreases in water temperature could create a shift to high turbidity state. This is because higher water temperature causes more intensive phytoplankton grazing by zooplankton. The model also shows that when the water temperature decreases, or the abundance of zooplankton-feeding fishes increases, the clear water phase in spring shifts to a later period. However, Jeppesen et al. (2003) argue that the aforementioned model does not take into consideration a number of important factors. For example, a rise in the water temperature causes increased phytoplankton growth, and favors Cyanobacteria, which are not grazed by small crustacean and may negatively affect the herbivorous zooplankton.

Scheffer & Van Nes (2007) point out that a question of climate change impact upon the aquatic ecosystems’ alternative stable regimes is still underexplored, and the results obtained by different authors are sometimes contradictory, so further studies in this area are essential.

**Changes in nutrient conditions.** In the context of alternative stable regimes theory an important question has been what the critical nutrient level would be for maintaining a clear water regime. Scheffer & Van Nes (2007) come to a conclusion that such threshold level will be specific for each aquatic ecosystem because it depends on different factors, such as lake size, depth, climate etc.

The nitrogen-to-phosphorus ratio (N:P-ratio) is an important factor, that may cause the aquatic ecosystems within the Dnieper basin to shift from one alternative stable regime to another. It is well known that their current hydrochemical conditions are marked by a reduction in inorganic nitrogen concentration, increase in phosphorus content and, consequently, a decline in N:P-ratio (Shcherbak et al., 2016; Yakushin et al., 2017).

To assess the impact of the N:P-ratio change upon the alternative stable regimes of the aquatic ecosystems of the Dnieper basin we have considered the relationship between the content of nitrogen, phosphorus and contour algal communities’ biomass.

Field studies in Kaniv Water Reservoirs showed that the minimums and the maximums of algae biomass on *Potamogeton perfoliatus* L. coincided with minimal and maximal nitrate content (Fig. 3). A direct correlation was detected between the nitrate content and the epiphytic algae biomass ($r = 0.56; p = 0.004$).

For example, when the nitrate content varied within 0.037–0.058 mg N ⩯ dm$^{-3}$, the epiphytic algae biomass made up 0.060–1.50 mg ⩯ 10 cm$^{-2}$ of the plant surface, and when the nitrate content was higher – 0.104–0.153 mg N ⩯ dm$^{-3}$, the epiphytic algae biomass reached 1.52–2.34 mg ⩯ 10 cm$^{-2}$ of the plant surface.

Meanwhile, the relationship between the epiphytic algae biomass and the phosphate content was marked by a more complicated pattern (Fig. 4).

The figure shows, that there were peaks of phosphate content, which coincided with maximums of epiphytic algae biomass (for example, 24.06.10, 09.06.11, 05.10.11), and peaks of phosphate content, during which the epiphytic algae biomass was low (for example, 08.07.09, 25.08.10, 17.08.11). It is noteworthy that “synchronous” peaks of phosphate content and epiphytic algae biomass were observed at the beginning of summer or in the middle of autumn, while “asynchronous” peaks were observed in the midsummer or late summer. This pattern may be explained by the fact that in the midsummer and late summer high phosphorus content causes intensive blooms of Cyanobacteria, which reduce water trans-
perfoliatus and when the nitrate content was higher – 0.104–0.153 mg N algae biomass reached 1.52–2.34 mg phosphate content was marked by a more complicated pattern (Fig. 4).

Meanwhile, the relationship between the epiphytic algae biomass and the their biomass becomes higher. Therefore, on photosynthesis – thus the ecosystem is in their photosynthesis and does not interfere with epiphytic algae growth, but on the other hand, phytoplankton biomass increases simultaneously. Phytoplankton has a competitive advantage over epiphytic algal communities with respect to solar energy, because, being free-floating, it has prior access to light before it reaches epiphytic algae (Hansson, 1988). Due to light extinction by phytoplankton, the aquatic ecosystem shifts to high turbidity regime, and epiphytic algae development is suppressed.

Fig. 3. Dynamics of contour algal communities’ biomass on Potamogeton perfoliatus L. (1) and nitrate content (2) in the lowland reservoir

Fig. 4. Dynamics of contour algal communities’ biomass on Potamogeton perfoliatus L. (1) and phosphate content (2) in the lowland reservoir
Our previous studies showed a strong direct correlation between epiphytic algae’s gross primary production and nitrate content in water ($r = 0.88$; $p = 0.008$) (Semenyuk & Shcherbak, 2017). The similar correlation has been observed for primary production – organic matter destruction ratio ($A/R$-ratio) ($r = 0.90$; $p = 0.005$), and specific primary production – daily $P/B$-coefficients ($r = 0.80$; $p = 0.03$). The relationship between epiphytic algae’s production parameters and phosphate content is of more complex, curvilinear pattern. The productivity of epiphytic algal communities reaches its maximum, when the phosphate content is within 0.051–0.086 mg P·dm$^{-3}$, and declines when the phosphate content deviates from this range.

The findings of our studies agree with literature data. It is known (Hansson, 1988; Lalonde & Downing, 1991; Vadéboncœur & Steinman, 2002) that in eutrophic water bodies light (rather than phosphorus concentration) can be the limiting resource for periphyton primary production, because high phytoplankton biomass shadows the light and suppresses the photosynthesis of epiphytic algae.

It is necessary to consider another important question related to algal communities’ response to changes in nutrient conditions. It is known that when phosphates are present in excess, algal growth is limited by nitrogen compounds, and when the nitrogen content decreases, a competitive advantage is gained by taxa, capable of fixing atmospheric nitrogen [N$_2$]. In other words, algae, which cannot fix molecular nitrogen, grow in proportion to the limits of the low nitrogen resources, while nitrogen-fixing algae may grow in proportion to the phosphorus available in excess. Such nitrogen-fixing taxa include heterocyst-containing Cyanobacteria, for example species from genera Anabaena, Aphanizomenon, Nostoc.

The findings of our previous studies show that blooms of heterocyst-containing Cyanobacteria occur in aquatic ecosystem of the Dnieper basin quite frequently. For example, the summer phytoplankton of the Dnieper Water Reservoirs, the Lower Dnieper, the Chornobyl Nuclear Power Plant Cooling Pond was dominated by Dolichospermum flosaquae (Brébisson ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek, D. scheremetiavieae (Elenkin) Wacklin, L.Hoffmann & Komárek, Aphanizomenon flosaquae Ralfs ex Bornet & Flahault, Cuspidothrix issatschenkoi (Usachev) P.Rajaniemi, Komárek, R.Willame, P.Hrouzek, K.Kastovská, L.Hoffmann & K.Sivonen, causing intensive blooms (Shcherbak, 2019; Semenyuk et al., 2020; Shcherbak et al., 2020).

Besides, we have detected the phenomenon of winter under-ice blooms by Aphanizomenon gracile Lemmermann in a pond at the place of a former peat quarry in the flood-land of the Trubizh River (Shcherbak et al., 2019).

It is important that similar mechanisms are pertaining to contour algal communities. When nitrogen is a limiting resource, the competitive edge is gained by taxa, which can fix atmospheric nitrogen and do not depend upon the nitrogen content in the aquatic environment. Such taxa include diatoms from Rhopalodiaceae family (species from genera Epithemia Kützing and Rhopalodia O. Müller), whose cells contain specific structures – the so called “spheroid bodies”. These “spheroid bodies” are nitrogen-fixing endosymbionts tracing their origin to Cyanobacteria from genus Cyanothece. The endosymbionts provide the diatoms with nitrogen compounds, when nitrogen is a limiting resource (Floener & Bothe, 1980; DeYoe et al., 1992; Müller, 1999; Marks & Power, 2001; Precht et al., 2004; Nakayama et al., 2010; Trapp et al., 2012).

Our previous studies in Kyiv Water Reservoir show that when the N:P ratio in water decreases, the biomass of species from Epithemia and Rhopalodia genera goes up (Semenyuk & Shcherbak, 2017).

To prove this pattern, we conducted the similar research for other Dnieper reservoirs located downstream (from Kaniv Water Reservoir to Kakhovka Water Reservoir).

The N:P ratio at each sampling site was calculated from the open data of surface water monitoring, published by the Ukrainian State Water Resources Agency at their official website “Monitoring and Ecological Assessment of Water Resources of Ukraine” (Моніторинг ..., 2024).

As a result, an inverse logarithmic relation between these two parameters was obtained (Fig. 5). When the N:P-ratio is above 15, the biomass of Rhopalodiaceae diatoms is low and makes up <1% of the total biomass. When N:P-ratio is minimal (equal to 4 or less), their share in the biomass reaches the maximum (13% of the total algal community biomass).

It is also necessary to point out, that mass vegetation of planktonic Cyanobacteria from genera Dolichospermum (=Anabaena), Aphanizomenon causes the aquatic ecosystem’s transition to high turbidity regime and aggravation of light conditions for epiphytic algae growth.
However, apart from ability to fix atmospheric nitrogen, species from *Epithemia* and *Rhopalodia* genera have another important biological trait – they are adapted to low level of solar radiation (Müller, 1999). Such shade tolerance allows these species to vegetate under poor light conditions, caused by cyanobacterial blooms.

Thus, the development of species from Rhopalodiaceae family, which are able to fix atmospheric nitrogen and are shade-tolerant, is an important mechanism sustaining functioning of epiphytic algal communities under high turbidity regime caused by an increase in the phosphate content and reduction in the N:P-ratio.

**Water-level drawdown.** The impact of water-level drawdown upon the alternative stable regimes of aquatic ecosystems was studied in the Chornobyl Nuclear Power Plant Cooling Pond. The large-scale water-level drawdown in the Chornobyl NPP Cooling Pond caused a decline in the quantitative development of periphytic algae. Before the drawdown (as of summer 2013) the algal periphyton biomass had made up 32.470±5.385 mg·10 cm⁻² of the substratum surface. After the water level drawdown almost by four meters the biomass has shrunk to a third of its initial value. For example, in summer 2016 the average biomass equaled to 9.854±3.030 mg·10 cm⁻², in summer 2017 – 10.682±2.084 mg·10 cm⁻², and in summer 2018 – 9.789±2.168 mg·10 cm⁻².

We believe that in this situation the water drawdown acted as an extreme event, which triggered a shift in the cooling pond’s alternative stable regime. With the water volume in the cooling pond becoming less, the nutrient concentration got higher, the spring warming of the water column accelerated, and the overgrowth of higher aquatic plants reduced. All this brought about intensive phytoplankton growth, decrease in Secchi-disk transparency and decline in the biomass of contour algal communities.

However, in response to the water-level drawdown in the Chornobyl NPP Cooling Pond and planktonic Cyanobacteria blooms, the periphytic algal communities activated the mechanisms aimed at maintaining their dynamic equilibrium. For example, there was an increase in the relative share of species from genera *Oscillatoria, Epithemia, Rhopalodia*, which are considered shade-tolerant (Mur et al., 1977; Scheffer et al., 1997; Müller, 1999), species from genera *Nitzschia, Navicula*, which can live in silted habitats, and β-α-, α-saprobic species. It can be said that periphytic algal communities shifted to a new equilibrium state.

The similar processes of a water body’s shift to high turbidity regime are known for Sevan Lake in Armenia. Artificial lowering of the water table, which begun as early as in 1930–1940s and lasted until 1980–1990s, brought about eutrophication of the lake ecosystem, algal blooms, aggravation of oxygen conditions and reduction of the Secchi-disk transparency in 4–5 times as compared with the period before the water-level drawdown (Parparov, 1990).
Mechanisms of epiphytic algal communities’ functioning in aquatic ecosystems of the Dnieper basin under different alternative stable regimes

Summarizing of our findings set forth above makes it possible to formulate the concept of this research, which is illustrated by Fig. 6. The concept is based on the alternative stable regimes theory (Scheffer et al., 1992, 1993; Scheffer & Carpenter, 2003; Scheffer & Van Nes, 2007) and describes the contour algal communities’ development under different alternative stable regimes in the aquatic ecosystems of the Dnieper basin and also may be applied to similar natural-artificial water bodies, in particular, water reservoirs in large lowland rivers.

**Conclusion**

Analysis of the long-term field data obtained in aquatic ecosystems of the Dnieper basin has made it possible to distinguish the major factors which can trigger aquatic ecosystems’ shift from clear water regime to high turbidity regime: climate change, changes in nutrient conditions and water-level drawdown.

In response to the complex effect of these changes contour algal communities activate the mechanisms aimed at mitigating the negative consequences of such impact and at maintaining the community’s dynamic equilibrium in the unfavorable conditions of high turbidity.

These mechanisms include changes in the ratio of phyla with a decrease in the diatoms’ share and increase in the shares of green and blue-green algae; increase in the abundance of nitrogen-fixing species; enlargement in the share of shade-tolerant species and species with high saprobity index.

The above-mentioned transformations in the structure of contour algal communities may be of practical value and can be used as reliable biological indicators of regional and global environmental changes.

![Fig. 6. Contour algal communities under different alternative stable regimes in aquatic ecosystems of the Dnieper basin: PFC – projective foliage cover, A – primary production, n – species richness, N – cell count, B – biomass, R – organic matter destruction, P/B – specific production, N – nitrogen, P – phosphorus](image)


References (translated & transliterated)


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