When Clear Water Lies: Filamentous Algae overgrow Macrophytes

Katrin Teubner[1]*, Markus Weinbauer*[2]

[1] *Department of Functional and Evolutionary Ecology, Unit Limnology, University of Vienna, Vienna, Austria , email: katrin.teubner@univie.ac.at*

[2] *Laboratoire d'Océanographie de Villefranche, LOV, Sorbonne Université & CNRS UMR7093 Institut de la Mer de Villefranche, IMEV, Villefranche-sur-Mer, France, email: markus.weinbauer@imev-mer.fr*

DOI: 10.5281/zenodo.17691569

Abstract

As primary producers, submerged macrophytes depend on the availability of ambient light within the water column. This study evaluates underwater vertical PAR profiles measured in May 2025 at seven floodplain lakes and channels in the Danube Delta Biosphere Reserve, Romania, focusing on the *depth of optimum light exposure* rather than solely on minimal light requirements (euphotic depth). Alongside submerged macrophytes, dense accumulations of filamentous algae frequently develop in the water column, creating a 'false transparency' effect in which visually clear water overestimates the light available at the macrophyte canopy. Effective management and restoration of the Danube Delta therefore require supporting macrophyte communities capable of establishing and persisting under low-nutrient conditions. Only such resilient stands – free from filamentous algal overgrowth – can ensure that open-water transparency once again reflects true ecological quality.

Introduction

The Danube Delta Biosphere Reserve in Romania is characterized by interconnected small riverine channels and shallow floodplain lakes (Nichersu et al. 2022). The shallowness of these water bodies and their short residence times – often only a few days for the Danube Delta lakes (Los 1998) – generally provide suitable habitat for macrophytes. Underwater light – both as a resource and a signalling cue – often governs macrophyte recovery in degraded shallow lakes. Accordingly, the underwater light climate is quantified here using optical measurements to assess light availability in the water column.

Measuring Lake Depth of Optimal Light Requirements for Macrophyte Development

Assessing optimal light requirements for macrophyte development in the Danube Delta is essential for understanding ecosystem functions. Minimal light thresholds – 1% of surface irradiance for planktonic autotrophs and 2–4% for macrophytes – indicate only survival (Teubner et al. 2022). In shallow lakes, macrophytes flourish only under near-optimal light, around 12% of surface irradiance (Teubner et al. 2020), which ensures sustained growth, competitive strength against phytoplankton, and exposure of canopy leaves near the water surface. Observations from the oxbow lake 'Alte Donau' show that when large sediment areas receive this optimal light, macrophytes expand rapidly, forming dense, structurally complex stands that act as a major seasonal phosphorus sink and create a three-dimensional habitat. Mature submerged macrophyte stands are thus recognized not only for their biomass and nutrient retention but also as a distinct structural habitat formation, forming a third ecological component alongside benthic and pelagic zones (Teubner et al. 2022). These submerged 'underwater meadows' in freshwater are analogous to marine underwater forests, providing extensive habitat at the water surface and throughout the water column for fish, invertebrates, and other biota. Understanding the underwater light climate in the Danube Delta is therefore key to predicting macrophyte growth, habitat formation, and ecosystem stability, for example in common species such as *Trapa natans L., Ceratophyllum demersum L., Nuphar lutea (L.)SM,* and *Stratiotes aloides L.*

Figure 1. LI-COR underwater spherical PAR sensor (left; PAR plane air sensor not shown; Lacul Babina) and measurement of underwater light below filamentous algal mats and leaves of Nymphaea alba, respectively (right, Lacul Ligheanca).

RESEARCH

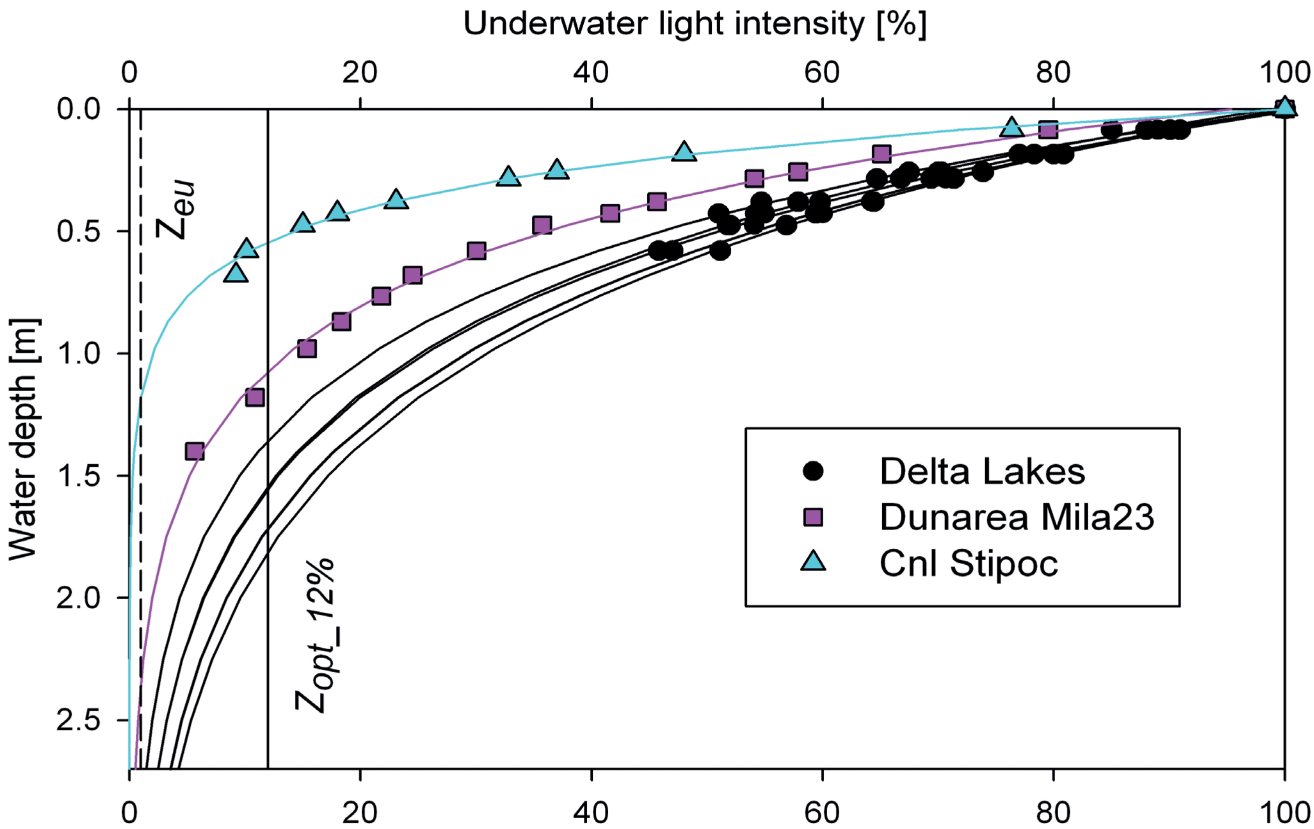

Figure 2. Underwater light profiles for Danube Delta Lakes (four floodplain lakes, Lacul Babina, L. Ligheanca, L. Vâcaru, L. Vâsins) and narrow natural watercourse connecting lakes of the Danube Delta, Gârla Lopatna), Danube oxbow waterbody at village Mila23 (Dunărea Veche at Mila23) and floodplain channel (Canal Stipoc). Data points indicate measurement depths, while the fitted curves extend beyond them to 2.70 m, corresponding to the maximum lake depth in the Danube Delta studied by Cristofor et al. (2003). Underwater light intensity of 1% (euphotic depth, z_{eu}) and of 12% surface ambient light (optimum light requirement for macrophyte growth, $z_{opt\_12\%}$) is indicated by dashed and solid line. Measurements from 8-11 May 2025.

Vertical Light Profiles Relevant to the Growth and Flourishing of Macrophytes

Measuring the underwater light climate in shallow lakes is challenging because Secchi disk readings are often inadequate. The Secchi disk has been used for over 200 years to estimate water clarity (Teubner et al. 2021), but it provides limited information in very shallow systems. Although widely applied, established first for marine and later freshwater observations, Secchi measurements are only meaningful where the Secchi depth is less than the actual water depth (Secchi depth survey for Danube Delta in Sarbu 2003). Entries such as 'Secchi disk visible at the bottom' cannot be used to calculate underwater light attenuation. In shallow floodplain lakes with soft, easily resuspended sediments, near-bottom Secchi readings are unreliable. Therefore, direct optical measurements using appropriate sensors are required to characterize the underwater light climate in these systems.

Underwater light profiles of Photosynthetically Active Radiation (PAR) were conducted with a 4π quantum sensor (LI-COR, at *fig. 1*). The light profiles in figure 2 were measured in open water adjacent to macrophyte stands, without shading effects from the aquatic plants, as macrophytes or filamentous algal mats. Curve fitting was extended to 2.70 m,

Parameter	Lacul Vârsina	Lacul Babina	Gârla Lopatna	Lacul Vâcaru	Lacul Ligheanca	Dunărea Mila23	Canal Stipoc
k_{PAR} [m^{-1}]	1.160	1.345	1.395	1.441	1.460	2.055	3.585
z_{eu} [m] $z_{macr\_4\%}$ [m]	**3.97** 2.78	**3.42** 2.39	**3.30** 2.31	**3.20** 2.23	**3.15** 2.20	**2.24** 1.57	**1.28** 0.90
$z_{opt\_12\%}$ [m]	**1.83**	**1.58**	**1.52**	**1.47**	**1.45**	**1.03**	**0.59**

Table1. Optical properties of water bodies in four Danube Delta lakes (lacul), a narrow natural watercourse (gârlă), an oxbow (Dunărea Veche at Mila23), and the Canal Stipoc, including mean vertical light attenuation coefficient (k_{PAR}), the euphotic depth at 1% surface ambient light (z_{eu}), the depth of minimum light requirement for macrophyte growth at 4% surface ambient light ($z_{macr\_4\%}$), and the depth of optimum light conditions for macrophyte growth at 12% surface ambient light ($z_{opt\_12\%}$, Teubner et al. 2020, 2022). All lakes and narrow natural watercourse are macrophyte dominated water bodies of low water flow velocity, different from the oxbow and channel.

Figure 3. Danube Delta floodplain lakes are characterized by dense submerged macrophyte meadows, typically formed by mixed species such as Potamogeton crispus and Elodea nuttallii. High water transparency, even in brownish waters coloured by dissolved humic acids, is perceived by humans as indicative of good water quality (Teubner at al. 2020) (top left, Lacul Ligheanca). Phytoplankton-induced turbidity reduces light availability in the water column and consequently suppresses the growth of submerged macrophytes (top right, oxbow Dunărea Veche Mila23). Filamentous algae can form veil-like, cottony structures in the water column or mats at the surface, and wave action can wash them ashore – making them easily visible (bottom left, Canal Catavaia). Small fishing boat navigating a narrow channel – Fishermen keep small channels open between lakes, supporting hydrological connectivity of the riverine lake system (Richardson 2021, Nichersu et al. 2022). In addition to trophic conditions, connectivity and flow velocity determine the survival of submerged macrophytes (bottom right, Canal Vârsina).

corresponding to the maximum lake depth reported for Danube Delta lakes by Cristofor et al. (2003), to cover the potential depth range in the system, even though most lakes measured here differ from those in the original study (except Lacul Babina). Because these Delta floodplain lakes are very shallow, seasonal water-level fluctuations strongly affect effective lake depth (Los 1998; Nichersu et al. 2022). During the five-day LI-COR survey May 2025, water levels were relatively high compared with typical seasonal conditions.

Vertical Light Attenuation in Macrophyte-Covered Lakes Compared to Channels

Vertical light profiles were measured in a total of seven water bodies, as shown in figure 2. Light intensity, which decreases exponentially with increasing depth below the water surface, differed substantially across the studied sites. The lakes showed that even at 1.5 m depth, about 10–12% of surface light remained, thus providing a large vertical zone where macrophytes can develop and thrive. Based on underwater light attenuation, the depth of optimum ambient light for macrophytes in the five lakes and the natural watercourse averaged 1.57 m, ranging from 1.45 to 1.83 m ($Z_{opt\_12\%}$ in *Table 1*). This indicates that – under the light conditions measured in open water near macrophyte stands – there is considerable potential for macrophytes to flourish and to form surface carpets or underwater meadows.

As shown in figure 2, at all floodplain lake sites the depth of optimum light exceeds the measured depth profiles, due to the shallowness of the sampling locations. The depth of the minimum light requirement for macrophytes growth, $Z_{macr\_4\%}$, goes much deeper, averaging 2.38 m (2.20–2.78 m). The average of euphotic depth, Z_{eu}, is with 3.41 m remarkably deeper (3.15–3.97 m). The denser the macrophyte stands grow, the more self-shading comes into play. In this study, we found that directly beneath the leaves of *Nuphar lutea,* close to the leaf surface, strong shading occurs and reduces ambient surface light by 97–99% (with k_{PAR} values ranging from 44.39 to 59.30 m^{-1}, n = 5 measurements, Lacul Vâcaru, 8 May 2025). However, in less dense stands, light availability increases again with depth because natural light can

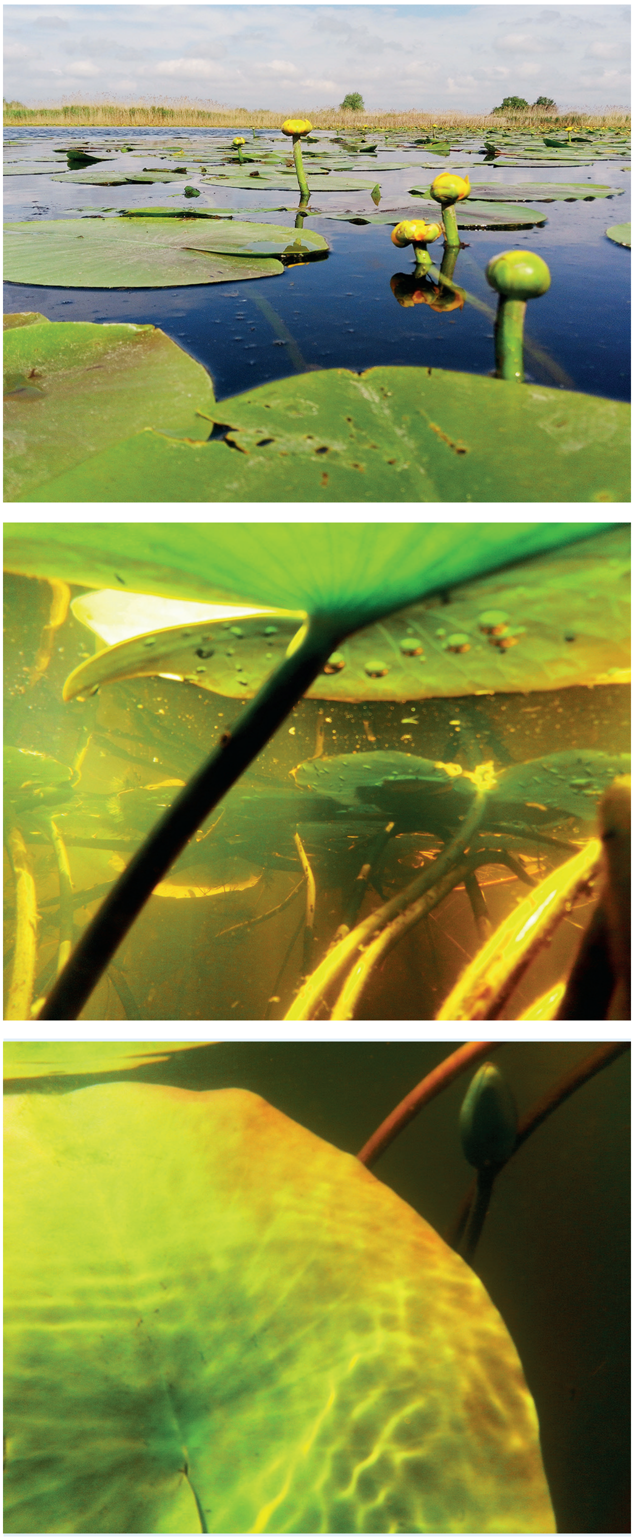

Figure 4. *Nuphar lutea viewed from above (top) and below the water (middle). The underwater view shows that the leaves provide shade near the water surface, but in sparse stands sunlight can still penetrate the shallow littoral zone, ensuring good light availability near the sediment layer. Nymphaea alba showing sunlight reflected on leaves (bottom), Lacul Vâcaru, 9 May 2025.*

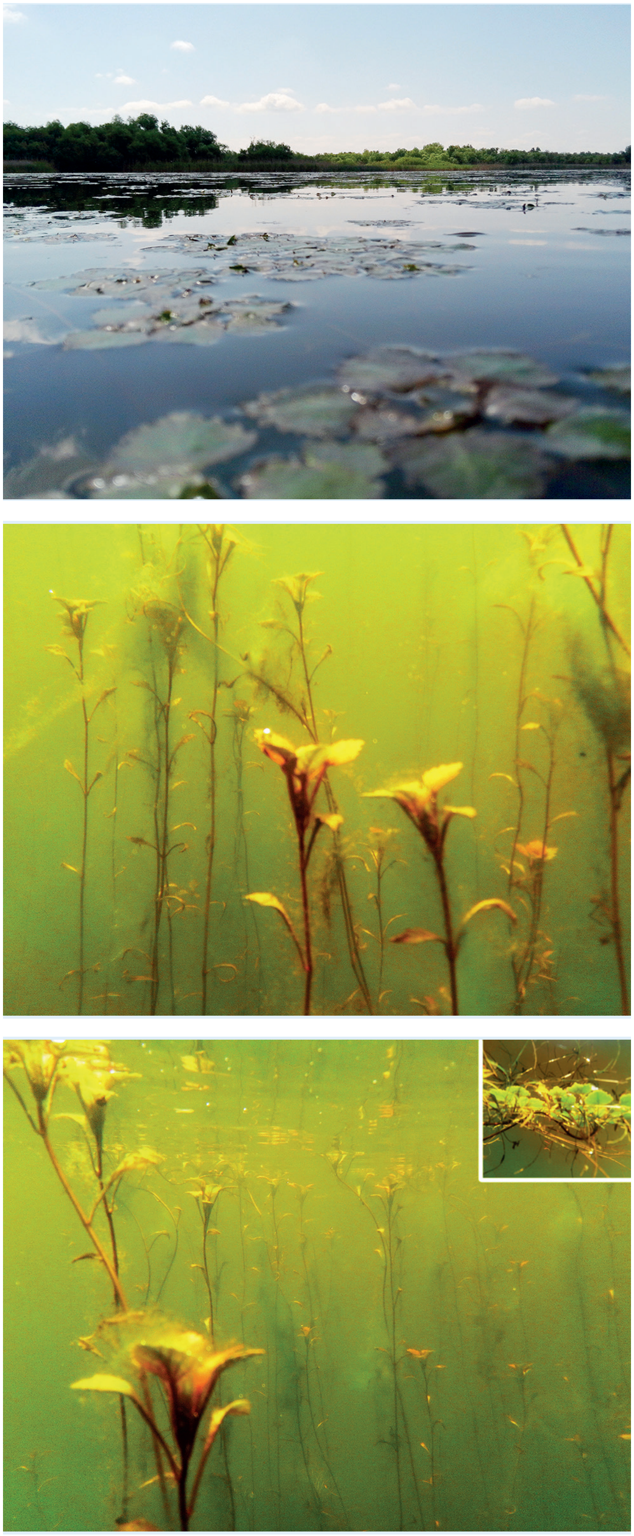

Figure 5. *Trapa natans viewed from above (top) and below the water surface (middle, bottom). Dark leaf pigmentation results from photo-protective pigments adapted to high light exposure above water (top). Young spring shoots, still submerged, serve as attachment structures for filamentous algae, which form veil-like, cottony layers that persist in riverine floodplain lakes (middle). During the spring growth phase, Trapa competes with other submerged macrophytes and filamentous algae for light, ends once it reaches the water surface. After this bottleneck – when sufficient light is achieved despite turbidity caused by planktonic and attached filamentous algae in the water column – Trapa forms surface biomass carpets, providing habitat for other wetland organisms. Natural watercourse Gârla Lopatna, 7 May 2025, bottom; inset: view from below on a freshly established carpet.*

pass through the loosely arranged leaves toward lake bottom (*fig. 4*, middle and bottom). This pattern differs from the usual vertical light decline in open water, as light attenuation increases with depth and light intensity decreases accordingly. It shows that single macrophyte plants – and even loose-leaf underwater canopies – do not cause substantial

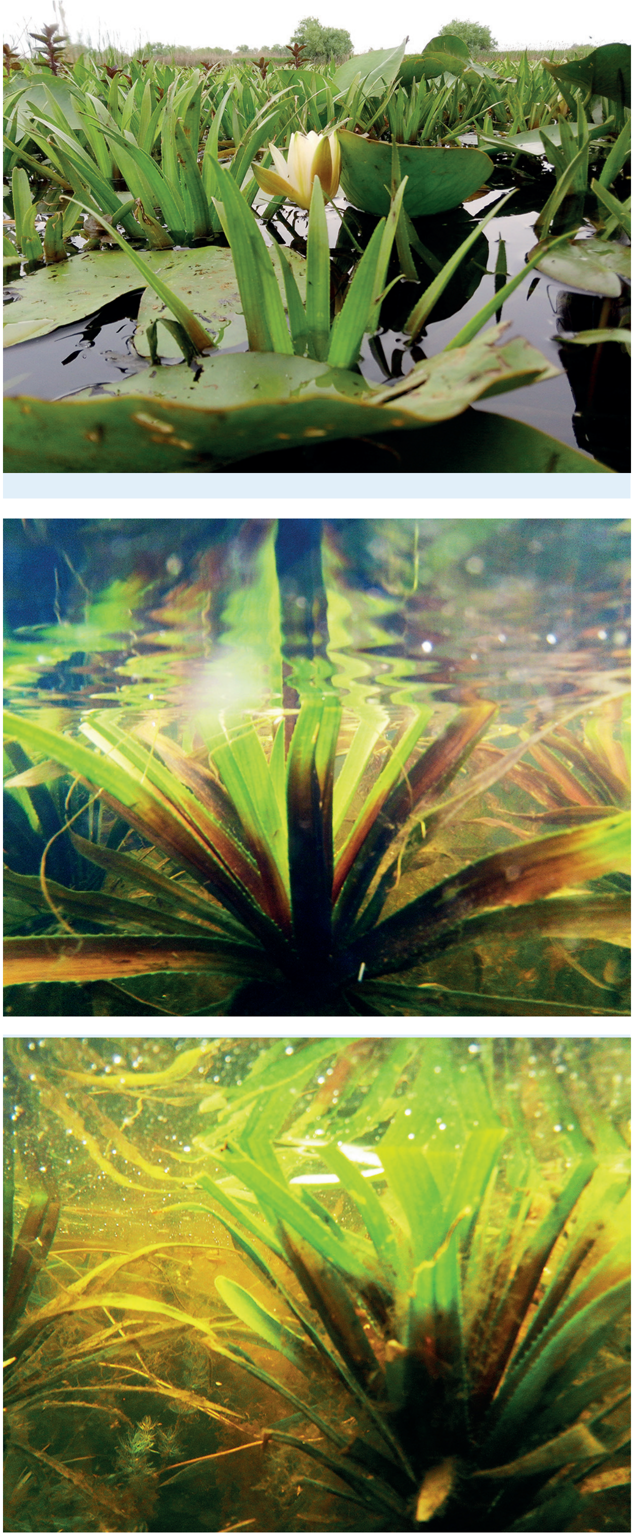

Figure 6. Stratiotes aloides seen from above (top) and underwater (middle and bottom). The stand in the middle photo is almost free of filamentous algae, unlike the bottom photo, which further shows a few shoots of Ceratophyllum demersum among dense stands of S. aloides, Lacul Vârsina, 10 May 2025.

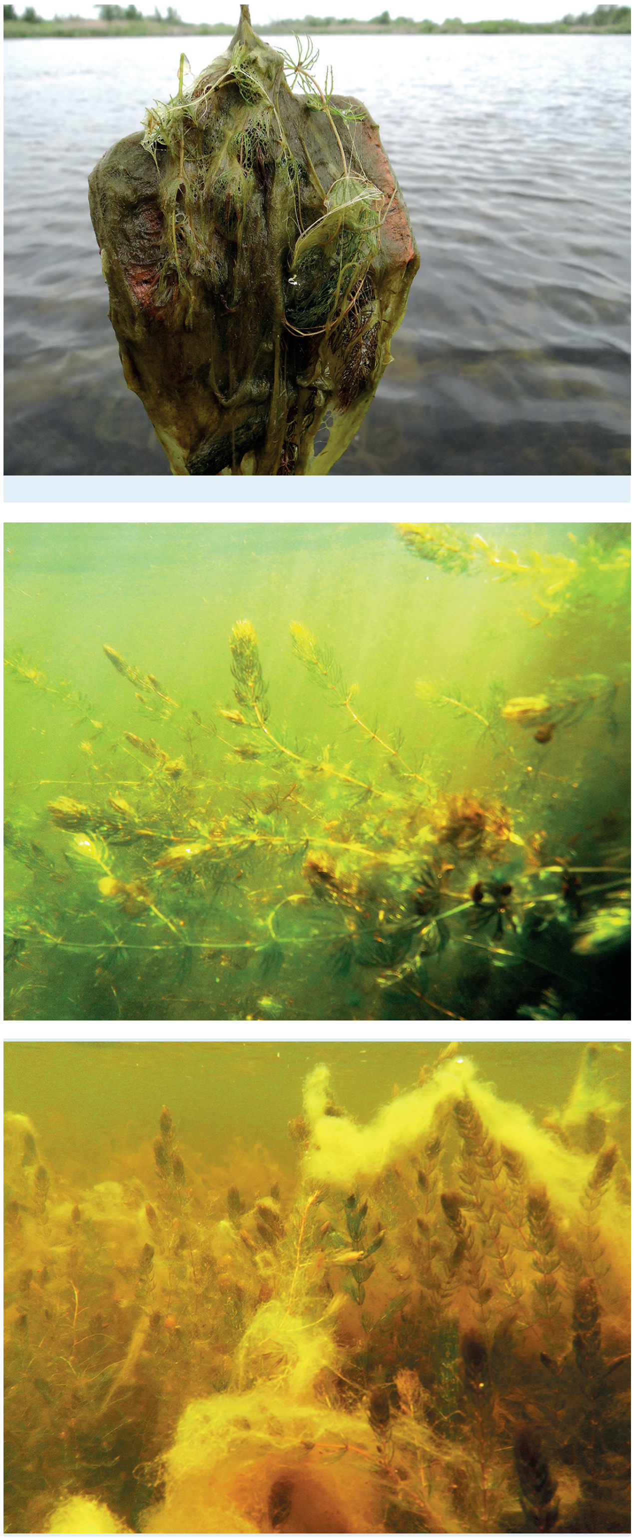

Figure 7. Ceratophyllum demersum sampled together with filamentous algae (top) and underwater stands viewed from a 'fish perspective' (middle and bottom). At first glance, the lake appears healthy due to its clear water, but extensive macrophyte stands are compromised, overgrown by filamentous algae. The middle photo shows a Ceratophyllum stand nearly free of filamentous algae, while the bottom photo depicts the common situation: the Ceratophyllum is covered by a dense, cotton-like layer of filamentous algae (10 May 2025, Lacul Babina).

shading below the water surface. It further implies that the scarcer the carpet of floating-leaved macrophytes, such as *Nuphar or Trapa*, the greater the light exposure reaching the sediment in shallow littoral zones, triggering the excessive growth of filamentous algae (Kemp et al. 2025).

The macrophytes observed at the measurement sites of these lakes included *Elodea nuttallii* (Planch.) H. St. in Lacul Ligheanca (*fig. 3*, top left), *Nuphar lutea* (L.)SM. and *Nymphaea alba* L. in Lacul Vâcaru (*fig. 4*), *Trapa natans* L. in the natural watercourse Gârla Lopatna (*fig. 5*), *Stratiotes* *aloides* L. in Lacul Vârsina (*fig. 6*), and *Ceratophyllum demersum* L. in Lacul Babina (*fig. 7*). It is worth noting that macrophytes often do not cover more than 40% of the lake area; a patchy mosaic of different species was common, and from other studies it is known that these patterns can vary seasonally and from year to year (Gaştecu 1993, 2021; Coops et al. 1999; Cristofor et al. 2003; Covaliov et al. 2003; Sârbu 2003; Schneider-Binder 2021; Janauer et al. 2021).

In contrast, in Canal Stipoc, light declined very rapidly, reaching only about 1% of surface intensity at roughly 1.5 m (*fig. 2*; Z_{eu} 1.28 m in *Table 1*). Such steep attenuation severely limits the depth zone in which macrophytes can grow under adequate light, as the minimum light requirement for macrophyte growth, $Z_{macr\_4\%}$, is met only down to 0.90 m, and the well-illuminated zone for optimal growth, $Z_{opt\_12\%}$, is even shallower at 0.59 m. Here, the $Z_{opt\_12\%}$ exceeds the measurement depth. Light attenuation at Dunărea Veche Mila23 fell between these extremes – between the lakes and Canal Stipoc – with moderate light attenuation, but as in Canal Stipoc, the $Z_{opt\_12\%}$ is shallower than the depth reached by the measured underwater light profile. It indicates that macrophyte growth cannot benefit from optimal light exposure at the canal bottom.

In the Canal Stipoc, surface-floating mats of filamentous algae were common along the channel banks. Measurements of shading beneath these mats showed a much wider range of attenuation compared with shading beneath *Nuphar leaves*, as both the thickness and areal extent of algal mats vary far more than those of individual leaves. The mean percentage of surface ambient light transmitted below the mats was 60.2%, with a median of 55.4%, ranging from 25.6% to 85.3% (Lacul Vâcaru, 8 May 2025, n = 5 measurements, *fig. 1*, right). Accordingly, light attenuation also varied widely, with k_{PAR} showing a mean of 9.3 m^{-1}, a median of 8.8 m^{-1}, and a range from 3.5 to 20.2 m^{-1}.

These patterns indicate that shallow Danube Delta lakes generally provide favourable light conditions for macrophyte expansion, if inferred from light attenuation in open water. In contrast, turbid channels such as Canal Stipoc, surrounded by degraded floodplains, restrict macrophyte growth to very shallow areas. This result aligns with the Secchi depth survey conducted in the Danube Delta by Sarbu (2003). Planktonic algal turbidity (*fig. 3,* top right), a major threat to submerged macrophytes caused by nutrient enrichment, is a common symptom of ecosystem deterioration, whereas sustainable restoration aims to re-establish submerged macrophytes and shift the system back toward a macrophyte-dominated, clear-water state (Teubner et al. 2018, 2020, 2021, Pall 2018).

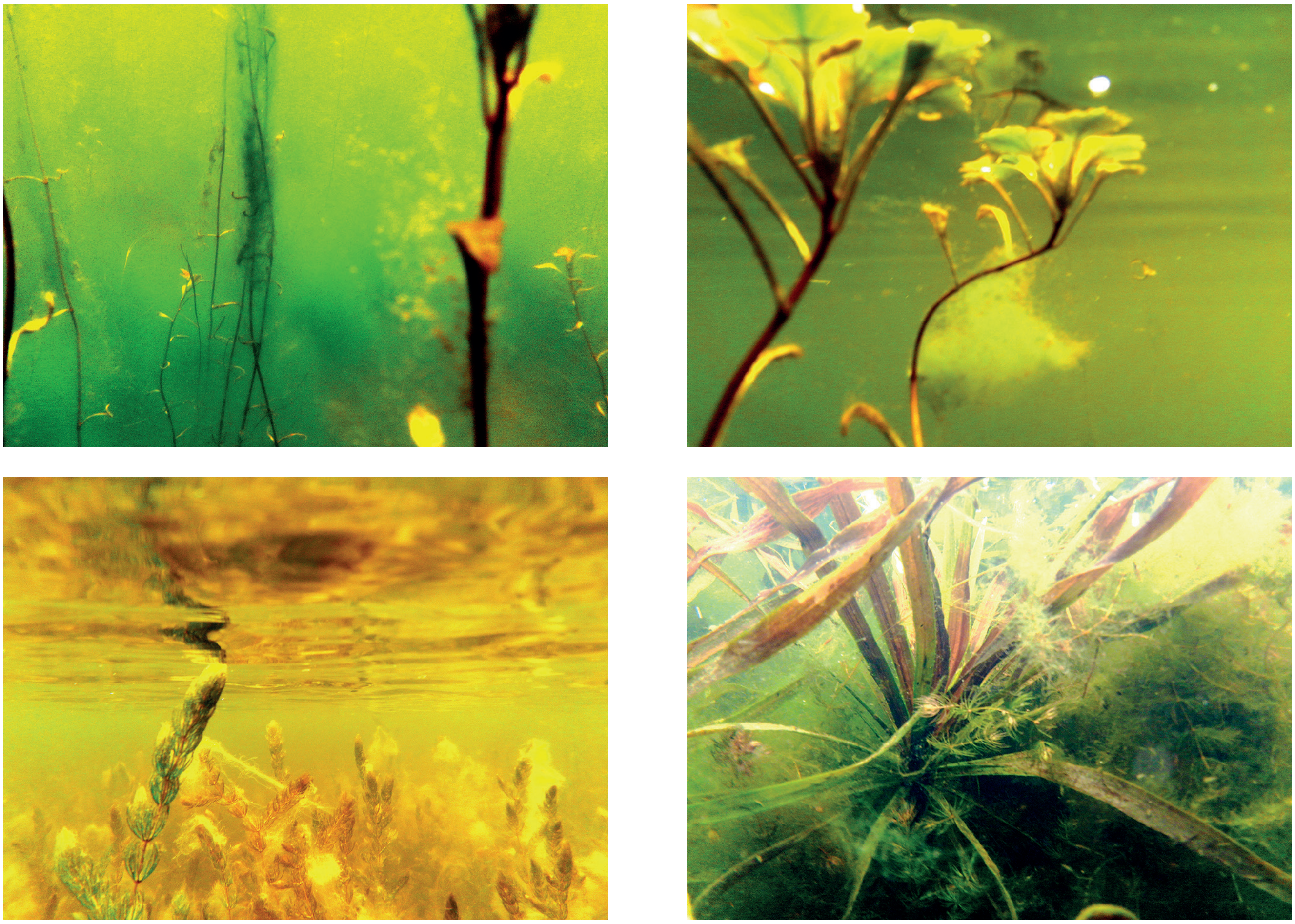

Figure 8. Summary of the concept of 'false water transparency': Apparent water clarity of water body can overestimate actual underwater light availability for stands of submerged macrophytes. Filamentous algal mats create patchy shading patterns when attached to macrophyte leaves or shoots. Shown here: Trapa natans (top left and right), Ceratophyllum demersum (bottom left), and Stratiotes aloides (bottom right).

'False transparency' can Mask early Signs of Macrophyte Decline.

Depth estimates for optimal macrophyte light requirements ($Z_{opt\_12\%}$), as well as for minimum requirements ($Z_{macr\_4\%}$, Z_{eu}), show that Danube Delta lakes offer favorable light conditions for macrophyte growth compared with other systems. Nonetheless, even ongoing recent reductions in nitrogen and phosphorus loads (Zaharia et al. 2022) have not resulted in corresponding increases in macrophyte abundance. The opposite trend was noted by Schneider-Binder (2021), who reported for example a clear decline in water chestnut despite remaining notable populations. Filamentous algae, however, appear to have proliferated in recent years, as observed by local fishermen, consistent with Covaliov et al. (2003), who noted low-abundance mats among macrophytes in June 2001, reflecting a trend reported globally. Conventional light assessments in the open water site of a lake – Secchi depth and open-water PAR profiles – however, do not account for shading generated by epiphytic filamentous algal mats, attached to macrophytes or floating at the lake water surface (*fig. 1*, right, *fig. 3*, bottom right). These algal species including *Cladophora glomerata, Hydrodictyon reticulatum*, and *Spirogyra* sp. in the Danube Delta (Covaliov et al. 2003) can even outcompete macrophytes under moderately eutrophic, warm, and clear-water conditions (Ozimek et al. 1991; Kemp et al. 2025). Droughts in the delta lead to a progressive loss of aquatic habitats (Jitariu et al. 2022), which at first glance compromises further stands of many submerged macrophyte species. In contrast, filamentous algae seem to gain a short-term advantage from increasingly shallow, warmer, and more transparent water bodies before these areas ultimately dry out due to prolonged aridity, driven by climate change and insufficient management to mitigate these global impacts.

The current Danube ecosystem status of a flourishing underwater, cotton-like layer of filamentous algae results in 'false transparency', where visually clear water overestimates actual light availability in the submerged macrophyte zone. Observations reveal that macrophytes such as *Trapa natans, Ceratophyllum demersum, Stratiotes aloides* (*fig. 8*), and even invasive species such as *Elodea nuttallii* (Lupu et al. 2025) are frequently covered by epiphytic filamentous algae during this May survey. The widespread occurrence of dense, veil-like algal structures and floating mats in the Delta indicates an increasing risk of macrophyte suppression. Restoration efforts mitigating further ecosystem degradation must therefore prioritise promoting macrophyte communities capable of thriving under low-nutrient conditions. Only then can open-water transparency return as a reliable indicator of ecological quality.

Acknowledgements:

The one week 'Water Transparency' field campaign was supported by the EU DANSER project (Grant agreement ID: 101157942). We also gratefully acknowledge the valuable insights provided by our fisherman field guide in the Danube Delta, as well as the warm hospitality and support received from Pavel and Aurica Marcov in Mila23.

References

Coops H, Hanganu J et al (1999). Classification of Danube Delta lakes based on aquatic vegetation and turbidity. Hydrobiologia 415(0), 187-191.

Covaliov S, Van Geest G et al (2003). Seasonality of macrophyte dominance in flood-pulsed lakes of the Danube Delta. Hydrobiologia 506(1-3), 651-656.

Cristofor S, Vadineanu A et al (2003). Long-term changes of submerged macrophytes in the Lower Danube Wetland System. Hydrobiologia 506(1), 625-634.

Gastescu P (1993). The Danube Delta: Geographical characteristics and ecological recovery. GeoJournal 29(1), 57-67.

Gastescu P (2021). The biodiversity of the Danube Delta Biosphere Reserve reflected in the structure of the ecosystems. In: Water resources and wetlands, pp. 1-19 5th Int Conf Wetlands, Tulcea (RO), http://www.limnology.ro/wrw2020/proceedings.html

Janauer GA, Exler N et al. (2021). Distribution of the macrophyte communities in the Danube reflects river serial discontinuity. Water 13(7), 918. DOI:10.3390/w13070918

Jitariu V, Dorosencu A et al. (2022). Severe drought monitoring by remote sensing methods and its impact on wetlands birds assemblages in Nuntași and Tuzla Lakes (Danube Delta Biosphere Reserve). Land 11(5), 672. DOI:10.3390/land11050672

Kemp HR, Zieritz A et al. (2025). Light and temperature as triggers for surface filamentous green algal blooms in shallow freshwater systems. Limnology and Oceanography. DOI:10.1002/lno.70169

Los, F. J. (1998). Hydrodynamical models of the Danube Delta. Report (T2298), WL Delft Hydraulics: 51 pages

Lupu G, Covaliov S et al. (2025). Status of biodiversity, reed habitats, sustainable exploitation of natural resources, invasive species, and socio-economic implications in DDBR in 2024. Scientific Annals of the Danube Delta Institute, 30, 141-162. DOI:10.3897/saddi.30.163613

Nichersu I, Constantinescu A et al. (2022). A Transdisciplinary Approach Using Danube River Multi-connectivity in Wetland Management. In: Negm, A., Zaharia L, Ioana-Toroimac, G (eds) The Lower Danube River. (pp. 405-442) Springer, Cham. DOI:10.1007/978-3-031-03865-5_14

Ozimek T, Pieczynska E et al. (1991). Effects of filamentous algae on submerged macrophyte growth: a laboratory experiment. Aquatic Botany 41, 301-315. DOI:10.1016/0304-3770(91)90050-F

Pall K (2018). Wax and Wane of Macrophytes. In: Dokulil M, Donabaum K, Teubner K (eds) The Alte Donau: Successful Restoration and Sustainable Management. Aquatic Ecology Series, vol 10. Springer, Cham. https://doi.org/10.1007/978-3-319-93270-5_8

Richardson T (2021). Displacing the Delta: Notes on the Anthropology of the Earth's Physical Features. In Delta Life: Dynamic Envir. Krause F, Harris M (eds) Oxford New York: Berghahn, 27-54.

Sarbu A (2003). Inventory of aquatic plants in the Danube Delta: a pilot study in Romania. Archiv für Hydrobiologie 147, 205-216.

Schneider-Binder E (2021). Ecological conditions of the Waterchestnut (Trapa natans L.) in the Danube Delta (Romania). TRSER 23(3), 1-16.

Teubner K, Kabas W et al. (2018) Phytoplankton in Alte Donau: Response to trophic change from hypertrophic to mesotrophic over 22 years. In: The Alte Donau: Successful restoration and sustainable management - An ecosystem case study of a shallow urban lake. Aquatic Ecology Series, vol 10. Springer, Cham,107–147. DOI:10.1007/978-3-319-93270-5_9

Teubner K, Teubner I et al. (2020.) New Emphasis on Water Transparency as Socio-Ecological Indicator for Urban Water: Bridging Ecosystem Service Supply and Sustainable Ecosystem Health. Frontiers in Environmental Science 8:573724. DOI:10.3389/fenvs.2020.573724

Teubner K, Teubner IE et al. (2021). New Emphasis on Water Clarity as Socio-Ecological Indicator for Urban Water – a short illustration. In: Rivers and Floodplains in the Anthropocene. Ext Abstracts 43rd IAD-conf. (10.17904/ku.edoc.28094), 70-78.

Teubner K, Teubner IE et al. (2022). Macrophyte habitat architecture and benthic-pelagic coupling: Photic habitat demand to build up large P storage capacity and bio-surface by underwater vegetation. Frontiers in Environmental Science 10:901924. DOI:10.3389/fenvs.2022.901924

Zaharia L, Țuchiu E et al. (2022). Variability of Nutrient Concentrations Along the Lower Danube River. In: Negm, A., Zaharia L, Ioana-Toroimac, G (eds) The Lower Danube River. (pp. 161-194). Springer, Cham. DOI:10.1007/978-3-031-03865-5_6