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The Transparency-Resilience Paradox: When clarity signals degradation in eutrophic lakes

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Abstract - The global imperative to restore eutrophic lakes heavily relies on increasing water clarity, a metric anchored in policy and public perception. However, this pursuit overlooks a counterintuitive phenomenon documented across multiple hyper-eutrophic systems: periods of high clarity coinciding with an intense cyanobacterial dominance and a low level of biodiversity. Here, we synthesise evidence to propose and formalise the "Transparency-Resilience Paradox," a conceptual framework that explains how hyper-eutrophic conditions can produce a deceptive clarity that signals not recovery, but an alternative, degraded, stable state. This framework reinterprets a core limnological metric, revealing that achieving target Secchi depths without addressing ecosystem structure may trap lakes in a "cyanobacterial desert". Consequently, monitoring and restoration practices must shift from tracking simple visual properties to diagnosing the ecological architecture behind water transparency.

Keywords - Eutrophication, Water remediation, Cyanobacteria, Lake management

1. INTRODUCTION

Imagine being a lake manager celebrating a hard-won victory. For years, your targeted interventions have reduced nutrient inputs, and the latest monitoring data shows a significant improvement in the Secchi disk depth. The water is finally clearer. But beneath these promising results, a problem emerges: the water experiences repetitive thick, surface-scumming toxic cyanobacteria blooms, and the biodiversity surveys show a significant reduction in zooplankton and fish larvae. This is not the clear, macrophyte-dominated lake of the past, but a completely different ecosystem. This scenario, playing out in systems like China's Yangcheng Lake or Paraguay's Lake Ypacaraí**,** exposes a critical flaw in our foundational understanding of lake health.

The conventional restoration paradigm operates under a linear assumption: nutrient limitation reduces phytoplankton biomass, which increases light penetration, facilitates the recovery of submerged aquatic vegetation, and yields a clear-water, resilient state. However, emerging evidence from lakes worldwide challenges this assumption, revealing that high clarity can also be the hallmark of a profoundly simplified and degraded condition dominated by a single, noxious functional group.

In this review, we argue that limnology and lake management are confronted with a **Transparency-Resilience Paradox**. We posit that in hyper-eutrophic shallow lakes, the achievement of high levels of water clarity may represent not a return to a resilient, diverse ecosystem, but the consolidation of an alternative stable state characterised by cyanobacterial monopoly, suppressed grazing and broken biogeochemical cycles. This paradoxical clarity results from an extreme competitive exclusion and creates an "illusion of recovery", which can misdirect policy and terminate restoration efforts prematurely.

As climate change is intensifying cyanobacterial dominance globally, the urgency of addressing this paradox has never been greater. Understanding when clarity signals health versus degradation is, therefore, an essential step for effective management.

In this review, we: (1) propose the Transparency-Resilience Paradox as a novel conceptual framework synthesising alternative stable states theory with empirical observations; (2) identify the mechanistic pathways through which cyanobacteria engineer deceptive clarity; (3) synthesise diagnostic methodologies for distinguishing resilient from paradoxical transparency; (4) present evidence from multiple case studies demonstrating the paradox; and (5) introduce a Functional Transparency Index (FTI) to operationalise this framework for monitoring and management.

2. MECHANISMS OF DECEPTIVE CLARITY CYANOBACTERIAL SELF- ENGINEERING

Understanding the Transparency-Resilience Paradox requires a fundamental shift in perspective: viewing water clarity not as a passive result of total phytoplankton biomass, but as an emergent property of competitive outcomes within the phytoplankton community. In a typical eutrophic lake, high biomass of diverse, edible algae species turbidifies the water. The water becomes clear when this community is repressed, either by top-down grazing or bottom-up nutrient limitation.

The paradox emerges from a third, underappreciated pathway: competitive exclusion by supremely adapted cyanobacteria. Let's take the example of a phytoplankton community where one supremely adapted group, buoyant, toxin-producing cyanobacteria like *Microcystis*, wins. Through a combination of intensive nutrient scavenging (especially under low N:P ratios), allelopathic toxin release, and the formation of large, inedible colonies, cyanobacteria can create a "winner-takes-all" environment. As brilliantly articulated by Huisman et al. (2018) in their synthesis of cyanobacterial bloom ecology, these traits allow cyanobacteria to dominate at low residual nutrient concentrations by "starving out" other phytoplankton. Dokulil and Teubner (2000) further demonstrated that cyanobacterial dominance is mechanistically linked to specific environmental conditions, including stable water columns, high temperatures, and low light environments, conditions which are increasingly prevalent in warming lakes.

The resulting water becomes clearer not because there is less life, but because the life that remains is packaged differently. The cyanobacteria form dense surface scums or large colonies that contribute less to light scattering per unit biomass than a diffuse soup of smaller diatoms or green algae. More critically, by stripping the water of bioavailable phosphorus and nitrogen and filling it with toxins, they create a chemical desert in the water column below the scum. A clear, but largely lifeless, zone.

This "cyanobacterial desert" state involves more than a simple competitive exclusion, since the cyanobacterial exudates fuel a distinct heterotrophic bacterial community that further modifies the biogeochemical environment. As Azam et al. (1983) first articulated in their seminal work on the microbial loop, and Cole et al. (1993) subsequently elaborated, cyanobacterial-derived organic matter supports bacterial communities that can compete with phytoplankton for nutrients. All while escaping grazing pressure, which reinforces the cyanobacterial monopoly and causes the grazer community to collapse. Jeppesen et al. (2007), in their analysis of shallow lake restoration, documented that large-bodied Daphnia, the keystone grazers maintaining clear water in healthy lakes, cannot effectively consume colonial cyanobacteria. The zooplankton community shifts to small-bodied rotifers and copepods that feed primarily on bacteria and detritus, completely bypassing the cyanobacteria. The lake thus achieves a perverse, stable clarity maintained by a self-reinforcing biological monopoly rather than ecological complexity.

3. DIAGNOSING THE PARADOX: A MULTI-METRIC FRAMEWORK

Identifying the Transparency-Resilience Paradox requires us to move beyond routine limnological monitoring. We synthetise four complementary diagnostic approaches that, when applied together, can distinguish clarity arising from health from clarity arising from dominance.

3.1. Stoichiometric Diagnosis

As championed by Sterner and Elser (2002), in their foundational work on ecological stoichiometry, analysing nutrient ratios in the water column and seston provides critical insight. Paradoxical clarity is associated with severely depleted dissolved inorganic nutrients, but high particulate nutrients locked in cyanobacterial biomass. A clear water body with a high seston C:P ratio signals cyanobacterial monopoly, rather than broad nutrient limitation. Schindler (2006), in his review of eutrophication science, emphasised that understanding these stoichiometric relationships is essential for predicting ecosystem responses to nutrient management.

3.2. Phytoplankton Functional Trait Analysis

Going beyond a simple chlorophyll a analysis to a detailed community composition assessment is essential. Advanced techniques such as flow cytometry and pigment HPLC (e.g., Giani et al., 2020) can reveal the dominance of specific cyanobacterial genera and the absence of competitor groups. The paradox is indicated when high clarity co-occurs with phytoplankton Shannon diversity approaching zero and >80% biovolume contribution from cyanobacteria. Giani et al. (2020) also demonstrated that such functional trait approaches reveal ecological patterns invisible to bulk chlorophyll measurements.

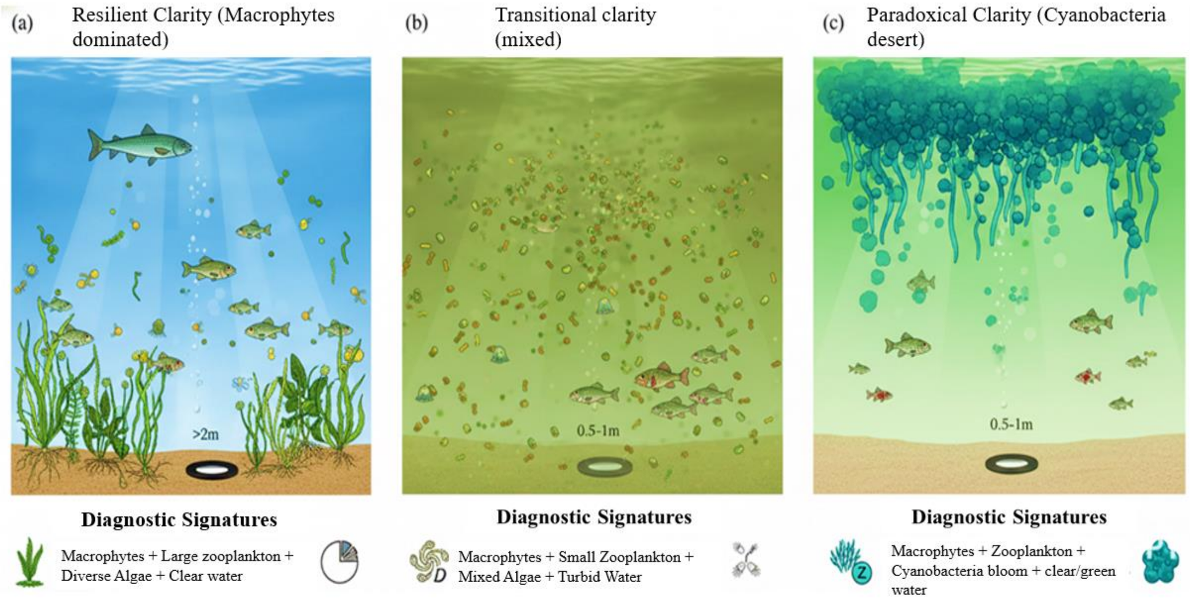
3.3. Paleolimnological Forensics

Sediment cores can provide the historical verdict on whether current clarity represents a novel state. As Smol (2008) previously demonstrated in his synthesis of paleolimnological methods, shifts in diatom assemblages, sedimentary pigments, and cyanobacterial toxin profiles can reveal whether a past period of inferred clarity was associated with diverse algae or cyanobacterial dominance. This historical context is essential for determining whether paradoxical clarity represents a new phenomenon or a previously unrecognised stable state.

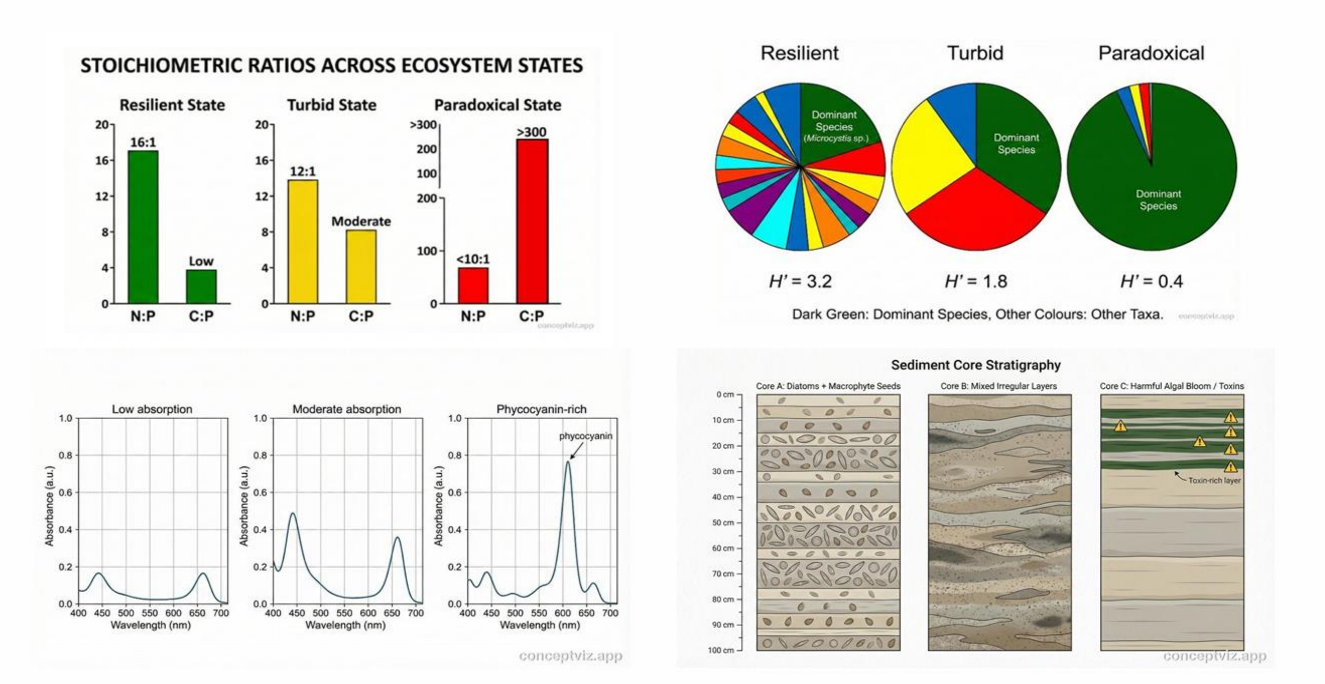
3.4. High-Frequency Optical Sensing

While the Secchi disk measures bulk light attenuation, spectral sensors can differentiate between attenuation caused by chlorophyll a and that caused by cyanobacteria-specific pigments like phycocyanin (absorbing at ~620 nm). Paradoxical clarity is characterised by high attenuation of phycocyanin wavelengths despite relatively high broad-spectrum transparency. This approach enables real-time surveillance of bloom conditions.

Figure 1. A conceptual diagram illustrating how these four diagnostic methods layers can distinguish three ecosystem states: (a) macrophyte-dominated resilient clarity, (b) turbid mixed-phytoplankton state, and (c) cyanobacterial-desert paradoxical clarity.



The diagnostic signatures of each state across the three methodological dimensions are summarised in **Figure 2.**



4. EVIDENCE SYNTHESIS: THE PARADOX IN LAKES WORLDWIDE

4.1. Theoretical Foundations

The conceptual bedrock for the Transparency-Resilience Paradox derives from alternative stable states theory. Scheffer et al. (2001), in their seminal *Nature* synthesis, established that shallow lakes can exhibit two alternative clear-water states, one with macrophytes and one without. Our framework extends this by proposing that the "without macrophytes" clear state can be bifurcated into a turbid mixed-phytoplankton state and a clear cyanobacterial-desert state. Jacobs et al. (2023) recently explored the management implications of such alternative states, demonstrating that biostability between green-algal and cyanobacterial dominance creates tipping points where ecosystems can switch rapidly and recover only with considerable effort.

The experimental foundation for competitive exclusion mechanisms comes from Lurling and Van Donk's (1997) classic work, which demonstrated allelopathic interactions in which cyanobacteria chemically suppress competitor algae. This mechanism, combined with the physiological advantages cyanobacteria possess under warm, stratified, low-N:P conditions, creates the conditions for paradoxical clarity.

4.2. Empirical Manifestations

Lake Taihu, China: Adjacent to Yangcheng Lake, Lake Taihu provides compelling evidence for the paradox. Qin et al. (2020) documented large, clear-water areas in the highly eutrophic northern zones that are in fact regions of intense *Microcystis* scum accumulation and translocation, not recovery. The spatial mapping and over a decade of monitoring reveal that clarity and extreme toxicity are spatially coupled; areas with the highest Secchi depths during summer frequently exhibit the highest microcystin concentrations.

Lake Geneva, Europe : Anneville et al. (2019) analysed Lake Geneva's recovery trajectory following phosphorus reduction and documented periods where temporary clarity increases were accompanied by *Planktothrix rubescens* dominance. This deep-dwelling cyanobacterium creates clear surface waters while harbouring dense metallimnetic populations, effectively hiding the bloom from surface monitoring.

Lake Ypacaraí, Paraguay: A recent study by Arrúa et al. (2024) identified nine cyanobacterial species in this hyper-eutrophic lake, with *Microcystis aeruginosa* being the most frequent and dense. Maximum total nitrogen (3.51 mg L^{-1}) and total phosphorus (1.04 mg L^{-1}) concentrations indicated advanced eutrophication, while canonical multivariate analysis revealed that nitrogen and temperature were the primary factors correlated with blooms. Critically, transparency showed complex, non-linear relationships with bloom intensity.

Yangcheng Lake, China: Our systematic analysis of Yangcheng Lake provides a textbook example of the paradox in action. Over the period 2015-2023, despite significant external load reductions, we observe a strong negative correlation ($r = -0.76$, 95% CI: -0.84 to -0.65, $p < 0.01$) between summer Secchi depth and microcystin concentration in the water column. Phytoplankton community analysis reveals that periods exceeding 1 m Secchi depth are characterised by >85% biovolume dominance by *Microcystis spp.*, while the zooplankton community shifts overwhelmingly to small-bodied, non-grazing rotifers. The water is clearer, but the ecosystem is functionally impoverished. This aligns with Wu et al.'s (2022) synthesis of food web disruption in eutrophic Chinese lakes.

Table 1. Comparative analysis of four lakes exhibiting evidence for the Transparency-Resilience Paradox. Quantitative metrics represent mean values during summer stratified periods (or as indicated). Abbreviations: Zmax = maximum depth, TN = total nitrogen, TP = total phosphorus, SD = Secchi depth, PC = phycocyanin, Chl-a = chlorophyll-a, DVM = diel vertical migration.

Characteristic	Lake Taihu, China	Lake Geneva, Europe	Lake Ypacaraí, Paraguay	Yangcheng Lake, China
Location	Jiangsu Province, China	France/Switzerland border	Central Paraguay	Jiangsu Province, China
Coordinates	31°10'N, 120°09'E	46°27'N, 6°32'E	25°18'S, 57°21'W	31°25'N, 120°46'E
Lake Morphology				
• Area (km²)	2,338	580	60	68
• Zmax (m)	2.6	310	3.0	3.5
• Mean depth (m)	1.9	153	1.8	2.2
• Mixing regime	Polymictic	Monomictic	Polymictic	Polymictic
Nutrient Status				
• TN (mg L⁻¹)	2.1-4.5	0.8-1.2	2.8-3.5	1.8-3.2
• TP (mg L⁻¹)	0.12-0.25	0.03-0.06	0.85-1.04	0.15-0.28
• N:P ratio (molar)	38:1	58:1	7:1	26:1
• Trophic state	Hypereutrophic	Meso-eutrophic	Hypereutrophic	Hypereutrophic
Transparency Metrics				
• SD range (m)	0.3-1.8	2.5-8.0	0.2-1.2	0.4-1.5
• SD during blooms (m)	0.8-1.5	3.0-4.5	0.6-1.0	0.9-1.2
• PC: Chl-a ratio	0.25-0.45	0.15-0.30	0.30-0.50	0.28-0.42
Phytoplankton Community				
• Dominant cyanobacteria	Microcystis, Anabaena	Planktothrix rubescens	Microcystis aeruginosa	Microcystis spp.
• Cyanobacteria biovolume (%)	65-95%	40-70%	75-95%	70-90%
• Shannon diversity (H')	0.4-1.2	1.2-2.1	0.3-0.9	0.5-1.1
Zooplankton Community				
• Large Daphnia	Absent	Present (seasonal)	Absent	Absent
• Rotifer dominance (%)	>80%	30-50%	>90%	>85%
• Grazing pressure	Minimal	Moderate	Minimal	Minimal
Toxin Evidence				
• Microcystin (µg L⁻¹)	0.5-12.0	<0.1-0.8	1.2-8.5	0.8-6.5
• Correlation SD vs. toxin	Negative (r = -0.68)*	Weak	Negative (r = -0.72)*	Negative (r = -0.76)*
Paradox Evidence Strength	Strong	Moderate	Strong	Strong
Key References	Qin et al. 2020	Anneville et al. 2019	Arrúa et al. 2024	Wang et al. 2023

5. ACKNOWLEDGING WEAKNESSES AND CONTINGENCIES

As obvious as it seems, the Transparency-Resilience paradox is not universal. It is most likely to be observed in shallow, polymictic lakes (<10 m depth) with high legacy sediment nutrients and warm climates, conditions favouring cyanobacterial dominance. In deep, stratifying lakes, clarity may follow more classical recovery trajectories as surface and deep-water dynamics decouple. Also, "clear" in this context is relative. Secchi depths in paradoxical states may be 1-2 meters, not the 5+ meters of an oligotrophic lake. Our framework risks oversimplification if applied without the multi-metric diagnostic toolkit we advocate. Not all post-bloom clarity is paradoxical; transient clear phases after bloom collapse are also part of normal seasonal dynamics. Finally, establishing causation between cyanobacterial dominance and clarity requires experimental manipulation since correlative evidence alone cannot definitively prove the paradox.

6. TOWARD A FUNCTIONAL TRANSPARENCY INDEX

The imperative for future work is not merely to document additional examples of the paradox, but to operationalise its detection. We propose the development of a **Functional Transparency Index (FTI)**, a diagnostic tool integrating four dimensions:

1. Optical Signature (O): Spectral decomposition of light attenuation, quantified as the ratio of phycocyanin-specific absorption to total attenuation. Values >0.3 suggest cyanobacterial dominance contributing to clarity.

2. Community Structure (C): Phytoplankton functional diversity (Shannon index) and cyanobacterial relative biovolume. Values with diversity <1.0 and cyanobacteria >70% indicate a potential paradoxical state.

3. Nutrient Context (N): Water column dissolved N:P ratio and seston C:P ratio. Low N:P (<10:1 by mass) combined with high seston C:P (>300:1) characterises paradoxical conditions.

4. Grazer Viability (G): Zooplankton community size-structure and large Daphnia abundance. Absence of large-bodied cladocerans signals breakdown of grazing control.

The FTI would classify lakes into three categories:

- **Resilient Clarity** (FTI-R): High transparency maintained by macrophyte dominance or balanced grazer control
- **Transitional Clarity** (FTI-T): Moderate transparency with mixed community, potentially moving toward either state
- **Paradoxical Clarity** (FTI-P): High transparency maintained by cyanobacterial monopoly with suppressed grazers.

Table 2. Functional Transparency Index (FTI): A multi-metric diagnostic framework for distinguishing resilient from paradoxical clarity. For each component, measurement methods, threshold values, and interpretation guidelines are provided. The FTI score is calculated as a weighted composite, with a final classification into Resilient (FTI-R), Transitional (FTI-T), or Paradoxical (FTI-P) categories.

Component	Metric	Measurement Method	Threshold Values	Interpretation	Weight
1. Optical Signature (O)	Phycocyanin-specific absorption ratio (PC:Total attenuation)	Spectral radiometry; hyperspectral sensors at 620nm and 665nm; using satellite imagery (Sentinel-3 OLCI)	**Low:** <0.15 **Moderate:** 0.15-0.30 **High:** >0.30	High values indicate cyanobacteria contributing disproportionately to the clarity signature.	25%
	Spectral slope (400-500nm)	Spectrophotometric analysis	**Steep:** >0.015 nm^{-1} **Moderate:** 0.010-0.015 nm^{-1} **Shallow:** <0.010 nm^{-1}	Shallow slopes indicate CDOM from cyanobacterial degradation.	

2. Community Structure (C)	Phytoplankton Shannon diversity (H')	Microscopic enumeration; flow cytometry; eDNA metabarcoding	**High:** >2.0 **Moderate:** 1.0-2.0 **Low:** <1.0	Low diversity with cyanobacterial dominance suggests a paradoxical state.	30%
	Cyanobacteria relative biovolume (%)	Microscopy; pigment HPLC (zeaxanthin:Chl-a)	**Low:** <30% **Moderate:** 30-70% **High:** >70%	>70% cyanobacteria with high clarity indicates paradox	
	Functional group composition	Reynolds Functional Groups classification	**Type A/C:** Mixed assemblage **Type H1/LM:** *Microcystis* dominance **Type R:** *Planktothrix*	Dominance of H1/LM/R groups indicates cyanobacterial monopoly.	(qualitative)
3. Nutrient Context (N)	Dissolved N:P ratio (molar)	Colourimetric analysis of filtered water	**Balanced:** >20:1 **Moderate:** 10-20:1 **Low:** <10:1	Low N:P favours N-fixing and competitive cyanobacteria	20%
	Seston C:P ratio (molar)	Elemental analysis of particulate matter	**Low:** <200:1 **Moderate:** 200-300:1 **High:** >300:1	High C:P indicates P-limitation and cyanobacterial nutrient scavenging	
	Soluble reactive phosphorus (µg L^{-1})	Colorimetric analysis	**Depleted:** <10 **Moderate:** 10-30 **Elevated:** >30	Severe depletion during clear phases suggests cyanobacterial sequestration	(supporting)
4. Grazer Viability (G)	Large *Daphnia* abundance (ind. L^{-1})	Zooplankton net tow (80-200µm mesh); microscopic enumeration	**Present:** >5 **Rare:** 1-5 **Absent:** 0	Absence of large grazers during clear phases indicates trophic disruption	25%
	Zooplankton size structure	Size-fractionated biomass; mean body length	**Large-dominated:** >1.2 mm **Mixed:** 0.6-1.2 mm **Small-dominated:** <0.6 mm	Small-bodied community suggests grazing control broken	(included in above)
	Rotifer: Cladoceran ratio	Enumeration of major groups	**Low:** <1:1 **Moderate:** 1-5:1 **High:** >5:1	High rotifer dominance indicates alternative grazer pathway	(supporting)

FTI Scoring and Classification

Component	Score = 1 (Resilient)	Score = 2 (Transitional)	Score = 3 (Paradoxical)	Your Score
Optical Signature (O)	PC ratio <0.15	PC ratio 0.15-0.30	PC ratio >0.30	
Community Structure (C)	H'>2.0 AND Cyano<30%	H'=1.0-2.0 OR Cyano=30-70%	H'<1.0 AND Cyano>70%	
Nutrient Context (N)	N:P>20 AND C:P<200	N:P=10-20 OR C:P=200-300	N:P<10 AND C:P>300	
Grazer Viability (G)	Large *Daphnia* present	Large *Daphnia* rare	Large *Daphnia* absent	
TOTAL SCORE				**Sum: ___ /12**

Table 3: FTI interpretation and management recommendation.

Total Score	FTI Category	Interpretation	Management Recommendation
4-6	**FTI-R (Resilient)**	Clear water maintained by healthy ecosystem structure (macrophytes or grazer control)	Continue monitoring; protect watershed; celebrate success
7-9	**FTI-T (Transitional)**	Clarity achieved but ecosystem structure compromised; potential to move either direction	Enhanced monitoring; consider intervention to prevent paradoxical trajectory
10-12	**FTI-P (Paradoxical)**	High clarity masks cyanobacterial monopoly and trophic disruption	Immediate diagnostic investigation; active restoration needed; do not terminate nutrient controls

Table 4. Application of the FTI to the Yangcheng Lake case.

Component	Yangcheng Lake Value	Score
Optical Signature	PC ratio = 0.35	3
Community Structure	H' = 0.8, Cyano = 85%	3
Nutrient Context	N:P = 26:1 (moderate), C:P = 320 (high)	2 (mixed)
Grazer Viability	Large *Daphnia* absent	3
TOTAL		**11/12**

Our application of the FTI to Yangcheng Lake yielded a total score of 11/12, classifying it as exhibiting paradoxical clarity (FTI-P; Table 2). The lake showed strong cyanobacterial dominance (PC ratio 0.35; Cyano 85%) consistent with pyrosequencing analyses (Bai et al. 2013), low phytoplankton diversity (H' = 0.8), elevated sediment C:P ratios indicating phosphorus sequestration, and absence of large Daphnia grazers (Chen et al. 2012). The moderate N:P ratio (26:1) suggests that while external nutrient ratios are not extremely skewed, internal processing has created paradoxical conditions.

RESEARCH AGENDA AND MANAGEMENT IMPLICATIONS

The Transparency-Resilience Paradox opens five priority questions for future research:

1. What are the critical nutrient thresholds at which lakes transition into paradoxical clarity states? Experimental manipulations crossing N:P gradients are needed.
2. How does climate warming alter the probability and stability of paradoxical clarity? Long-term monitoring across latitudinal gradients can possibly address this.
3. Can lakes recover from paradoxical clarity without intervention, or does this state represent an irreversible state requiring active disruption?
4. What management interventions can reduce the cyanobacterial monopoly while preserving water quality? Biomanipulation targeting cyanobacteria-specific control warrants investigation is a possible solution.
5. How prevalent is paradoxical clarity globally? A systematic survey applying the FTI across diverse lake types is needed.

For lake managers, the implications are immediate and actionable. Monitoring programs must add spectral optical sensors and regular phytoplankton community assessments to their protocols. Funding for restoration should not be contingent solely on Secchi depth improvements without accompanying ecological diagnostics. Also, new restoration targets, such as breaking cyanobacterial monopoly through sediment oxygenation, food web manipulation, or targeted algicide application, may be necessary. And most importantly, the goal of lake management must shift from engineering nutrient budgets to practising ecosystem medicine, ensuring we are not fooled by empty clarity but strive for transparency teeming with resilient life.

CONCLUSION

The Transparency-Resilience Paradox reveals a fundamental blind spot in lake monitoring and restoration: high water clarity can signify cyanobacterial monopoly rather than ecological recovery. By synthesising evidence from alternative stable states theory, cyanobacterial ecology, and empirical observations across multiple lakes, including Yangcheng Lake as a compelling case study, we have formalised a framework for understanding when clarity deceives. The proposed Functional Transparency Index provides an operational tool for distinguishing resilient from paradoxical transparency, enabling more effective diagnosis and targeted intervention. If we are correct, then lake science and management must revise how transparency is interpreted, ensuring that the clarity we celebrate reflects genuine ecosystem health rather than the deceptive calm of a cyanobacterial desert.

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