Clarifying the trophic state concept to advance macroscale freshwater science and management

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Abstract

For over a century, ecologists have used the concept of trophic state (TS) to characterize an aquatic ecosystem's biological productivity. However, multiple TS classification schemes, each relying on a variety of measurable parameters as proxies for productivity, have emerged to meet use-specific needs. Frequently, chlorophyll a, phosphorus, and Secchi depth are used to classify TS based on autotrophic production, whereas phosphorus, dissolved organic carbon, and true color are used to classify TS based on both autotrophic and heterotrophic production. Both classification approaches aim to characterize an ecosystem's function broadly, but with varying degrees of autotrophic and heterotrophic processes considered in those characterizations. Moreover, differing classification schemes can create inconsistent interpretations of ecosystem integrity. For example, the U.S. Clean Water Act focuses exclusively on algal threats to water quality, framed in terms of eutrophication in response to nutrient loading. This usage lacks information about non-algal threats to water quality, such as dystrophication in response to dissolved organic carbon loading. Consequently, the TS classification schemes used to identify eutrophication and dystrophication may refer to ecosystems similarly (e.g., oligotrophic and eutrophic), yet these categories are derived from different proxies. These inconsistencies in TS classification schemes may be compounded when interdisciplinary projects employ varied TS frameworks. Even with these shortcomings, TS can still be used to distill information on complex aquatic ecosystem function into a set of generalizable expectations. The usefulness of distilling complex information into a TS index is substantial such that usage inconsistencies should be explicitly addressed and resolved. To emphasize the consequences of diverging TS classification schemes, we present three case studies for which an improved understanding of the TS concept advances freshwater research, management efforts, and interdisciplinary collaboration. To increase clarity in TS, the aquatic sciences could benefit from including information about the proxy variables, ecosystem type, as well as the spatiotemporal domains used to classify TS. As the field of aquatic sciences expands and climatic irregularity increases, we highlight the importance of re-evaluating fundamental concepts, such as TS, to ensure their compatibility with evolving science.

Introduction

Trophic state (TS) is a fundamental concept in the aquatic sciences that describes an ecosystem's characteristic biological productivity. Operationally, productivity can be challenging to estimate because spatial and temporal heterogeneities within ecosystems can substantially influence waterbody-wide productivity. Therefore, several proxies and formulations for classifying TS have emerged since the beginning of the 20th century (Box 1; Table 1). Nutrients, chlorophyll, and Secchi disk depth are common proxy variables for evaluating TS, whereas alternative formulations rely on true color, organic carbon, biomass estimates, and even microbial community composition (Table 1). Depending on data availability, TS may be expressed as a discrete group, a continuous index, or even a probability of being assigned to a discrete group, where each formulation communicates information about uncertainty in the classification (Nojvan et al. 2019). The proxies measured, and consequent classifications of TS, can also differ between ecosystem types and regions (Table 1). In lakes and reservoirs, Hutchinson (1957) focused on hypolimnetic oxygen depletion rates. Lindeman (1942) and Horne and Goldman (1983) focused on TS as phases of a waterbody's ontogeny. Carlson (1977) focused solely on autochthony (i.e., primary production), whereas Naumann (1917), Thienemann (1921), and Wetzel (2001) focused on both autochthony and allochthony. In rivers and streams, the TS concept has likewise focused on productivity as a function of autochthony and allochthony, but more specifically, the ratio of photosynthesis-to-respiration at the scale of river reach (Odum 1956, Dodds and Cole 2007). Dodds (2006) classified TS on the probability of observing a given phosphorus, nitrogen, or chlorophyll concentration in a river reach, where benthic and pelagic algae can be independently considered.

Regardless of the exact TS classification scheme, scientists, managers, and the public rely upon these simplified discretizations to characterize complex ecosystem processes, thereby allowing for scientific progress when detailed data are lacking (Kraemer 2020). In this sense, TS is a fundamental ecosystem characteristic that can be inferred from basic water quality data. Such simplifications are important for generalizing our understanding of ecosystem function, when often only discrete observations of ecosystems are available (Palmer and Febria 2012). Wetzel (2001) demonstrates this point by using TS to make broad predictions about how and why water quality constituent depth profiles, such as dissolved oxygen and pH, differ between stratified oligotrophic and eutrophic lakes (Figure 1). Although these generalities may not always apply to every ecosystem, the TS concept is a useful, conceptual framework that can predict water quality conditions when direct measurements are sparse. For example, depth profiles are uncommon relative to grab samples from surface waters, yet consistent depth profile patterns for given trophic states allow us to infer profile dynamics from limited depth-profile data sets (Figure 1). These uses of trophic state have even extended to policy, where the language of TS is included in Sections 106 and 314 of the U.S. Clean Water Act (33 U.S.C. 1252 et seq.) for the "identification and classification [of lakes] according to eutrophic condition," and eutrophic conditions can trigger "procedures, processes, and methods…to control sources of pollution and…to restore [water quality]." In each of these instances, proxy variables are related to a trophic state classification, which is then used to predict ecosystem productivity, function, and integrity.

Over the last half century, the proxies used to classify TS have become synonymous with productivity, potentially leading to TS being, as Hutchinson (1957) warned, "[a] terminology that is so widely and often so inaccurately employed in discussing productivity." For example, oligotrophic lakes and rivers are associated with low biological productivity, which is associated with low phosphorus and nitrogen concentrations. Consequently, nutrient concentrations become the defining feature of an ecosystem's TS, rather than the biological productivity itself. This conceptual merger of biological productivity with its measured proxies can be beneficial for projecting ecological information across landscapes. However, it can also lead to confusion, where, for example, reference to a TS category may actually translate to value ranges of the proxy variable. In these instances, the same word in reference to a given TS classification can create miscommunication, where multiple individuals may refer to the same TS classification but through the lenses of different proxies. Confusion can be further compounded when different classification schemes suggest diverging expectations for ecosystem function, such as characteristic oxyclines across various TS classification schemes throughout the contiguous U.S. (Figure 1). Regardless of how “oligotrophic” is defined, oxycline and thermocline profiles produce anticipated orthograde curves. In contrast, eutrophic profiles are visually similar, yet the most distinctive clinograde curves are observed in dystrophic and mixotrophic lakes (Figure 1), systems that are less well studied than eutrophic lakes (Leech et al. 2018). These incongruences between expected ecosystem functioning call into question the extent to which autotrophic-focused metrics, such as Trophic State Index (TSI), might discourage consideration of heterotrophic processes that likewise influence ecosystem patterns and processes. In this vein, clarifying language in TS classification has potential consequences for how both water quality conditions and ecosystem function are perceived.

Without an epistemological evolution, the fields of aquatic ecology and water quality management run the risk of developing divergent understandings of ecosystem function. Considering the pace and magnitude of climatic uncertainty, clarifying existing TS categories can allow for more standardized approaches to understanding the structure and function of aquatic ecosystems over past and future decades. To illustrate the usefulness of a clear and consistent, yet dynamic, conceptual framework for advancing the aquatic sciences, we detail three instances where clarifying the TS concept can guide aquatic research and management. In each case study, we highlight the clarity gained by combining emerging scientific themes, data streams, and technologies with the TS concept. Moreover, we demonstrate that conveying (1) the proxy variables and classification scheme employed, (2) the spatial and temporal domains of the proxy data, and (3) the ecosystem type considered are three concrete steps towards clarifying the TS concept. Communicating these pieces of information is an initial step in ensuring scientific reproducibility, thereby furthering the aquatic sciences, water resource management, and interdisciplinary collaboration.

Clarifying the TS concept can enhance our understanding of aquatic ecosystems across seasons and biomes

Especially in northern, temperate regions, the rise of under-ice studies has expanded our understanding of biological productivity beyond open water seasons (Hampton et al. 2015, 2017). Oligotrophic lakes, such as Lake Baikal (Kozhova and Izmest'eva 1998), can experience multi-week, under-ice algal blooms that attain biomass comparable to eutrophic systems (Popovskaya 2000). Conversely, eutrophic lakes may experience decreased primary production when light-blocking snow is located on ice or as ice becomes opaque (Garcia et al. 2019, Kivilä et al. 2023), which can drive wintertime chlorophyll concentrations toward levels typically observed in oligotrophic lakes (Kalinowska and Karpowicz 2020). In both cases, TS classifications based on samples collected under-ice may differ from those based on samples collected during open water conditions, which can alter interpretations of the dominant processes in the waterbody. Given surface waters' rapid warming (O'Reilly et al. 2015, Huang et al. 2024) and declining ice cover worldwide (Sharma et al. 2019), an emphasis on how wintertime dynamics influence TS classifications can help refine our expectations of ecosystem change. For example, diminishing ice cover over coming decades could reduce algal productivity by both hindering ice-obligate algal communities and suppressing growth of open-water water taxa, even though psychrophilic and psychrotolerant blooms can occur (Reinl et al. 2023). Therefore, ice loss may homogenize the anticipated behaviors of eutrophic and oligotrophic water bodies during winter, with both ecosystems being similarly productive during ice-free winters and only diverging in summer. Thus, clarifying the TS concept can present a conceptual framework upon which seasonal investigations of waterbody productivity lead to new hypotheses.

In contrast to temperate ecosystems, tropical aquatic ecosystems have less pronounced seasonal variation in temperature and photosynthetically available radiation but are highly driven by hydrological variation in the dry and wet seasons (Cunha et al. 2021). In this case, TS schemes from temperate lakes are inadequate in tropical lakes. The productivity of Brazilian lakes, for example, is influenced by lake water level, water column stability changes, allochthonous nutrient loading, and turbidity related to dry-wet seasonal shifts (Gagliardi et al. 2019, Cunha et al. 2021, Brighenti et al. 2024). This alternative framing of seasonality based on dry-wet periods rather than cold-warm periods diverges from anticipated conceptual models of how eutrophic and oligotrophic lakes function, such as via the build-up and breakdown of thermoclines and oxyclines (Figure 1). Consequently, these contrasting frameworks for characterizing intra-annual variation in productivity further complicate the comparability of TS assessments made across biomes when using a single classification system.

To clarify the TS concept, the spatial and temporal domains of classifications are especially important. If we assume that TS is based on cyclical degrees of autotrophy and heterotrophy (Wetzel 2001), characterizing TS relative to an annual baseline is necessary. While estimates of TS solely based on summertime productivity in temperate lakes can be useful for water quality management, such estimates cannot always be extrapolated across seasons or ecosystems. As most TS assessments are currently based on summertime productivity, our current understanding of characteristic productivity is likely biased towards summertime conditions and temperate regions. Yet, the growth of our understanding of wintertime and tropical productivity highlights how important seasonality can be for holistically understanding and inferring waterbody productivity and function. As the field of aquatic sciences continues to expand into seasons and geographic locations that are less well represented in the literature (Mejia et al. 2018, Barbosa et al. 2023, Rogers et al. 2023), we can build on decades of research using the TS concept to create opportunities for scaling the TS concept beyond the specific periods and biomes used to lay its foundations. Thus, we could further assess how aquatic ecosystems function, how this functionality varies regionally and seasonally, and how to contextualize regional ecosystems' functioning within global patterns.

Clarifying the TS concept can inform freshwater management across aquatic ecosystems

For management purposes, the language of TS has been used to classify water quality characteristics to represent ecosystem functions and services. For example, eutrophic conditions may be desirable for increasing fish production (Rast and Thornton 1996). Conversely, hypereutrophic conditions may promote widespread anoxia, which can lead to fish kills. Even though TS is classified via a subset of proxy variables, the TS classification can imply a suite of generalizable expectations for ecosystem function and integrity. These expectations may not empower precise characterization across ecosystems or prescribe specific actions but can be used for flagging ecosystems for targeted investigation, thereby aiding managers to prioritize ecosystems for restoration efforts. When applied across landscapes and geopolitical boundaries, TS categories can aid managers as a high-level comparative and contextual tool to communicate ecosystem integrity without the need for relying on specific water quality parameters.

Because various TS classification schemes rely on different proxy variables (Table 1), categories detectable by each scheme can narrow the focus of how water quality is perceived and communicated. For example, managers may use Secchi disk depth to calculate TSI (Carlson 1977), and then use TSI to identify waterbodies that are hypereutrophic and at greater risk of cyanobacterial blooms. However, Secchi disk depth can also indicate high concentrations of suspended inorganic sediments or highly colored waters (Cunha et al 2021). Such highly colored dystrophic lakes are not necessarily at a similar risk of cyanobacterial blooms and present a different suite of management implications despite having overlapping Secchi disk depth ranges with eutrophic lakes. This incongruence can be consequential for water quality estimates because mixotrophic lakes, as defined by the Nutrient Color Paradigm (NCP), also have elevated risk of cyanobacterial blooms (Leech et al. 2018). Continental-scale data demonstrate that Secchi disk depth can fail to differentiate eutrophic, mixotrophic, and dystrophic lakes (Figure 2).

Translation across TS schemes can be challenging. For example, TSI-derived classifications do not identify dystrophic and mixotrophic states, unlike NCP, creating different interpretations of TS class occurrences at landscape scales (Figure 3). The Upper Midwest and Northern Appalachians (U.S.; Omernik 1987) are two ecoregions that highlight extremes in TS classification differences (Figure 3). Among TSI-derived metrics using total phosphorus, Secchi disk depth, chlorophyll, rotifer abundance, and crustacean zooplankton abundance, 41% and 35.4% of lakes in the Upper Midwest and Northern Appalachians would be classified as eutrophic, respectively, whereas NCP suggests 10.4% and 3.7% of lakes as eutrophic, respectively. Conversely, NCP suggests that 51.5% and 58.3% of lakes in the Upper Midwest and Northern Appalachians would be classified as dystrophic or mixotrophic, underscoring both the prevalence of high dissolved organic carbon in these ecosystems and the potential for management to overlook a widespread water quality concern (Solomon et al. 2015).

Even when TS classification schemes are conceptually comparable, irregularities in sample collection may limit the extent to which TS classifications are interchangeable. In particular, samples necessary for linking classification schemes may not be co-located or collected contemporaneously. For example, TSI and Ecological State (ES) can rely upon total phosphorus, Secchi disk depth, and chlorophyll measurements, measurements that may be more commonly collected relative to the true color or dissolved organic matter/carbon (DOM, DOC) measurements needed for the NCP (Box 1). TSI and ES, then, might allow for finer-scale assessments, but less frequent true color or DOM data collection may be too coarse for comparative analyses. Given potential problems with translating across TS classification schemes, clarifying the proxy data used to assign a TS classification ensures the interpretability of TS classifications. Further, ensuring clear and consistent proxy data across classification schemes will improve our ability to quantify expected variability in TS over space and time, thereby optimizing successive management decisions.

Clarifying the TS concept can benefit interdisciplinary collaboration

Progress in the aquatic sciences has benefited from a suite of disciplines, and other disciplines reciprocally benefit from the aquatic sciences. Scientists and managers can maximize these benefits by providing greater consistency and clarity to avoid confusion in their applications across disciplines. In particular, a limitation for field-based methods is the capacity to upscale *in situ* observations across landscapes due to limited time, funding, and personnel. Emerging technologies and tools, such as remote sensing and machine learning techniques, have enabled progress in extending localized insights across continental and interannual scales. Although these techniques have historically focused on understanding structural components of aquatic ecosystems (e.g., mixing), they are beginning to address water quality and ecosystem functional change (Calamita et al. 2024). Consequently, these approaches may provide the most tractable paths for understanding macroscale water quality patterns, if grounded in clear and sound limnology that guides interpretation.

Remote sensing is a pertinent example of a discipline that has implemented the TS concept to understand aquatic ecosystem change from local-to-global and monthly-to-decadal scales. For example, Wang et al. (2018), Gilarranz et al. (2022), and Sillen et al. (2024) quantified TSI based on chlorophyll a (TSI_{CHLA}) and its associated variability from remotely sensed surface reflectance for hundreds of lakes worldwide. Werther et al. (2021) and Meyer et al. (2024) also developed models to classify TS from remote sensing surface reflectance across broad spatial scales, but Meyer et al. (2024) used the NCP to classify TS whereas Werther et al. (2021) used TSI_{CHLA}. Together, the range and number of remote sensing studies aimed at evaluating ecosystem productivity indicates the incorporation of the TS concept into remote sensing-based approaches, yet few studies consider how different TS classification schemes may hinder communication and comparison of results.

This lack of clarity could lead to diverging perceptions of ecosystem integrity across scales that are otherwise not feasible to manually sample, thereby undermining the strength of remote sensing's capacity to sample large spatial scales. For example, *in situ* data may indicate oligotrophic status for both a river and a lake, but the characteristics of TS in those ecosystem types are different. In lakes, oligotrophic conditions are associated with low pelagic productivity in the water column, resulting in high reflectance values in the blue portion of the spectrum and lower values in the green portion. In rivers, oligotrophic conditions often are associated with high benthic productivity, resulting in high reflectance values in the green portion of the spectrum and lower values in the blue portion. Even within a given ecosystem type, varying TS formulations may mask water quality change. For example, dominant wavelength is a powerful remotely sensed metric that can suggest autotrophic productivity in lakes (Topp et al. 2021a, 2021b, Yang et al. 2022, Sillen et al. 2024) and rivers (Gardner et al. 2021). However, dominant wavelength can fail to capture organic matter concentrations in lakes, making dystrophic and mixotrophic lakes indistinguishable from oligotrophic and eutrophic lakes, respectively (Figure 4). Thus, insights made from dominant wavelength may be limited to assessing remotely sensed TSI-based classifications as opposed to NCP-based classifications. Because remote sensing of inland water quality has historically had weak connections with limnology, hydrology, and ecology (Bukata 2013, Topp et al. 2020), there is potential for remote sensing science to obfuscate distinct ecological states, especially when both states may be referred to by same word (i.e., "eutrophic"). If limnological expertise is not included in the modeling framework or considered when applying models across ecosystems, remotely sensed water quality observations may offer spurious conclusions about water quality distribution and trends.

Beyond remote sensing, the proliferation of data collection methods in aquatic ecosystems has significantly expanded, including automated buoys, platforms, and *in situ* sensors. This wealth of information from multiple sources has enabled the creation of diverse machine learning methods for better understanding complex aquatic ecosystem dynamics. However, in instances where TS classification schemes vary across training datasets or only focus on specific dimensions of water quality, machine learning methods may not robustly form generalizable models capable of classifying diverse aquatic ecosystems. When limnological knowledge is integrated into machine learning models, such as in knowledge-guided machine learning (Appling et al. 2022, Karpatne et al. 2024), consistent and well documented classification schemes can aid in reflecting anticipated ecosystem dynamics. For example, Hanson et al. (2020) used knowledge-guided machine learning to model phosphorus dynamics in a lake over 20 years, where the integrated model replicated a downward trend in lake TP concentrations and, by extension, reduction in eutrophy. Regardless of the exact implementation, consistent and clear communication of TS classifications schemes used to develop training datasets would maximize the predictive accuracy of these data-driven models.

New information gathered via emerging technologies may deepen our understanding of aquatic ecosystem properties across scales but will also demand periodic re-evaluation of how TS classification is operationalized. Remote sensing and data-driven modeling can expand spatial and temporal domains that may be impractical to manually sample. Clarification of the TS concept can enable researchers using remote sensing and data-intensive modeling to take advantage of the rich history of limnological principles (Topp et al. 2020). Effectively integrating limnology and technical aspects of remote sensing and machine learning will require investment and cross-pollination of communities. This blending of communities will need to overcome disciplinary barriers and norms, including jargon, concepts, and even data formats. Many grassroot efforts, such as the Community for Data Science and Open Science in the Aquatic Sciences and "Hacking Limnology" Workshop Series (Meyer and Zwart 2020, Meyer et al. 2021), are breaking down these divides. Given the rapid growth of remote sensing and machine learning techniques for water quality assessment, further clarification of TS can benefit the increasing interdisciplinarity of limnology by disentangling concepts for non-limnologists, thereby enabling broader uptake and insights.

Moving Forward: Clarifying the TS concept to advance the freshwater sciences

For many ecologists, TS is often the first conceptual framework for understanding aquatic ecosystems. Similarly, for many policy makers and water managers, TS is often a guiding paradigm to qualitatively evaluate water quality and prioritize ecosystems for restoration (e.g., 33 U.S.C. 1252 et seq.; Carlson 1977). Even though TS may not be as specific or prescriptive as individual ecosystem characteristics, TS provides a generalized conceptual framework to compress complex, interconnected processes into a single metric. TS then becomes a tool to infer ecosystem processes when data may be limited; however, there may be nuanced inconsistencies across applications. We highlight how TS can be a useful conceptual framework for evaluating ecosystem function, yet we demonstrate a clear need to re-evaluate and expand this conceptual framework to include less well sampled ecosystems, water quality parameters, biomes, and seasons. Without this clarification, miscommunication amongst limnologists and collaborators has potential to offer spurious conclusions of water quality and ecosystem change and to limit scientific reproducibility.

Given divergent TS schemes and end-user needs, convergent understanding of TS will require at least three pieces of metadata: (1) the ecosystem type, (2) the proxy data, and (3) the spatial and temporal domains of the proxy data. Each component provides detail on how TS can be understood in a given ecosystem. The ecosystem type details the dominant processes at play within an ecosystem. The proxies used for a classification scheme detail how a TS classification is determined, its comparability to other ecosystems, and the balance of autotrophy and heterotrophy considered. Defining the spatial and temporal domains of the proxy data allows for nuanced understanding of a classification, where inferences can be conveyed based on the temporal scales, geographic regions, and biomes considered. When provided, these metadata could empower robust assertions of landscape level patterns (Figure 3), consistency in usage (Figure 4), and even re-evaluation of core expectations for each TS (Figure 1). In cases when metadata are thoroughly documented, such as for the U.S. Environmental Protection Agency National Lakes Assessment, multiple TS classifications schemes may be applied to more holistically understand implications of divergent definitions across macroscales. Regardless of the level of detail given to each metadata criterion, communicating these pieces of information is an initial step forward in improving clarity among TS concepts.

Ultimately, how the TS concept is implemented will likely stem from the task at hand. In the case of management, TS may be used to characterize water quality, prioritize water bodies for additional investigation, and communicate those water quality characteristics to decision makers. In the case of scientific investigations, varying classification schemes may be applied to fully characterize ecosystems occurring at a particular spatial or temporal scale. As a foundational concept, understanding trophic states expected over macroscales is necessary for a global understanding of freshwater systems that moves beyond that derived from northwestern Europe and northeastern North America (Dodds et al. 2019). A wealth of existing literature has already underscored the importance of including understudied regions (Santoso and Toruan 2020) and seasons (Hampton et al. 2015), and increased data sharing and publication practices will likely expedite the pace and scope of understanding limnological function worldwide (*sensu* Wulder et al. 2012). Global change is pushing ecosystems into novel states, and understanding the characteristics, particularly trophic states, of fresh waters across a range of climate conditions is necessary to predict ecosystem trajectories.

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Author Contribution Statement

MFM conceived the idea for the manuscript and provided leadership throughout its development. MFM, BMK, SEH, AIP, AKF, TVK, RL, IAO, SNT, and LSB, contributed to the design of the manuscript. MFM and BMK wrangled and harmonized data for the manuscript. RMP, BMK, and MFM contributed to table and figure development. All co-authors contributed either to writing or critically editing the manuscript.

Open Research Statement

No new data were generated for this paper. All U.S. Environmental Protection Agency National Lakes Assessment data are available at https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys. All R scripts necessary for producing figures are included in the project's GitLab repository (Meyer et al. 2025).

Conflicts of Interest

The authors declare no conflicts of interest.

Table 1: Aggregation of select Trophic State classification schemes. Note that Nürnberg (1996) likewise contains an extensive list of trophic state classification schemes, a portion of which are included in this list. Additionally, some trophic state indices mentioned in this table contain uncommon metrics, such as sediment bacterial abundance, but have complex formulations that do not necessarily fit the format of this table. For completeness, we added their reference and ranges to this table, but future users are encouraged to refer to the primary literature for those indices' calculations. Abbreviations in "Index Name" are coded as follows: "TSI" – "Trophic State Index", "TS" – "Trophic State", "NCP" – "Nutrient-Color Paradigm", "QI" – "Q Index", "PTSI" – "Phyto-See-Index", "TLI" – "Trophic Level Index", "SBTI" – "Sediment Bacterial Trophic Index". Abbreviations in "Variables Used and Value Limits" are coded as follows: "TP" – "Total Phosphorus in µg/L", "SDD" – "Secchi Disk Depth in m", "Chl" – "Chlorophyll a in µg/L", "Max Chl" – "Maximum Chlorophyll a in µg/L", "Min SDD" – "Minimum Secchi Disk Depth in m", "TN – Total Nitrogen in µg/L", "Color" – "True Color in Platinum Cobalt Units", "CDOC" – "Colored Dissolved Organic Carbon in m^{-1}", "PB" – "Phytoplankton Biomass in mg/L", "PTSI" – "Phyto-See-Index", "SBTI" – " Sediment Bacterial Trophic Index", "AF" – "Anoxic Factor in days per summer", "AHOD" – "Areal Hypolimnetic Oxygen Depletion in $mg \cdot m^{-2} \cdot d^{-1}$", "GPP" – "Gross Primary Production in mmol $O_2 \cdot m^{-2} \cdot d^{-1}$", "R" – "Respiration in mmol $O_2 \cdot m^{-2} \cdot d^{-1}$", " Mean Benthic Chl" – "Mean Benthic Chlorophyll a in mg m^{-2}", "Max Benthic Chl" – "Maximum Benthic Chlorophyll a in mg m^{-2}", " Sestonic Chl" – "Sestonic Chlorophyll a in µg/L", "cDOM" – "Chromophoric Dissolved Organic Matter at a_{254}". TS Groups are coded as follows: "Oligo" – "Oligotrophic", "Meso" – "Mesotrophic", "Eu" – "Eutrophic", "Hypereu" – "Hypereutrophic", "Ultraoligo" – "Ultraoligotrophic", "Supereu" – "Supereutrophic", "Poly" – "Polytrophic", "Ultramicro" – "Ultramicrotrophic", "Micro" – "Microtrophic". Abbreviations in "Data Type" are coded as follows: "Cont" – "Continuous", "Cat" – "Categorical", "Prob" – "Probabilistic". Abbreviations in "Zone Sampled" are coded as follows: "Epi" – "Epilimnion", "Sed" – "Sediment", "Hypo" – "Hypolimnion", "Ben" – "Benthic", "Ses" – "Seston". Numbers in "references" are coded as follows: (1) Carlson (1977), (2) Cunha et al. (2013), (3) Vollenweider and Kerekes (1982), (4) Lamparelli (2004), (5) Sakamoto (1966), (6) Webster et al. (2008), (7) Williamson et al. (1999), (8) Padisák et al. (2006), (9) Mischke (2015), (10) Burns et al. (1999), (11) Wood et al. (2023), (12) Nürnberg (1996), (13) Nürnberg and Shaw (1998), (14) Dodds (2007), (15) Dodds and Cole (2007), (16) Dodds et al. (1998), (17) Gianello et al. (2024), (18) Zhang et al. (2018)

Index Name	**Data Type**	**Geography**	**Season**	**Type**	**Zone Sampled**	**TS Groups**	**Variables Used and Value Limits**	**Reference**
TSI	Cont	Midwest United States	Summer	Lakes	Epi	Oligo	SDD > 4 TP <12 Chl <2.6	(*1*)
						Meso	SDD 2-4 TP 12-24 Chl 2.6-7.3	
						Eu	SDD 0.5-2 TP 24-96 Chl 7.3-56	

						Hypereu	SDD <0.5 TP > 96 Chl >56	
TSI	Cat Cont	Brazil	All	Reservoirs	Epi	Ultraoligo	TP < 15.9 Chl < 2	(*2*)
						Oligo	TP 16-23.8 Chl 2.1-3.9	
						Meso	TP 23.9-36.7 Chl 4-10	
						Eu	TP 36.8-63.7 Chl 4-10	
						Supereu	TP 63.8-77.6 Chl 20.3-27.1	
						Hupereu	TP >77.6 Chl >27.2	
TS	Cat Cont Prob	Worldwide	NA	Lakes and Reservoirs	Epi	Ultraoligo	TP 0-4 Chl < 1 Max Chl < 2.5 SDD >12 Min SDD > 6	(*3*)
						Oligo	TP 4-10 Chl 1-2.5 Max Chl 2.5-8 SDD 6-12 Min SDD 3-6	
						Meso	TP 10-35 Chl 2.5-8 Max Chl 8-25 SDD 3-6 Min SDD 1.5-3	
						Eu	TP 35-100 Chl 8-25 Max Chl 25-75 SDD 1.5-3	

							Min SDD 0.7-1.5	
						Hupereu	TP >100 Chl >25 Max Chl >75 SDD <1.5 Min SDD <0.7	
TS	Cat Cont	Brazil	All	Reservoirs	Epi	Ultraoligo	TP < 8 Chl < 1.2	(*4*)
						Oligo	TP 8.1-19 Chl 1.3-3.2	
						Meso	TP 19.1-52 Chl 3.3-11	
						Eu	TP 52.1-120 Chl 11.1-30.6	
						Supereu	TP 120.1-233 Chl 30.7-69.1	
						Hupereu	TP >233 Chl >69.2	
TS	Cat Cont	Japan	All	Lakes	Epi	Oligo	TP 2- 20 TN 20- 200	(*5*)
						Meso	TP 10-30 TN 100-700	
						Eu	TP 10-90 TN 500-1300	
NCP	Cat	Maine, New Hampshire, Michigan, Wisconsin (United States)	Summer	Lakes	NA	Oligo	TP < 30 + Color < 20	(*6*)
						Eu	TP > 30 + Color < 20	
						Dys	TP < 30 + Color > 20	
						Mixo	TP > 30 + Color > 20	
NCP	Cat	United States, Argentina	Summer	Lakes	Epi	Oligo	TP < 10 + CDOC < 25	(*7*)
						Eu	TP > 10 + CDOC < 25	

						Dys	TP < 10 + CDOC > 25	
						Mixo	TP > 10 + CDOC > 25	
QI	Cat Cont	Hungary	All	Lakes	Epi	Excellent Good Medium Tolerable	PB < 1 PB 1-4 PB 4-8 PB > 8	(*8*)
PTSI	Cat Cont	Germany	All	Lakes and Reservoirs	Epi	Oligo	PTSI < 1.5	(*9*)
						Meso	PTSI 1.5-2.5	
						Eu	PTSI 2.5-3.5	
						Poly	PTSI 3.5-4.5	
						Hyper	PTSI >4.5	
TLI	Cat Cont	New Zealand	NA	Lakes	Epi	Ultramicro	Chl <0.33 SDD >25 TP <1.8 TN <34	(*10*)
						Micro	Chl 0.33-0.82 SDD 15-25 TP 1.8-4.1 TN 34-73	
						Oligo	Chl 0.82-2.0 SDD 15-7 TP 4.1-9.0 TN 73-157	
						Meso	Chl 2-5 SDD 2.8-7 TP 9.0-20 TN 157-337	
						Eu	Chl 5-12 SDD 1.1-2.8 TP 20-43 TN 337-725	

						Supereu	Chl 12-31 SDD 0.4-1.1 TP 43-96 TN 725-1558	
						Hypereu	Chl >31 SDD <0.4 TP >96 TN >1558	
SBTI	Cat Cont	New Zealand	NA	Lakes	Sed	Micro	SBTI <2	(*11*)
						Oligo	SBTI 2-3	
						Meso	SBTI 3-4	
						Eu	SBTI 4-5	
						Supereu	SBTI 5-6	
						Hypereu	SBTI >6	
TS	Cat Cont	Worldwide	Summer	Lakes	Epi Hypo	Oligo	TP <10 TN <350 Chl <3.5 SDD >4 AF <20 AHOD <250	(*12*, *13*)
						Meso	TP 10-30 TN 350-650 Chl 3.5-9 AF 20-40 AHOD 250-400	
						Eu	TP 30-100 TN 650-1200 Chl 9-25 AF 40-60 AHOD 400-550	
						Hypereu	TP >100 TN >1200 Chl >25 AF >60	

							AHOD >550	
TS	Cat Prob	Worldwide	All	Lotic	Ben	Oligo	TP <25 TN <325	(*14*)
						Meso	TP 25-60 TN 325-700	
						Eu	TP >60 TN >700	
TS	Cat Cont Prob	United States	Summer	Lotic	Ben	Oligo	GPP <6.25 R <119 GPP/R <0.19	(*15*)
						Meso	GPP 6.25-37.5 R 119-243 GPP/R 0.19-0.63	
						Eu	GPP >37.5 R >243 GPP/R >0.63	
TS	Cat Cont Prob	United States	Summer	Lakes	Epi	Oligo	GPP <13 R <35 GPP/R <0.68	(*15*)
						Meso	GPP 13-34 R 35-46 GPP/R 0.67-0.9	
						Eu	GPP >34 R >46 GPP/R >0.9	
TS	Cat Cont Prob	Worldwide	All	Lotic	Ben Ses	Oligo	Mean Benthic Chl <20 Max Benthic Chl <60 Sestonic Chl <10 TP <25 TN <700	(*16*)

						Meso	Mean Benthic Chl 20-70 Max Benthic Chl 60-200 Sestonic Chl 10-30 TP 25-75 TN 700-1500	
						Eu	Mean Benthic Chl >70 Max Benthic Chl >200 Sestonic Chl >30 TP >75 TN >1500	
TS	Cat Cont	Argentina		Lakes	Epi	Ultraoligo	cDOM <3	(*17*)
						Oligo	cDOM 3-40	
						Meso	cDOM 40-45	
						Eu	cDOM >45	
TS	Cat Cont Prob	China		Lakes	Epi	Oligo	cDOM <4	(*18*)
						Meso	cDOM 4-10	
						Eu	cDOM 10-23	
						Hypereu	cDOM >23	

Figure 1: Daytime temperature (blue) and dissolved oxygen (turquoise) depth profiles for all lakes in the 2017 U.S. Environmental Protection Agency (EPA) National Lakes Assessment (NLA) sampling campaign across four trophic state classification schemes. Dissolved oxygen concentrations have been scaled relative to temperature values so that profiles approximately overlap, similar to those portrayed in Wetzel (2001). Lines are drawn using locally estimated scatterplot smoothing (loess) fits across all lakes within each trophic state classification, where confidence envelopes (gray) signify increasing uncertainty in the model fit. Broadly, oligotrophic lakes all demonstrate anticipated orthograde curves, whereas eutrophic lakes do not demonstrate distinctive clinograde curves relative to those observed in explicitly dystrophic, mixotrophic, or hypereutrophic lakes. Data for TS classifications come from the 2017 EPA NLA sampling campaign (U.S. Environmental Protection Agency 2017a, 2017b). Further details on how this analysis was conducted, including information on the EPA NLA's sampling design are included in the "Supplemental Methods" file as well as the R scripts "strat_check.R" and "depth_profile_plots_condensed.R" in the companion software release (Meyer et al. 2025).

Figure 2: Boxplots representing characteristic Secchi disk depths for lakes from the U.S. Environmental Protection Agency (EPA) 2012 and 2017 National Lake Assessment (NLA) and their associated trophic categories as determined by Nutrient Color Paradigm (NCP) and Trophic State Index (TSI). Boxplots are colored by the trophic category. Boxplots representing NCP-based categories have diagonal hatches, whereas boxplots lacking diagonal hatches represent TSI-based categories. Boxplot lines represent quartile statistics, and points outside lines represent outliers. Secchi disk depth, total phosphorus, and true color data come from the EPA NLA (U.S. Environmental Protection Agency 2011, 2012, 2017a, 2017b). TSI delineations were made following guidelines in Carlson (1977). NCP delineations were made following thresholds established in Webster et al. (2008) and Leech et al. (2018). Further details on the EPA NLA sampling design are included in the “Supplemental Methods” file. This figure was created using the R script “secchi_depth_boxplots.R” provided in the companion software release (Meyer et al. 2025).

Figure 3: Map (A) and aggregated percentages in Omernik Level III aggregated ecoregions (B) of lake trophic state using various classification schemes. Classification schemes shown here are not necessarily the most common but are intended to reflect the diversity of potential schemes. Notably, trophic state classifications can produce dramatic differences in anticipated frequency and abundance of a given trophic state. For example, the Nutrient Color Paradigm (NCP) tends to identify far fewer eutrophic lakes in the Northern Appalachian (3.7% of lakes) and Upper Midwest (10.7%) ecoregions, relative to TSI-based metrics (35.4% and 41% on average, respectively). Trophic state classifications are based on chlorophyll a (TSI_{CHLa}), total phosphorus (TSI_{TP}), and Secchi Disk Depth (TSI_{SDD}), rotifer abundance (TSI_{ROT}; Ejsmont-Karabin 2012), and crustacean zooplankton abundance (TSI_{CR1}; Ejsmont-Karabin and Karabin 2013), as well as the NCP. Data for TS classifications come from the 2017 U.S. Environmental Protection Agency (EPA) National Lakes Assessment (NLA) sampling campaign (U.S. Environmental Protection Agency 2017a, 2017b). Further details on the EPA NLA sampling design are included in the "Supplemental Methods" file. This figure was created using the R script "lts_refinement_map.R" provided in the companion software release (Meyer et al. 2025).

Figure 4: Mean and standard deviation of dominant wavelengths and true color (Platinum-Cobalt Units) ranges across trophic state classifications. When assessed with trophic state index grouping (A), mean dominant wavelength largely separates oligotrophic, mesotrophic, eutrophic, and hypereutrophic lakes, although substantial variation within and overlap between classifications exist. Unlike dominant wavelength, true color values for trophic state index classifications substantially overlap between classifications. When assessed with nutrient-color paradigm groupings (B), dominant wavelength separates autotrophic groups but masks dystrophic and mixotrophic lakes with oligotrophic and eutrophic lakes, respectively. When viewed across a gradient (C), dominant wavelength is a powerful metric for assessing autotrophic productivity, yet variation within groups can likely contribute noise to classification models trained on solely remotely sensed surface reflectance data. Data for TS classifications come from the 2017 U.S. Environmental Protection Agency (EPA) National Lakes Assessment (NLA) sampling campaign (U.S. Environmental Protection Agency 2017a, 2017b). Further details on how this analysis was conducted, including information on the EPA NLA sampling design are included in the "Supplemental Methods" file as well as the "rs_ts_differences.R" R script in the companion software release (Meyer et al. 2025).

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Box 1: A comparison of selected lake TS classification schemes

Several classification schemes have been adopted to classify trophic states, including those mentioned in Table 1 and others (e.g., Dodds and Whiles 2019). Although we cannot compare all these approaches, we have compared three approaches to illustrate how differences in definition of TS can lead to divergent interpretations if considered independently and without context. Together, the TS classifications offer broader insights into the trophic state concept.

Trophic State Index (TSI), developed by Carlson (1977) and subsequently refined, has been used as a descriptor of water quality in lentic waterbodies and has been frequently adopted by management agencies, including the U.S. Environmental Protection Agency (U.S. Environmental Protection Agency 1990). TSI provides both a continuous metric and a categorical grouping but only indicates autotrophic productivity. Furthermore, TSI has been adapted to accommodate values typical to a given location. For example, in Brazil, TSI relationships have been adapted to classify tropical reservoirs to consider the overall greater productivity of tropical ecosystems compared to other climate zones (Cunha et al. 2013). Proxies of this scheme are Secchi disk depth, total phosphorus, and chlorophyll a; classifications include oligotrophic, mesotrophic, eutrophic, and hypereutrophic.

Nutrient-color paradigm (NCP) groups lakes based on water clarity (measured as carbon concentration, water color, or absorption coefficient) and autotrophic capacity. Rohde (1969) first arranged the four quadrants of the NCP, placing autochthony on the horizontal axis and allochthony on the vertical axis. This second dimension discriminates “oligotrophic” (low autochthony, low allochthony) and “eutrophic” (high autochthony, low allochthony) lakes from “dystrophic” (low autochthony, high allochthony) lakes and “mixotrophic” (high autochthony, high allochthony) lakes.

Proxies of this scheme are total phosphorus and carbon concentration, water color, or absorption coefficient; classifications include oligotrophic, eutrophic, dystrophic, and mixotrophic.

Ecological State (ES) is a component of the European Union's Water Framework Directive (WFD; Commission and Environment 2014), which introduces a planning process and assessment schema to manage, protect, and improve the surface and subsurface water environment. Ecological state is an assessment of the structure and function of surface waters. ES accounts for the abundance of aquatic flora and fish fauna, the availability of nutrients, and aspects like salinity, temperature, and presence of chemical pollutants. Notably, ES includes benthic variables as well as water column conditions. As defined in the WFD, ES refers not to a specific level of a variable or a characteristic of an ecosystem but rather to a change from the baseline undisturbed state. Proxies of this scheme include but are not limited to total phosphorus, dissolved oxygen, water temperature, and macrophyte density; classifications include bad, poor, moderate, good, and high.

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