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Clarifying the trophic state concept to advance freshwater science, management, and interdisciplinary collaboration across spatial and temporal scales

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Abstract (345 of 350 words)

For over a century, ecologists have used the concept of trophic state (TS) to characterize an aquatic ecosystem's biological productivity. Because measuring productivity can be challenging within an ecosystem and across landscapes, multiple TS classification schemes, each relying on a variety of proxies for productivity, have emerged to meet use-specific needs. Most commonly, chlorophyll a, phosphorus, and Secchi depth are used to discriminate TS based on autotrophic production, whereas phosphorus, dissolved organic carbon, and true color are used to discriminate TS based on autotrophic and heterotrophic production. Both classification schemes aim to characterize an ecosystem's function broadly, but the relative emphasis on heterotrophic and autotrophic processes masks nuances in how an ecosystem's function is understood. Moreover, differing classification schemes can create inconsistent understanding and can lead to narrowed interpretation of ecosystem integrity. For example, the U.S. Clean Water Act focuses exclusively on threats to autotrophic 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, which can then be used to contextualize, compare, and project ecosystems across scales. However, to emphasize the consequences of using multiple TS classification schemes, we present three scenarios 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 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. Therefore, several proxies for identifying TS have emerged over the 20th century (Box 1; Table 1). Nutrients, chlorophyll, and Secchi disk depth (SDD) are common proxies for evaluating TS, whereas alternative formulations rely on true color, organic carbon, biomass estimates, and even microbial community composition (Table 1). Proxy usage and consequent discretization of TS can also differ between ecosystem types and regions (Table 1). In lakes and reservoirs, Hutchinson (1957) focused on hypolimnetic oxygen depletion rates as driven by productivity. Lindeman (1942) and Horne and Goldman (1983) focused on TS as phases of a waterbody's ontogeny, which are identified by net ecosystem exchange. 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 disparate, basic water quality data. Such simplifications are pivotal for generalizing our understanding of ecosystem function, thereby aiding researchers and managers alike to move beyond how ecosystems are structured differently and into investigations of why ecosystems function differently (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 oxygen, carbon dioxide, pH, nitrogen, phosphorus, iron, manganese, and redox potential, differ between stratified oligotrophic and eutrophic lakes. Although these generalities may not always apply to every ecosystem, the TS concept can be used to create a general predictive framework that can project water quality conditions when data 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 (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 project ecosystem productivity, function, and integrity.

Over the last half century, the proxies used to variously 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 reference to a TS category may actually translate to relative 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 lens of disparate proxies. Confusion can be further compounded when disparate classification schemes suggest diverging expectations for ecosystem function, such as characteristic oxyclines across various trophic state classification schemes (Figure 1). Regardless of how oligotrophic is defined, all oxycline and thermocline profiles produce anticipated orthograde curves. In contrast, all eutrophic profiles are visually similar, yet the most idealized clinograde curves are observed in dystrophic and mixotrophic lakes (Figure 1), which tend to be less reported relative to eutrophic conditions. These unexpected incongruences call into question the extent to which autotrophic-focused metrics, such as Trophic State Index, might channel thought away from 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.

Given how TS classification schemes have emerged and transformed over the past century, we attempt to re-evaluate and clarify how new insights inform and evolve our current understanding of existing TS categories. Without this 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 standardized understanding of how aquatic ecosystems are structured and function over past and future decades. To illustrate how a clear and consistent, yet dynamic, conceptual framework could be useful 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 underscore how combining emerging scientific themes, data streams, and technologies with the TS concept can be helpful for clarifying the scope of the science at hand as well as the TS concept itself. Moreover, we demonstrate how descriptions of TS will benefit from including both the proxies used (e.g., nutrient concentrations, water transparency, chlorophyll biomass), and the spatial area and temporal period represented. Communicating these pieces of information is an initial step in improving clarity in TS assessments and ensuring scientific reproducibility, thereby furthering the development of aquatic sciences, water resource management, and interdisciplinary collaboration.

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

TS is intended to represent whole-year net ecosystem productivity (Wetzel 2001), yet the TS concept has historically focused on summertime characteristics of Northern Hemisphere temperate lakes. A broader view of TS across biomes and seasons demands consideration of how seasonal climate variation influences the proxies used to classify a given TS (Dodds et al. 2019). In particular, investigations of wintertime dynamics and tropical ecosystems illustrate how TS can be understood differently from insights derived from summertime data from northern, temperate lakes. Considering tropical lakes and winter conditions can help clarify the temporal and spatial domains of TS. Temporally, a recent emphasis in wintertime productivity helps clarify the TS concept during a time when even historically well-studied ecosystems are less sampled. Spatially, a recent emphasis in tropical ecosystems helps clarify the TS concept for ecosystems that are productive year-round but seasonality is driven by relative change in precipitation. Together, these case studies offer a guide for how TS can provide a null hypothesis for less well studied geographies and seasons, and reciprocally, how these same geographies and seasons can improve the TS conceptual framework's usefulness and generality.

The rise of under-ice studies has expanded our understanding of biological productivity beyond open water seasons (Hampton et al. 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 and increased heterotrophy 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 ecosystem production towards an oligotrophic classification (Kalinowska and Karpowicz 2020). In both cases, the inclusion of winter productivity can be consequential for how a lake is classified, and therefore, how the dominant processes in the waterbody may be interpreted. 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 aid in understanding how a warming winter may influence annual dynamics. For example, diminishing ice cover over coming decades could hinder ice-obligate algal communities, yet cold temperatures may suppress overall growth rates of open-water water taxa during winter, even though episodic psychrophilic and psychrotolerant blooms can occur (Reinl et al. 2023). Ice loss, then, may homogenize the behavior of eutrophic and oligotrophic water bodies during winter, with both ecosystems being similarly productive during winter and diverging in the summertime. 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. Additionally, if TS is represented on an annual basis, yearlong growth conditions in tropical lakes could cause substantially more annual productivity than temperate lakes with the same mean or summertime algal biomass. The productivity of Brazilian lakes, for example, is influenced by 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 time periods rather than cold-warm periods, further complicates the comparability of TS assessments made across biomes through the same classification system.

When expanding the TS concept outside of northern, temperate lakes, the spatial and temporal domains of classifications become increasingly 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 be extrapolated temporally or spatially. As most TS assessments are currently based on summertime productivity, our current understanding of characteristic productivity is likely biased towards summertime conditions in temperate regions. Yet, the growth of our understanding of wintertime and tropical productivity highlights how important seasonality can be for holistically understanding and inferring the function of waterbody productivity worldwide.

As the field of aquatic sciences continues to expand into seasons and geographic locations that are poorly 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 time periods and biomes used to lay its foundations. More work on seasonality and in areas that have received less attention will allow a more nuanced view of TS. 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 function 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 prediction across ecosystems or prescribe specific actions, but they are useful 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.

As 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 SDD to calculate trophic state index (TSI; Carlson 1977), and then use TSI to identify waterbodies that are hypereutrophic and at greater risk of cyanobacterial blooms. However, SDD can also indicate high concentrations of suspended inorganic sediments or highly colored waters (Cunha et al 2021). 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), and coordinated, continental-scale sampling campaigns have shown how SDD can be indiscernible from eutrophic, mixotrophic, and dystrophic lakes categorized by TSI_{SDD} or NCP (Figure 2).

Beyond individual constituents, the categories differentiated by various classifications schemes makes translating across schemes challenging, if possible. For example, TSI-derived classifications do not identify dystrophic and mixotrophic states, unlike NCP. These incongruences amongst classification schemes can mask landscape-wide understanding of TS frequency and spatial distribution (Figure 3). The Upper Midwest and Northern Appalachians are two ecoregions that highlight extremes in understanding (Figure 3). Amongst TSI-derived metrics using total phosphorus, SDD, chlorophyll, rotifer abundance, and crustacean zooplankton abundance, 41% and 35.4% of lakes in the Upper Midwest and Northern Appalachians should be eutrophic, respectively, whereas NCP suggests 10.4% and 3.7% of lakes should be eutrophic. Conversely, NCP suggests that 51.5% and 58.3% of lakes in the Upper Midwest and Northern Appalachians should be 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 can be interchanged. In particular, samples necessary for linking classification schemes may not be co-located or collected contemporaneously, making classification schemes non-interchangeable. For example, TSI and Ecological State (ES) can rely upon total phosphorus, SDD, and chlorophyll data, which may be more frequently collected by monitoring programs relative to the true color or dissolved organic matter/carbon (DOM, DOC) data 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 tandem analyses.

Given the limited ability to translate across TS classification schemes, clarifying the proxy data used to assign a TS classification ensures the interpretability of TS classifications. Without the potential to compare across classification schemes, landscape wide assessments of TS may signal diverging understanding of water quality and ecosystem integrity. Further, ensuring the translatability across classification schemes will improve our understanding about TS and the ability to quantify expected variability in TS over space and time, thereby optimizing successive management decisions.

Clarifying the TS concept can increase the interdisciplinarity of the aquatic sciences

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 demonstrated exceptional progress in extending localized insights across continental scales. Consequently, these techniques may be the most tractable paths for understanding macroscale water quality patterns. However, without tandem technological and limnological expertise, their insights may be shortsighted.

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_{CHLA} and its associated variability from remotely sensed surface reflectance for hundreds of lakes worldwide. Werther et al. (2021) and Meyer et al. (2024) 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 adoption of the TS concept into remote sensing literatures, 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, 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 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. Consequently, models trained exclusively on data from lakes would erroneously classify oligotrophic rivers and vice-versa, if limnological expertise is not included in the modeling framework. As remote sensing approaches continue to expand the spatial and temporal coverage of aquatic ecosystem monitoring, stronger links need to be made between aquatic and remote sensing science to take full advantage of remotely sensed data sources.

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. For example, Werther et al. (2021) trained multiple machine learning models to examine the relationship between remote sensing surface reflectance and TSI_{CHLA} for 50 lakes worldwide. Although this approach yielded effective results for the majority of lakes, it frequently misclassified highly turbid waterbodies, implying that classification schemes including elements of both autochthony and allochthony may offer a more generalizable scheme for understanding water quality. Where machine learning may be able to integrate limnological knowledge into the model, such as in knowledge-guided machine learning (KGML; Appling et al. 2022, Karpatne et al. 2024), consistent and well documented classification schemes can aid in reproducing ecosystem dynamics. For example, Hanson et al. (2020) used KGML 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. The potential exists for model predictions to extend beyond phosphorus dynamics alone. Regardless of the exact implementation, consistent and clear communication of TS classifications schemes used in developing training datasets will 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. However, remote sensing and data-driven modeling currently may not take full advantage of the rich history of limnological principles, such as TS, without clear consideration of the processes, data, and operational definitions underlying those principles. Furthermore, clarification of TS can benefit the 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 constituent concentrations, 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. But, there may be nuanced inconsistencies across usage. While we are not proposing a unified classification scheme, we aim to highlight how TS can provide a conceptual framework for understanding less well studied ecosystems across spatial and temporal scales. Defining the spatial and temporal domains of the TS classification allows for nuanced understanding of a classification, where inferences can be conveyed based on the scales considered. The power of using TS as a framework to generalize, and to scale, relies on understanding of the proxies employed in the chosen classification scheme. Without consideration for these nuances, future scientific progress may lack comparability with previous or tandem efforts.

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). Initial steps in this direction have been stymied by lack of publicly-available data from areas with less well-established monitoring and scientific research networks. Global climate change is pushing ecosystems into novel states, and understanding the characteristics, particularly trophic states, of freshwaters across a range of climate conditions is necessary to predict how these ecosystems will change in the future.

Ultimately, how the TS concept is implemented will likely stem from the task at hand. In the case of management, TS may be a tool to characterize water quality, prioritize water bodies for additional investigation, and to 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. Beyond any single approach to classifying TS, there is a need for the aquatic sciences to continuously re-evaluate existing classification schemes; otherwise, diverging TS frameworks can hinder the growth of basic and applied science, interdisciplinarity across fields, and robust adoption by a suite of end users.

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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.

Data Availability Statement

No new data were generated for this paper. All US EPA NLA data are available at https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys.

Conflicts of Interest

The authors declare no conflicts of interest.

Table 1: Aggregation of select Trophic State classification schemes.

Index Name	Data Type	Geography	Season	Type	Zone Sampled	Variables Used	Reference
Trophic State Index	Continuous	Midwest United States	Summer	Lakes	Epilimnion	Secchi Disk Depth Chlorophyll-a Total Phosphorus	Carlson (1977)
Trophic State Index	Categorical Continuous	Brazil	All	Reservoirs	Epilimnion	Total Phosphorus Chlorophyll-a	Cunha et al. (2013)
Trophic State	Categorical Continuous Probabilistic	Worldwide	NA	Lakes and Reservoirs	Epilimnion	Total Phosphorus Chlorophyll-a Maximum Chlorophyll-a Secchi Disk Depth Minimum Secchi Disk Depth	Vollenweider and Kerekes (1982)
Trophic State Model Index	Categorical Probabilistic	Argentina Brazil Colombia Ecuador Mexico Puerto Rico Texas (United States) Venezuela	All	Lakes	Epilimnion	Total Phosphorus	Salas and Martino (1991)
Trophic State	Categorical Continuous	Brazil	All	Reservoirs	Epilimnion	Total Phosphorus Chlorophyll-a	Lamparelli (2004)
Trophic State	Categorical Continuous	Japan	All	Lakes	Epilimnion	Total Phosphorus Total Nitrogen	Sakamoto (1966)
Nutrient Color Paradigm	Categorical	Maine, New Hampshire,	Summer	Lakes	NA	True Color Total Phosphorus	Webster et al. (2008)

		Michigan, Wisconsin (United States)					
Nutrient Color Paradigm	Categorical	United States, Argentina	Summer	Lakes	Epilimnion	Chromophoric Dissolved Organic Carbon-absorption at 320 nm Total Phosphorus	Williamson et al. (1999)
Q index	Categorical Continuous	Hungary	All	Lakes	Epilimnion	Phytoplankton Biomass	Padisák et al. (2006)
Phyto-See-Index	Categorical Continuous	Germany	All	Lakes and Reservoirs	Epilimnion	Phytoplankton Composition Phytoplankton Biomass	Mischke (2015)
Trophic Status	Categorical	Denmark	Summer	Lakes	Epilimnion	Phytoplankton Biomass	Nygaard (1949)
Trophic Level Index	Categorical Continuous	New Zealand	NA	Lakes	Epilimnion	Chlorophyll-a Secchi Disk Depth Total Phosphorus	Burns et al. (1999)
Sediment Bacterial Trophic Index	Categorical Continuous	New Zealand	NA	Lakes	Sediment	Bacterial 16sRNA	Wood et al. (2023)
Planktonic Trophic Index	Categorical Continuous	Europe	Summer	Lakes	Epilimnion	Phytoplankton Abundance	Phillips et al. (2013)
Trophic State Index	Categorical Continuous	Wisconsin (United States)	All	Lakes	Epilimnion	Secchi Disk Depth Specific Conductivity Total Organic Nitrogen Total Phosphorus Chlorophyll-a Pearson's Cation Ratio	Shannon and Brezonik (1972)

Trophic State	Categorical Continuous	Worldwide	Summer	Lakes	Epilimnion Hypolimnion	Chlorophyll-a Total Phosphorus Total Nitrogen Anoxic Factor Areal Hypolimnetic Oxygen Depletion Secchi Disk Depth	Nürnberg (1996) Nürnberg and Shaw (1998)
Trophic State	Categorical Probabilistic	Worldwide	All	Lotic	Benthic	Total Nitrogen Total Phosphorus	Dodds (2007)
Trophic State	Categorical Continuous Probabilistic	United States	Summer	Lotic	Benthic	Gross Primary Production Ecosystem Respiration	Dodds and Cole (2007)
Trophic State	Categorical Continuous Probabilistic	United States	Summer	Lakes	Epilimnion	Gross Primary Production Ecosystem Respiration	Dodds and Cole (2007)
Trophic State	Categorical Continuous Probabilistic	Worldwide	All	Lotic	Benthic Seston	Benthic Chlorophyll-a Sestonic Chlorophyll-a Total Phosphorus Total Nitrogen	Dodds et al. (1999)

396

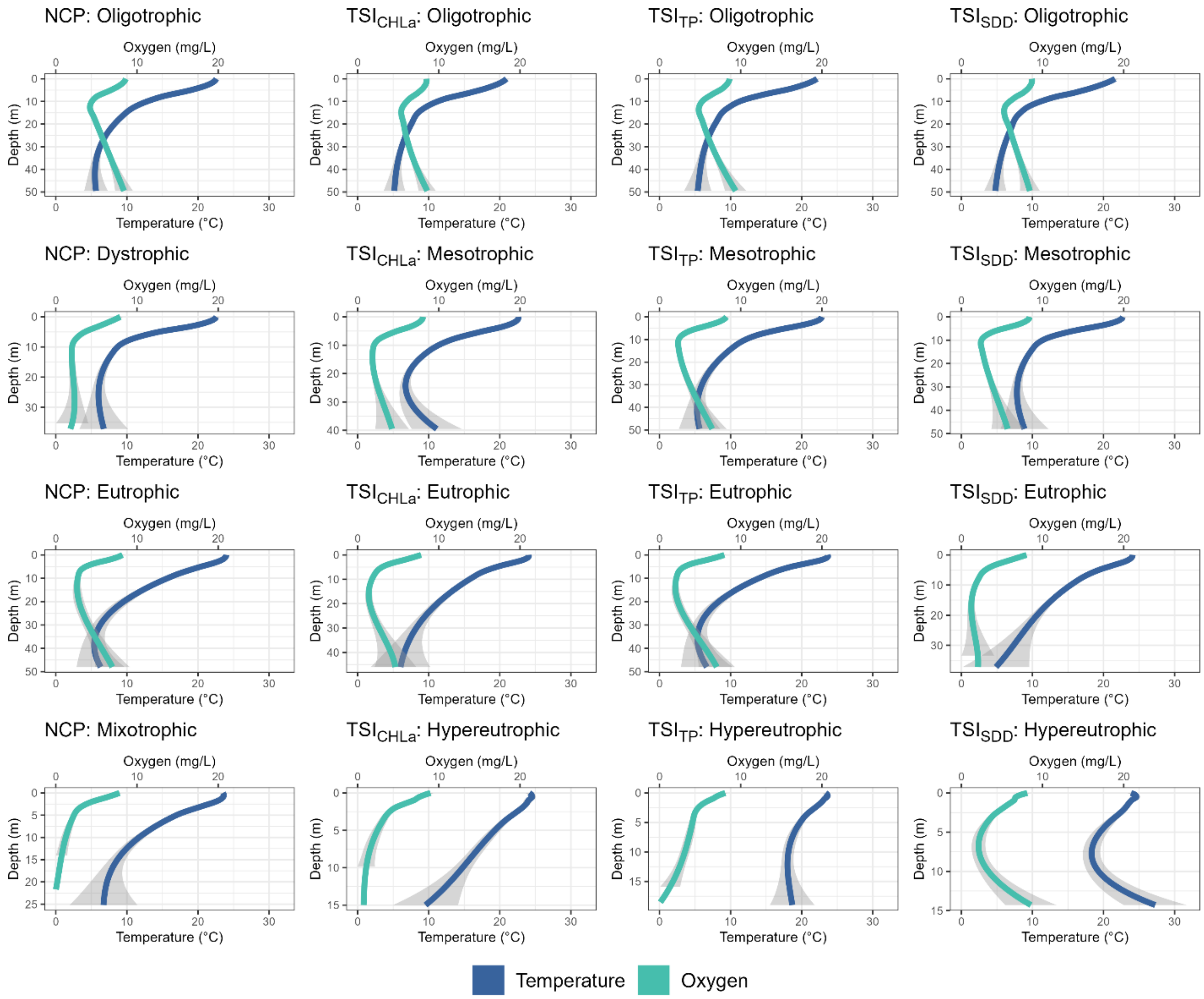


Figure 1: Temperature (blue) and dissolved oxygen (turquoise) depth profiles for all lakes in the 2017 NLA sampling campaign across four trophic state classification schemes. Dissolved oxygen concentrations have been scaled relative to temperature values so that profiles approximately overlap, similar to those portrayed in Wetzel (2001). Lines are drawn using loess fits across all lakes within each trophic state classification, where confidence envelopes signify increasing uncertainty in the loess-fit. Broadly, oligotrophic lakes all demonstrate anticipated orthograde curves, whereas eutrophic lakes do not demonstrate marked clinograde curves relative to those observed in explicitly dystrophic, mixotrophic, or hypereutrophic lakes. Data for TS classifications come from the 2017 US EPA NLA sampling campaign (USEPA 2017a, 2017b).

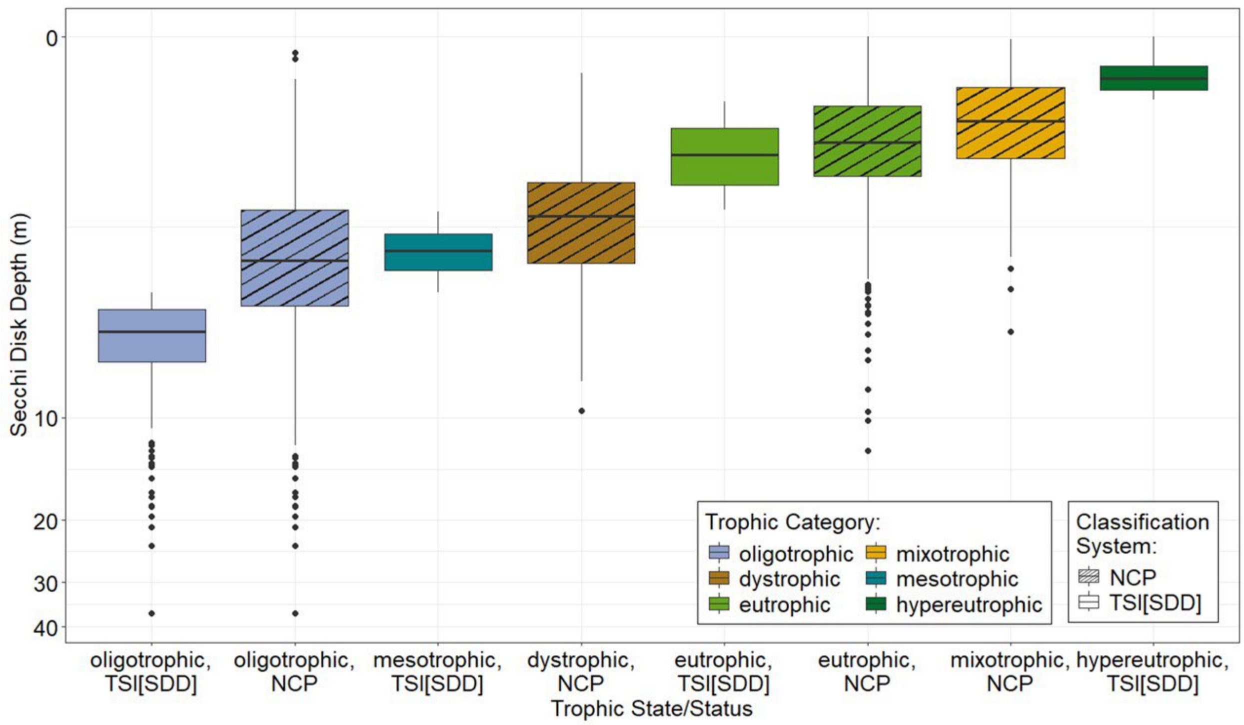


Figure 2: Boxplots representing characteristic Secchi disk depths for lakes from the U.S. Environmental Protection Agency's 2012 and 2017 National Lake Assessment and their associated trophic categories as determined by Nutrient Color Paradigm (NCP) and Trophic State Index (TSI). Boxplots are colored by the trophic category. Boxplots representing NCP-based categories have diagonal hatches, whereas boxplots lacking diagonal hatches represent TSI-based categories. Secchi Disk Depth, Total Phosphorus, and True Color data come from the U.S. Environmental Protection Agency's National Lake Assessment (USEPA 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).

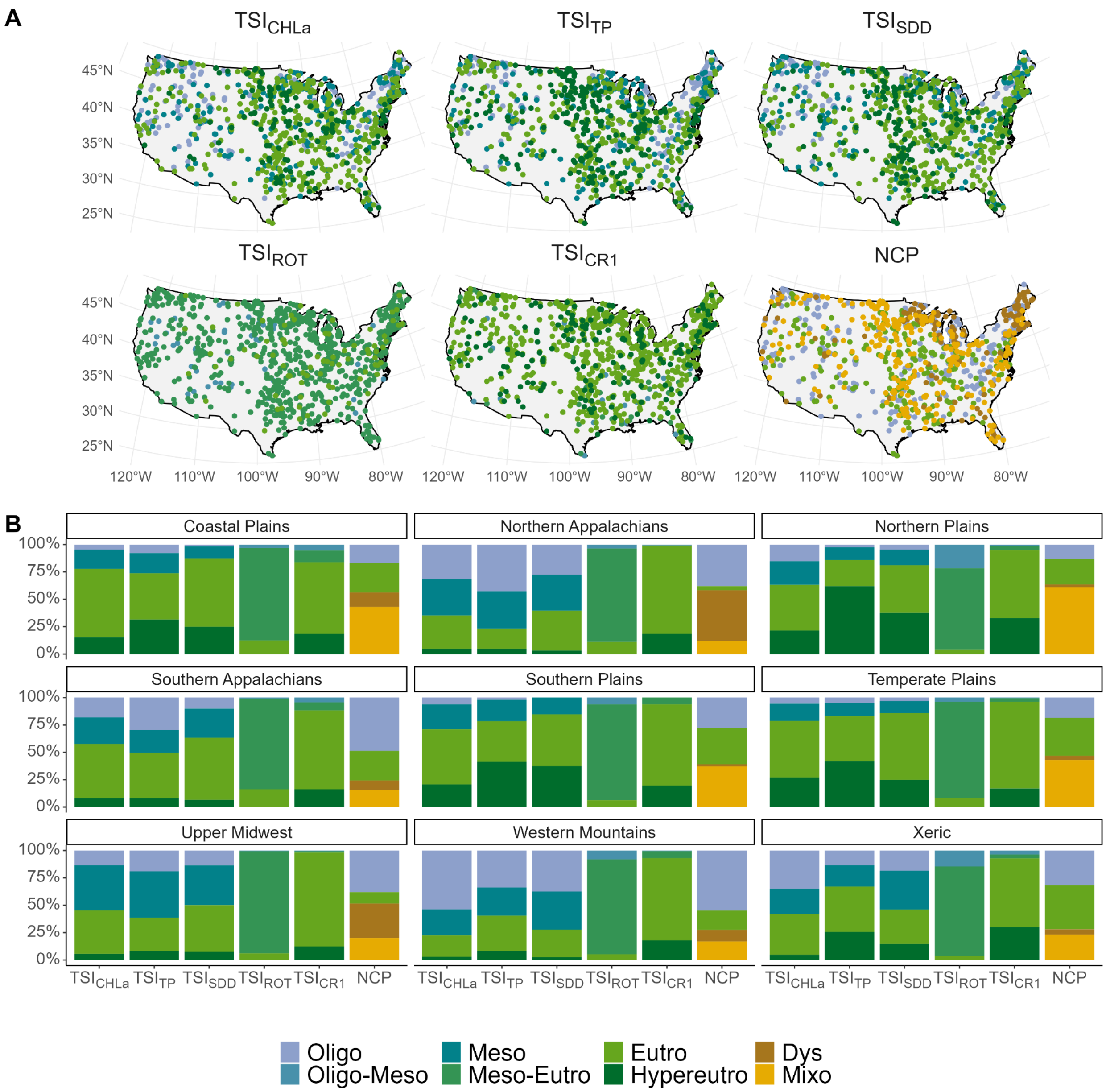


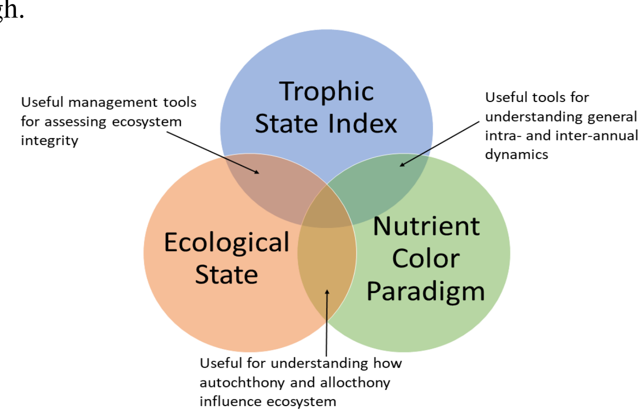
Figure 3: Map (A) and aggregated percentages in Omernik Level III aggregated ecoregions (B) of lake trophic state using various classification schemes. Classification schemes shown here are not necessarily the most common but are intended to reflect the diversity of potential schemes. Notably, trophic state classifications can produce dramatic differences in anticipated frequency and abundance of a given trophic state. For example, the 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 Nutrient-Color Paradigm (NCP). Data for TS classifications come from the 2017 US EPA NLA sampling campaign (USEPA 2017a, 2017b).

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 (USEPA 1990). It 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 take into account 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), 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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