Clarifying the trophic state concept to advance limnology, management, and interdisciplinary collaboration

Michael F. Meyer[1,2], Benjamin M. Kraemer[3], Carolina C. Barbosa[4], Davi G.F. Cunha[5], Walter K. Dodds[6], Stephanie E. Hampton[7], César Ordóñez[8], Rachel M. Pilla[9], Amina I. Pollard[10], Joshua A. Culpepper[11], Alexander K. Fremier[12], Tyler V. King[13], Robert Ladwig[2], Dina M. Leech[14], Shin-Ichiro S. Matsuzaki[15], Isabella A. Oleksy[4], Simon N. Topp[16,17], R. Iestyn Woolway[18], Ludmila S. Brighenti[19], Kate C. Fickas[20,21], Brian P. Lanouette[22], Julie C. Padowski[12], Jianning Ren[23], Xiao Yang[24]

[1.] U.S. Geological Survey, Madison, WI, USA
[2.] University of Wisconsin, Madison, WI, USA
[3.] University of Freiburg, Freiburg, Germany
[4.] University of Wyoming, Laramie, WY, USA
[5.] Universidade de São Paulo, São Carlos, SP, Brazil
[6.] Kansas State University, Manhattan, KS, USA
[7.] Carnegie Institution for Science, Pasadena, CA, USA
[8.] University of Geneva, Geneva, Switzerland
[9.] Oak Ridge National Laboratory, Oak Ridge, TN, USA
[10.] U.S. Environmental Protection Agency, Washington, D.C., USA
[11.] York University, Toronto, ON, Canada
[12.] Washington State University, Pullman, WA, USA
[13.] U.S. Geological Survey, Boise, ID, USA
[14.] Longwood University, Farmville, VA, USA
[15.] National Institute for Environmental Studies, Tsukuba, Ibaraki, Japan
[16.] U.S. Geological Survey, Carrboro, NC, USA
[17.] Current Address: Upstream Tech, Carrboro, NC, USA
[18.] Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK
[19.] Universidade do Estado de Minas Gerais, Divinópolis, MG, Brazil
[20] U.S. Geological Survey, Sioux Falls, SD, USA
[21.] University of California - Santa Barbara, Santa Barbara, CA, USA
[22.] Upper Skagit Indian Tribe, Sedro Woolley, WA, USA
[23.] University of Nevada - Reno, Reno, NV, USA
[24.] Southern Methodist University, Dallas, TX, USA

Significance Statement

Trophic state (TS) characterizes a waterbody's biological productivity and depends on its morphometry, physics, chemistry, biology, climate, and history. However, multiple TS operational definitions have emerged to meet use-specific classification needs. These differing operational definitions can create inconsistent understanding, can lead to miscommunication, and can result in siloed management strategies for TS. For example, some regulatory agencies use TS to signify ecological integrity as opposed to biological productivity, where TS classification may trigger intervention efforts. These inconsistencies may be compounded when interdisciplinary projects employ varied TS frameworks. To emphasize the consequences of using multiple TS classification schemes, we present three scenarios for which an improved understanding of the TS concept could advance limnological research, management efforts, and interdisciplinary collaboration. As the field of limnology continues to expand, we highlight the importance of re-evaluating even the most fundamental limnological concepts, such as TS, to ensure congruence with evolving, cutting-edge science.

Introduction

Trophic state (TS) is a fundamental concept in limnology that describes a waterbody's characteristic productivity. Conceptually, TS is an integration of internal and external drivers that influence a waterbody's biological productivity. But operationally, productivity can be challenging to estimate, and therefore, several proxies for identifying TS have emerged over the 20th century (Box 1; Supplemental Table S1). In lentic ecosystems, Hutchinson (1957) focused on hypolimnetic oxygen depletion rates as driven by production. 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 on autochthony, whereas Naumann (1917), Thienemann (1921), Wetzel (2001), and Dodds and Cole (2007) focused on characteristic productivity as a function of both autochthony and allochthony. In lotic ecosystems, 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).

Over decades, the proxies used to classify TS have become synonymous with its conceptual definition, potentially leading TS to be "[a] terminology that is so widely and often so inaccurately employed in discussing productivity" (Hutchinson 1957). However, limnology and water management relies upon these categorizations to simplify complex processes into a single metric (Kraemer 2020). Furthermore, these categories can be an expedient way to convey complex information and to guide policy and mitigation efforts. As science advances, there arises an increasing need to re-evaluate how the use of multiple proxies and classification schemes may alter our understanding of ecosystem productivity.

Given the pervasiveness of the TS concept for categorizing aquatic ecosystems, the use of several related, yet diverging, classification schemes hinders effective communication. As new developments in limnology, management, and technologies (e.g., remote sensing estimates of aquatic chlorophyll) continue to emerge, it becomes essential to re-evaluate and clarify how the most cutting-edge science informs and evolves existing categories. Without this epistemological evolution, the fields of limnology and water quality management run the risk of developing divergent understandings of how ecosystems function. Here, we detail three instances where clarifying the TS concept can impact the scope of limnology and management efforts. We showcase how descriptions of TS could benefit from including (1) the ecosystem type considered, (2) the proxies used to compute TS, and (3) the spatial region and temporal period that are 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 limnology, water resource management, and interdisciplinary collaboration.

Clarifying the TS concept can enhance our understanding of limnology

One of the most powerful ways we can clarify the TS concept is by testing how TS estimates vary across seasons or latitudinal zones outside those used in its original formulations. For example, the TS concept was historically crafted around characteristics of northern temperate lakes, which tend to freeze and experience strong seasonal shifts in precipitation and air temperature. However, a broader view across biomes and seasons demands consideration of how climate and geology influence trophic state (Dodds et al. 2019). Limnological studies often focus on summer; however, winter studies have highlighted how decreased lake ice cover can trigger a cascade of ecological and environmental consequences that influence TS (Sharma et al. 2019; Hébert et al. 2021). Under-ice chlorophyll-a concentrations can reach those of summertime concentrations, where under-ice algae can develop blooms and be vital resources for grazing invertebrates (Hampton et al. 2017). Moreover, summertime productivity for seasonally freezing lakes can be a function of antecedent winter conditions, where decreased ice cover can lead to decreased summertime productivity (Hrycik et al. 2021).

What information do we lose by focusing on summer conditions? In other words, “Is a eutrophic lake still eutrophic in the winter?" This distinction depends on how one classifies “eutrophic.” For lakes that seasonally freeze, eutrophic lakes may be equally productive in winter, but this productivity is neither immediately visible nor frequently considered. For eutrophic lakes experiencing reductions in ice cover, winter may be an ecological reset. In this instance, diminishing ice cover over coming decades could hinder ice-obligate algal communities. However, cold temperatures may suppress warm water taxa during winter. Ice loss, then, may homogenize the behavior of eutrophic and oligotrophic waterbodies during winter, but the trophic state still remains a classification system that relies on summertime productivity.

In contrast to temperate ecosystems, tropical aquatic ecosystems have less pronounced seasonal variation in temperature and radiation but are driven by hydrological variation in the dry and wet seasons (Cunha et al 2021). Therefore, the productivity of these aquatic systems can be influenced by water level changes and the allochthonous nutrient loading related to the seasonal shifts. With this alternative framing of seasonality, the comparability of TS assessments made across biomes becomes even less clear.

When expanding the TS concept across biomes and seasons, the spatial and temporal domains of classifications become essential. If we assume that TS is based on cyclical degrees of autotrophy and heterotrophy (Wetzel 2001), characterizing TS on an annual baseline is necessary. If we assume that TS reflects summertime productivity, then only summertime estimates are necessary. As most TS assessments are already based on summertime productivity, our current understanding of characteristic productivity is likely limited to summertime and primarily in temperate regions. Yet, the growth of our understanding of wintertime and tropical productivity highlights how important seasonality can be for holistically understanding waterbody productivity worldwide. These disparate spatial and temporal domains raise the question “Given strong differences in characterizing seasonality, how comparable are TS estimates across biomes?”

As limnology 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 create opportunities to expand the TS concept beyond the specific time periods and biomes used to lay its foundations. By looking at lower latitudes and non-summertime seasons, we can further assess how limnological ecosystems function, how this functionality varies regionally and seasonally, and how to contextualize regional ecosystem functioning within global patterns.

Clarifying the TS concept can benefit freshwater management

For management purposes, TS can classify ecosystems in relation to water quality and ecosystem services. For example, eutrophic conditions may be desirable for increasing fish production. Conversely, hypereutrophic conditions may promote anoxia, which can lead to fish kills. In a drinking water context, source water protection is an instance where TS classifications can connect water quality characteristics to services. Eutrophic water supplies have higher filtration needs, a higher likelihood of creating health hazards from algal toxins and disinfection byproducts, more taste and odor problems, and greater treatment costs (Cooke and Kennedy 2001). Dystrophic waters characterized by a dark brown color and high carbon also require greater disinfection; however, high concentrations of organic matter can result in carcinogenic byproducts following the disinfection process (Mukundan and Van Dreason 2014). Clarified understanding of metrics within a TS classification scheme may help to predict measures of interest, such as cyanobacterial biomass, within source waters (Fernandez-Figueroa et al. 2021).

Owing to incongruences in TS classification schemes, categories detectable by each scheme can narrow the focus of which water quality aspects are monitored. For example, managers may use Secchi disk depth (SDD) to calculate trophic state index (TSI), and then use TSI to identify waterbodies that are hypereutrophic and at greater risk of cyanobacterial blooms. However, autochthony-focused metrics define this classification, whereas dystrophic and mixotrophic systems are not distinguished. This incongruence can be consequential for water quality estimates because mixotrophic lakes may have elevated risk of cyanobacterial blooms (Leech et al. 2018), yet their SDD can be indiscernible from eutrophic and dystrophic lakes (Figure 1). Even when TS classification schemes are interoperable, they can be insensitive to capturing marked water quality changes. For example, a marginal change in phosphorus concentrations can propel a waterbody across a class boundary (Meyer et al. 2023). These realities can make TS-based classifications complex measurements of ecological change, where a meaningful classification change may correspond to a marginal water quality change.

Spatial and temporal heterogeneities can further confound TS classifications and influence the scales required for management efforts. Spatially, sample collection tends to occur at the waterbody's center, failing to capture heterogeneous conditions, especially in nearshore and benthic habitats (Vadeboncoeur et al. 2021). For lotic ecosystems, samples collected near riparian vegetation may influence TS signals due to hyporheic exchange or terrestrial-aquatic connections. In instances where spatial heterogeneities are monitored, resulting TS classifications may not be consistent across a waterbody. How these spatial heterogeneities might be communicated and interpreted will depend on the resolution of tools available to measure TS and resources of local management agencies to act on that information.

Temporally, samples for monitoring TS tend to be collected as snapshots in time, and a lack of contemporaneously collected samples can hinder the ability to crosswalk classification schemes. For example, TSI and Ecological Status (ES) can rely upon total phosphorus, SDD, and chlorophyll data, which are abundant across monitoring programs relative to true color or dissolved organic matter/carbon (DOM, DOC) data needed for nutrient-color paradigm (NCP; Box 1). TSI and ES, then, might allow for finer-scale temporal assessments for a waterbody, but less frequent true color or DOM data collection may miss details used in NCP classifications. Further, the focus of TSI on autotrophic components of an ecosystem makes translating from TSI-derived TS estimates to NCP-derived TS estimates challenging, which can skew understanding of TS frequency and spatial distribution across landscapes (Figure 2).

Clarifying the spatial, temporal, proxy data, and classification scheme limitations of TS refines management effectiveness and water quality reporting. TS classification schemes that account for variation across spatial and temporal scales as well as TS classification schemes may identify a waterbody as, for example, "generally oligotrophic with hot spots or hot moments of mixotrophy". Ensuring consistent TS proxies can suggest drivers of TS, thereby optimizing successive management decisions. From this fusion of data and TS classification schemes, management can better contextualize individual waterbodies and address drivers of those water quality conditions.

Clarifying the TS concept can increase the interdisciplinarity of limnology

Limnology has benefited from a suite of disciplines. Similarly, other disciplines can benefit from limnology. Limnologists can maximize these benefits by providing greater consistency in usage of concepts and categorizations to avoid confusion in their applications across disciplines.

Remote sensing is a pertinent example of a technology that has enabled the integration of limnological concepts into multidisciplinary research. Legleiter et al. (2022) used remotely sensed hyperspectral data in tandem with genus-level, pigment signatures to detail cyanobacterial abundance within a reservoir. Gardner et al. (2021), Topp et al. (2021), and Yang et al. (2022) used lake surface water color as a metric of whole-ecosystem productivity. Wang et al. (2018) and Gilarranz et al. (2022) quantified TS and its associated variability from remotely sensed surface reflectance for hundreds of lakes worldwide. Many of these studies refer to the TS concept, but few explain what specific proxies or spatio-temporal scales are used to characterize ecosystems. This lack of clarity could lead to spurious conclusions. Remotely sensed aquatic surface reflectances may imply oligotrophic status for both a river and a lake, but the limnological processes associated with those classifications may be completely different. In a lake, oligotrophic conditions could imply low productivity in the water column, thereby showing strong blue reflectance, whereas lotic systems with stable hydrology and low turbidity can have high benthic algal productivity and green reflectance under oligotrophic conditions. Although remote sensing approaches have the potential to revolutionize the spatial and temporal coverage of trophic state monitoring, stronger links need to be made between limnological and remote sensing science to take full advantage of remotely sensed data sources.

Data science techniques, such as Knowledge-Guided Machine Learning (KGML), have started integrating limnological processes to understand complex system 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. That study focused on characterizing patterns related to TS (i.e., TP), yet the potential exists for model predictions to extend beyond individual constituents and into holistic ecosystem characteristics. Consistent and clear communication of TS classifications schemes used in developing training data will maximize the predictive accuracy of these data-driven modeling approaches.

New information gathered via emerging technologies may deepen our understanding of aquatic ecosystem properties across scales but also will demand re-evaluation of how TS classification is operationalized. Remote sensing and data science can expand spatial and temporal domains that may be physically impossible to sample. Consequently, these techniques may provide the most tractable paths to understanding broadscale patterns in aquatic productivity. However, remote sensing and data science may not take full advantage of the rich history of TS within limnology without clear consideration of the processes and operational definitions underlying TS. Further clarification of TS can benefit the interdisciplinarity of limnology by clarifying concepts for non-limnologists, thereby enabling broader insights.

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

For many limnologists, TS is often the first conceptual model for understanding limnetic processes. The casual mention of TS can carry immense meaning to a limnologist, but there may be inconsistencies across usage. Although we are not proposing a unified classification scheme, we aim to underscore that clarity in TS classifications can benefit limnology, management, and interdisciplinary collaboration.

Given divergent TS schemes and end-user needs, three pieces of metadata are critical when reporting TS: (1) the ecosystem type, (2) the proxies used to compute TS, and (3) the spatial region and temporal period that are represented with the TS classification. Each informatic details how TS can be understood in a given ecosystem. “Ecosystem Type” can describe how lotic or lentic a waterbody may be, and estimates of hydrologic residence time may further explain drivers behind a waterbody’s TS (e.g., Hotchkiss et al. 2018). The proxies used for a classification scheme detail how a TS estimate is generated, its comparability to other ecosystems, and the balance of autotrophy and heterotrophy considered. Finally, 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 in the TS formulation. 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 stem from the task at hand. In the case of management, TS may be a tool to characterize water quality, to identify drivers dictating water quality, and to communicate that water quality characteristic to decision makers. In the case of scientific investigations, varying classification schemes may be applied to characterize ecosystems occurring at a particular spatial or temporal scale. Beyond any single approach to classifying TS, there is a need for limnology to re-evaluate existing classification schemes; otherwise, the implications of these diverging schemes 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.

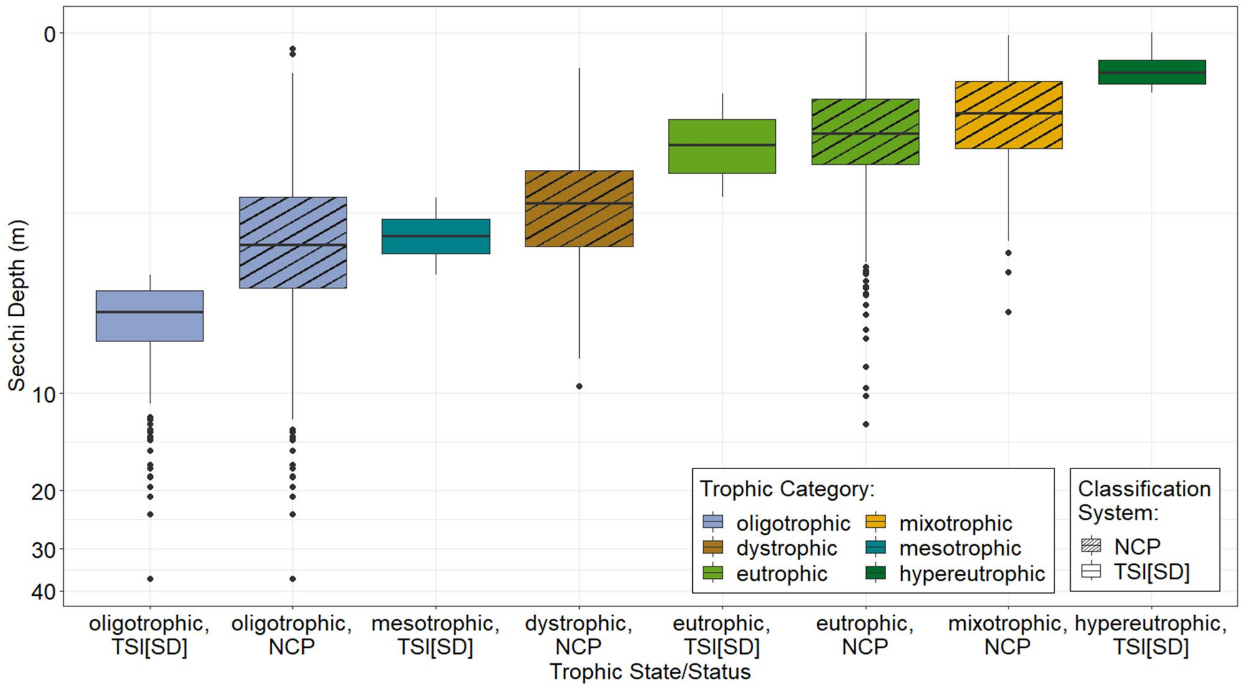


Figure 1: Boxplots representing characteristic Secchi disk depths for lakes from the U.S. Environmental Protection Agency’s 2012 and 2017 National Lake Assessment and their associated trophic categories as determined by NCP and TSI. Boxplots are colored by the trophic category. Boxplots representing 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; b). TSI delineations were made following guidelines in (Carlson 1977). NCP delineations were made following thresholds established in (Webster et al. 2008; Leech et al. 2018).

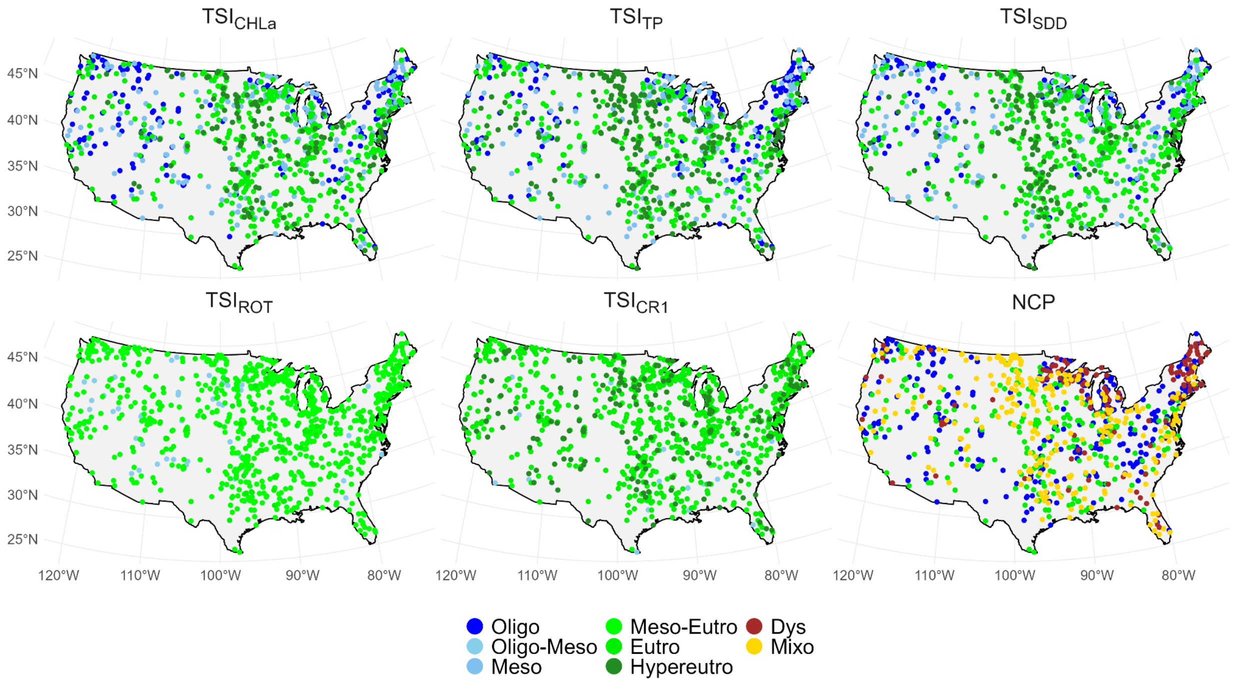


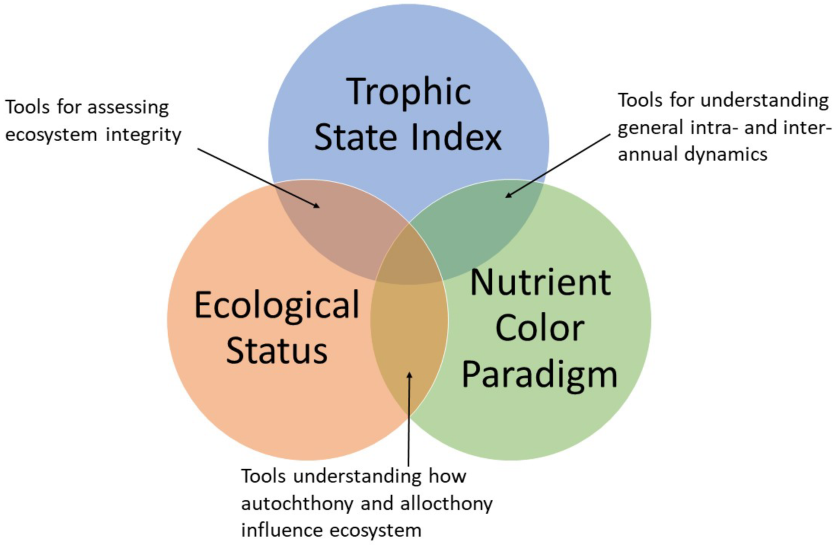
Figure 2: Map of lake trophic state using various classification schemes. Trophic state classification schemes include trophic state index (TSI) based on chlorophyll a (TSI$_{CHLa}$), total phosphorus (TSI$_{TP}$), and Secchi disk depth (TSI$_{SDD}$), rotifer abundance (TSI$_{ROT}$; (Ejsmont-Karabin and others 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; b).

Box 1: A comparison of selected lake TS classification schemes

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).

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.

Ecological Status (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 status 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.



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Supplemental Information for "Clarifying the trophic state concept to expand limnology, management, and interdisciplinary collaboration"

Michael F. Meyer[1,2], Benjamin M. Kraemer[3], Carolina C. Barbosa[4], Davi G.F. Cunha[5], Walter K. Dodds[6], Stephanie E. Hampton[7], César Ordóñez[8], Rachel M. Pilla[9], Amina I. Pollard[10], Joshua A. Culpepper[11], Alexander K. Fremier[12], Tyler V. King[13], Robert Ladwig[2], Dina M. Leech[14], Shin-Ichiro S. Matsuzaki[15], Isabella A. Oleksy[4], Simon N. Topp[16,17],R. Iestyn Woolway[18], Ludmila S. Brighenti[19], Kate C. Fickas[20,21], Brian P. Lanouette[22], Julie C. Padowski[12], Jianning Ren[23], Xiao Yang[24]

1. U.S. Geological Survey, Madison, WI, USA
2. University of Wisconsin, Madison, WI, USA
3. University of Konstanz, Konstanz, Germany
4. University of Wyoming, Laramie, WY, USA
5. Universidade de São Paulo, São Carlos, SP, Brazil
6. Kansas State University, Manhattan, KS, USA
7. Carnegie Institution for Science, Pasadena, CA, USA
8. University of Geneva, Geneva, Switzerland
9. Oak Ridge National Laboratory, Oak Ridge, TN, USA
10. U.S. Environmental Protection Agency, Washington, D.C., USA
11. York University, Toronto, ON, Canada
12. Washington State University, Pullman, WA, USA
13. U.S. Geological Survey, Boise, ID, USA
14. Longwood University, Farmville, VA, USA
15. National Institute for Environmental Studies, Tsukuba, Ibaraki, Japan
16. U.S. Geological Survey, Carrboro, NC, USA
17. Current Address: Upstream Tech, Carrboro, NC, USA
18. Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK
19. Universidade do Estado de Minas Gerais, Divinópolis, MG, Brazil
20 U.S. Geological Survey, Sioux Falls, SD, USA
21. University of California - Santa Barbara, Santa Barbara, CA, USA
22. Upper Skagit Indian Tribe, Sedro Woolley, WA, USA
23. University of Nevada - Reno, Reno, NV, USA
24. Southern Methodist University, Dallas, TX, USA

This supplemental document contains a compiled list of trophic state (TS) classification schemes. For each TS, we collated: (1) the index's name, (2) the data format required to implement a classification scheme, (3) the geography where the scheme was developed, (4) the season during which the scheme was developed, (5) the ecosystem type for which the scheme was developed, (6) the mixing zone and (7) spatial zone from which the scheme was developed.

Index Name	Data Format	Geography	Season	Ecosystem Type	Mixing Zone	Spatial Zone	Reference
Trophic status	Categorical	Worldwide	all	Estuaries	NA	pelagic	(Lee and Jones 1981)
Trophic state index	Continuous	Midwest United States	summer	lakes	epilimnion	pelagic	(Carlson 1977)
Trophic state model	Categorical; Probabilistic	Tropical	all	lakes	epilimnion	pelagic	(Salas and Martino 1991)
Trophic state	Categorical; Continuous	Japan	all	lakes	epilimnion	pelagic	(Sakamoto 1966)
Nutrient color paradigm	Categorical	Americas	Summer	lakes	epilimnion	NA	(Williamson et al. 1999)
Trophic status	Categorical	United States	Summer	lakes	epilimnion	pelagic	(USEPA 2007, 2012, 2017)
Q index	Categorical; Continuous	Hungary	all	lakes	epilimnion	pelagic	(Padisák et al. 2006)
Trophic status	Categorical	Denmark	Summer	lakes	epilimnion	pelagic	(Nygaard 1949)
Water quality index	Continuous	United States	Summer	lakes	epilimnion	pelagic	(Harkins 1974)
Canadian Council of Ministers of the Environment (CCME) Water Quality Index	Categorical; Continuous	Canada	All	lakes	epilimnion	pelagic	(Saffran et al. 2001)
Modified Canadian Council of Ministers of the Environment (CCME) Water Quality Index	Categorical; Continuous	Canada	All	lakes	epilimnion	pelagic	(Khan et al. 2004)
Planktonic trophic index	Categorical; Continuous	Europe	Summer	lakes	epilimnion	pelagic	(Phillips et al. 2013)
Trophic index number	Categorical; Continuous	United States		lakes	epilimnion	pelagic	(Stachelek et al. 2018)

Trophic state	Categorical; Continuous; Probabilistic	United States	Summer	lakes	Epilimnion	pelagic	(Dodds and Cole 2007)
Trophic state	Categorical; Continuous	Canadian and Worldwide	Summer	lakes	epilimnion, hypolimnion	pelagic	(Nürnberg and Shaw 1998)
Nutrient color paradigm	Categorical	North temperate	Summer	lakes	NA	NA	(Webster et al. 2008)
Trophic state	Categorical; Continuous	North American temperate lakes	All	lakes	Sediment core	Sediment core	(Stockner 1972)
Trophic state	Categorical; Continuous; Probabilistic	Temperate		lakes and reservoirs	epilimnion	pelagic	(Vollenweider and Kerekes 1982)
Phyto-See-Index	Categorical; Continuous	Germany	all	lakes and reservoirs	epilimnion	pelagic	(Mischke 2015)
Organization for European Economic Cooperation Trophic Status Index	Categorical; Probabilistic	Worldwide	all	lakes and reservoirs	epilimnion	pelagic	(Vollenweider and Kerekes 1982)
Lake condition index	Categorical	Wisconsin		Large lakes			(Lueschow et al. 1970)
Trophic state	Categorical; Probabilistic	Worldwide	all	lotic	benthic	benthic	(Dodds 2007)
Trophic state	Categorical; Continuous; Probabilistic	United States	Summer	lotic	benthic	benthic	(Dodds and Cole 2007)
Trophic state	Categorical; Continuous; Probabilistic	Worldwide temperate ecosystems	Seasonal	lotic	benthic/ sestonic	benthic	(Dodds et al. 1998)
Trophic state index	Categorical; Continuous; Probabilistic	United States	Summer	Non-saline lakes, reservoirs and ponds		pelagic	(Farnaz Nojavan et al. 2019)

Trophic state index	Categorical; Continuous	Tropics/Subtropics	all	reservoirs	epilimnion	pelagic	(Cunha et al. 2013)
Trophic state	Categorical; Continuous	Tropical	all	reservoirs	epilimnion	pelagic	(Lamparelli 2004)
EU Water Framework Directive Ecological Status	Categorical		all	rivers, lakes, marine			(Commission and Environment 2012)
Lake evaluation index	Continuous	United States	Summer		epilimnion	pelagic	(Porcella et al. 1980)
Trophic state	Categorical; Continuous						(Zafar 1959)
Florida trophic state index	Continuous	Florida					(Brezonik 1984)
Florida trophic state index	Categorical; Continuous	Florida					(Shannon and Brezonik 1972)
Water Quality Index	Categorical; Continuous	Laurentian Great Lakes					(Chow-Fraser 2006)
Trophic level index	Categorical; Continuous	New Zealand					(Burns et al. 1999)

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