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ECOSYSTEMS

Ecosystem Consequences of Changing Inputs of Terrestrial Dissolved Organic Matter to Lakes: Current Knowledge and Future Challenges

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ABSTRACT

Lake ecosystems and the services that they provide to people are profoundly influenced by dissolved organic matter derived from terrestrial plant tissues. These terrestrial dissolved organic matter (tDOM) inputs to lakes have changed substantially in recent decades, and will likely continue to change. In this paper, we first briefly review the substantial literature describing tDOM effects on lakes and ongoing changes in tDOM inputs. We then identify and provide examples of four major challenges which limit predictions about the implications of tDOM change for lakes, as follows: First, it is currently difficult to forecast future tDOM inputs for particular lakes or lake regions. Second, tDOM influences ecosystems via complex, interacting, physical-chemical-biological effects and our holistic understanding of those effects is still rudimentary. Third, non-linearities and thresholds in relationships between tDOM inputs and ecosystem processes have not been well described. Fourth, much understanding of tDOM effects is built on comparative studies across space that may not capture likely responses through time. We conclude by identifying research approaches that may be important for overcoming those challenges in order to provide policy- and management-relevant predictions about the implications of changing tDOM inputs for lakes.

Key words: lake; ecosystem; dissolved organic matter; dissolved organic carbon; terrestrial inputs; allochthonous; environmental change; review.

INTRODUCTION

Terrestrially derived dissolved organic matter (terrestrial DOM or tDOM) is increasingly recognized as a fundamental control on lake ecosystem structure

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and function (Jones 1992; Kullberg and others 1993; Williamson and others 1999; Prairie 2008). Like other major drivers such as nutrient concentrations and fishing pressure, tDOM has far-reaching effects on freshwater ecosystems. These effects occur at multiple levels of biological organization, ranging from cellular chemical stress to ecosystem biogeochemical cycles (Steinberg and others 2006; Prairie 2008). Furthermore, tDOM concentrations vary widely across the landscape, and inputs of tDOM to surface waters have changed substantially over the past several decades in many north temperate and boreal regions (Hanson and others 2007; Monteith and others 2007; Figure 1).

Given these two observations—that tDOM concentrations fundamentally shape lake ecosystems, and that these concentrations are changing through time—what are the implications for the future structure and function of these systems? Despite our considerable understanding of the role of tDOM in lakes, this is a surprisingly difficult question to answer. In this paper, we briefly review the effects of tDOM on lake ecosystems and the causes of recent changes in tDOM concentrations. We draw from several excellent reviews as well as more recent work, integrating perspectives from watershed hydrology, physical limnology, biogeochemistry, microbial and food web ecology, and other fields. We then focus on exploring four challenges that currently make predictions about the implications of changing tDOM inputs difficult, and conclude by suggesting some research avenues that may help to overcome these challenges.

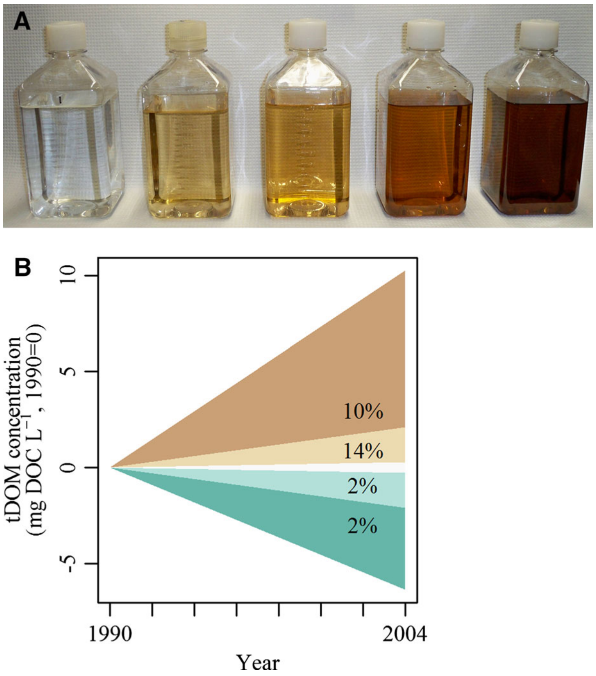

Figure 1. **A** The differences in color between these samples of water from five different lakes are due to different concentrations of terrestrially derived dissolved organic matter (tDOM). **B** Concentrations of tDOM in surface waters have changed over the past several decades in many surface waters. Numbers show the proportion of 500 lakes in which the tDOM trends from 1990 to 2004 falls within the shaded region. Increases greater than 0.02 mg DOC L^{-1} y^{-1} were observed in 24% of lakes. Redrawn from Monteith and others (2007) using data from the ICP Waters program (adapted by permission from Macmillan Publishers Ltd: Monteith and others 2007, copyright 2007).

WHAT IS tDOM AND HOW DOES IT ENTER LAKES?

Terrestrial DOM includes a diverse and variable suite of substances that originate from the tissues of terrestrial plants, is typically modified in the soil environment, and is ultimately transported to lakes by groundwater and surface water. Plant materials, including structural compounds like cellulose and lignin, are modified by interactions with minerals and microorganisms in the soil environment, where conditions like pH, temperature, and redox potential regulate solubility and rates of decomposition (Thurman 1985). The interaction of these physical and biological processes alters the chemical composition of soil organic matter, yielding a mixture of substances of diverse molecular size, age, and biological availability (Neff and Asner 2001). Although some of these substances are mineralized or sequestered in the soil, a substantial portion can be exported to aquatic systems. This export from the watershed ranges from 1 to 10 g C m^{-2} y^{-1} or higher, depending on the ecosystem (Mulholland 2003), and globally constitutes about half of terrestrial net ecosystem production on an annual basis (Battin and others 2009). Hydrology is an important control on export, both as the vehicle for transporting organic matter and because wet soils accumulate organic matter faster than they mineralize it and so have more available for export (Freeman and others 2001a). Export may vary among nearby watersheds due to differences in hydrology or in other factors such as terrestrial NPP, watershed size, or the areal extent of wetlands and their proximity to surface waters (Gergel and others 1999; Canham and others 2004; Jansson and others 2008).

The diverse chemical composition of tDOM, and the spatial and temporal variability in that composition, makes it difficult to fully and simply

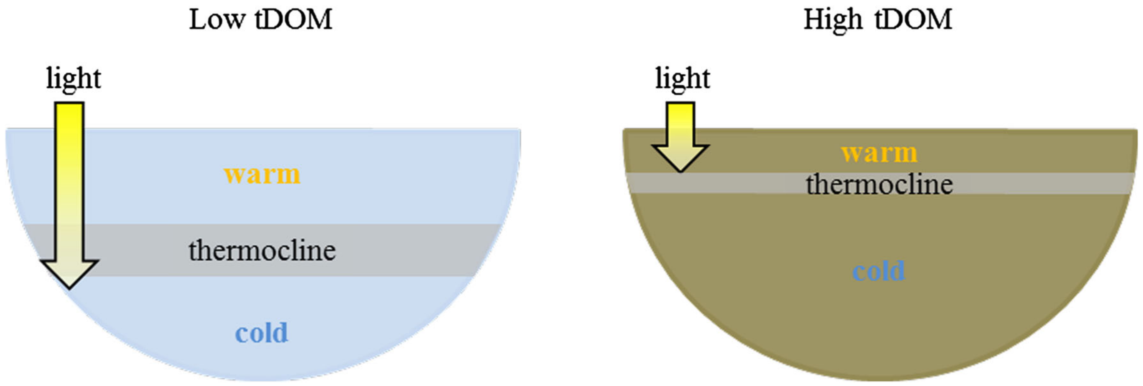

Figure 2. Light is extinguished rapidly with depth in a high-tDOM lake with dark water (*right*), and much less rapidly in a low-tDOM lake (*left*). Consequently, the water volume and bottom area capable of supporting photosynthesis are much lower in the high-tDOM lake. High-tDOM lakes also have steeper and shallower thermal gradients between warm oxygenated surface water and cold, potentially deoxygenated deep water. These differences strongly impact metabolic rates, biogeochemical processes, and animal habitat.

characterize (Sleighter and Hatcher 2007; Minor and others 2014). In general, however, a large fraction of the terrestrial DOM that is exported to aquatic ecosystems is comprised of humic substances (that is, humic and fulvic acids) that contain aromatic hydrocarbons including phenols, carboxylic acids, quinones, and catechol (McDonald and others 2004). These molecules are relatively resistant to microbial degradation by virtue of their molecular structure and high C:N and C:P ratios (McKnight and Aiken 1998). They also absorb light strongly in the ultraviolet and short wavelength visible region of the spectrum, giving water a brown, tea-stained color that affects light and heat penetration (Jones 1992). Operationally, DOM concentrations are often measured in terms of dissolved organic carbon, or DOC.

A FUNDAMENTAL CONTROL ON LAKE ECOSYSTEM STRUCTURE AND FUNCTION

Two properties of the complex suite of molecules that comprise tDOM have major implications for the structure of lake ecosystems.

First, tDOM absorbs solar radiation at particular wavelengths, changing the vertical distribution of light and heat (Kirk 1994; Fee and others 1996) (Figure 2). Light and temperature control metabolic rates, primary productivity, biogeochemistry, the distribution of organisms, and a host of other processes in lakes. In many lakes, terrestrial DOM is the primary regulator of water column transparency to the portion of shortwave energy (visible and ultraviolet light) that penetrates the near-surface layer (Morris and others 1995; Williamson and others 1996). All else being equal, higher tDOM concentrations drive faster light extinction and a vertical distribution of heat that is more heavily weighted toward the surface, unless there is sufficient mixing energy (most often in the form of wind shear) to prevent stratification (Pérez-Fuentetaja and others 1999; Houser 2006). Faster light extinction limits light availability to primary producers and alters interactions between visual predators and their prey. Warmer surface water results in stronger outward energy fluxes, so high-tDOM lakes are generally colder overall (Tanentzap and others 2008; Read and Rose 2013). The surface-weighted distribution of heat in low-transparency lakes also means that thermal stratification occurs closer to the surface and tends to be more stable (Kling 1988; Read and Rose 2013; Palmer and others 2014); more stable stratification reduces the amount of vertical mixing and alters vertical gradients of dissolved oxygen and other chemicals (Imberger 1998; Wüest and Lorke 2003; MacIntyre and others 2006). This affects biogeochemical reaction rates and habitat suitability for aerobic organisms.

Second, loads of tDOM are an energetic input to the base of the lake food web and can support catabolic and anabolic metabolism (del Giorgio and Peters 1994; Pace and others 2004) (Figure 3). A portion of the load occurs as low-molecular weight compounds that can be rapidly consumed by heterotrophic bacteria (Berggren and others 2010). More recalcitrant, high molecular weight compounds comprise the majority of the load, but even these are slowly degraded and consumed if

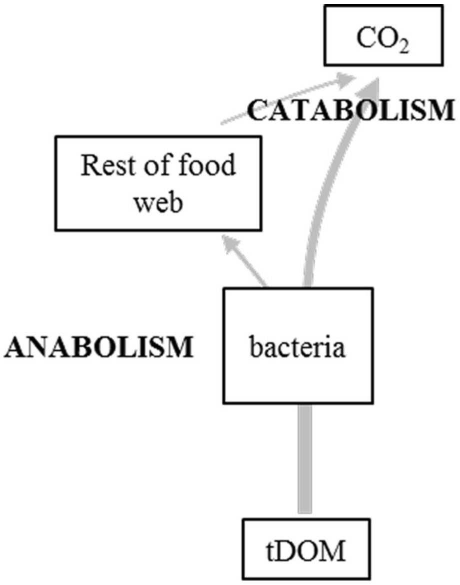

Figure 3. Terrestrial DOM provides a substrate for anabolic and catabolic metabolism, helping to support lake food webs and influencing carbon emissions to the atmosphere.

residence times are sufficient (Moran and Hodson 1990; Tranvik 1990; Volk and others 1997; Tranvik 1998; Aitkenhead-Peterson and others 2003; Young and others 2005). Photochemical reactions can also modify the lability of tDOM inputs (Geller 1986; Tranvik and Bertilsson 2001). Terrestrial DOM consumed by heterotrophic bacteria follows one of two pathways. Some is incorporated into cellular structures and thus becomes available to higher consumers like zooplankton and fishes, which may derive substantial portions of their biomass from terrestrial sources in lakes with large tDOM inputs (Grey and others 2001; Karlsson and others 2003; Pace and others 2004; Matthews and Mazumder 2006; Taipale and others 2008; Brett and others 2009; Cole and others 2011; Solomon and others 2011; Tanentzap and others 2014). Some is respired as CO_2, adding to the pool of inorganic carbon dissolved in lake water. This contributes to a net flux of CO_2 from the water to the atmosphere in many lakes with large tDOM inputs (Hope and others 1996; Sobek and others 2003; Larsen and others 2011b). These contributions of tDOM to metabolic processes in lakes are variable but sometimes quite large.

TERRESTRIAL LOADS TO AQUATIC SYSTEMS ARE CHANGING

Terrestrial DOM loads and concentrations have increased over the past several decades in many north temperate and boreal surface waters, in a phenomenon sometimes referred to as ''browning'' (Skjelkvale and others 2005; Roulet and Moore 2006; Kritzberg and Ekstrom 2012; SanClements and others 2012; Figure 1B). Temporal trends vary among systems, and include patterns of stable or decreasing DOC concentrations. For instance, Schindler and others (1997)observed decreasing DOC in a set of lakes experiencing long-term drought. Nonetheless, across broad regional and intercontinental scales, the majority of systems have experienced increases in DOC concentrations (Monteith and others 2007; Winterdahl and others 2014). For instance, trends in DOC from 1990 to 2004 were positive in 70% of 522 surveyed waters in North America and Europe, and DOC concentrations over roughly this period increased by 91% on average in monitored streams and lakes in the United Kingdom (Evans and others 2005; Monteith and others 2007).

A number of mechanisms related to climate change, atmospheric deposition, hydrology, and other drivers have been proposed as contributors to observed changes in DOC, and their relative importance has been debated (Evans and others 2006; Roulet and Moore 2006; Clark and others 2010). These mechanisms include (1) factors influencing the quantity and quality of plant-derived soil organic matter, such as climate effects on terrestrial net primary productivity and vegetation communities and nitrogen deposition effects on the characteristics of plant-derived organic matter and belowground C and N processing (Pregitzer and others 2004; Larsen and others 2011a); (2) factors influencing the solubility of soil organic matter, such as the impact of sulfate deposition on soil chemistry and the impact of temperature on extracellular enzyme activity in peat soils (Freeman and others 2001a; Clark and others 2005; De Wit and others 2007; Monteith and others 2007; Erlandsson and others 2008); and (3) factors influencing the hydrologic transport of tDOM to surface waters, including inter-annual or decadal-scale variation in precipitation and runoff patterns (Hongve and others 2004; Erlandsson and others 2008; Haaland and others 2010). Current synthesis suggests that many of these mechanisms play a role at certain spatial and temporal scales, but that the primary driver for decadal-scale increases, where observed, is linked to decreases in atmospheric sulfate deposition as a result of emissions regulations in North America and Europe (Monteith and others 2007; Erlandsson and others 2008; Clark and others 2010). These decreases seem to be changing soil chemistry in ways that increase the solubility of tDOM (Clark and others 2005; De Wit and others 2007).

HOW WILL CHANGING tDOM LOADS AFFECT LAKES?

It is clear that important ecosystem processes as diverse as carbon cycling, fish production, and drinking water provisioning could be strongly impacted by changes in tDOM inputs. Yet as we describe in this section, despite the considerable existing literature, four fundamental gaps in our understanding make concrete predictions about such ecosystem responses challenging.

Challenge 1: Uncertainty About Future tDOM Loads

The impact on lake ecosystems of any future changes in tDOM inputs will depend first and foremost on the magnitude of those changes. The tDOM increases observed over the past few decades have been substantial in some regions, as described above. Future changes as a result of shifts in sulfate deposition and climate could also be substantial, but our ability to forecast those changes is currently limited.

Changes in sulfate deposition will affect tDOM loads at very broad spatial scales. In North America and Europe, deposition reductions will likely cease to be a major driver of increasing loads as legislated emission targets are met and soils recover. In fact, in these regions, the observed changes in tDOM concentrations over recent decades may represent recovery to a more pre-industrial state, rather than a novel disturbance; continued development of paleolimnological techniques for inferring past DOC concentrations could help address this question (Rouillard and others 2011; Bragée and others 2013). Conversely, in industrializing countries rapidly increasing emissions may drive decreases in tDOM loads in downwind regions with acid-sensitive soils. Soil heterogeneity, patchiness of emissions sources, atmospheric transport mechanisms, and other factors will create local heterogeneity in these broad-scale patterns.

Superimposed on these effects, climate change will increasingly alter the processes that drive tDOM loading. The net effect of climate change on tDOM loads in a particular location or region is difficult to predict, given the complexity of the processes that generate and transport tDOM and the potential for effects at time scales ranging from years to centuries (Table 1). For instance, warmer temperatures will favor not only greater inputs to the soil OM pool via increased terrestrial primary production but also greater removals from that pool via increased soil respiration (Wu and others 2011), and the transport of that OM to lakes in the form of tDOM will vary in both quantity and quality depending on precipitation patterns and hydrology. Hydrologic change may also alter transport of iron, which, like tDOM, contributes to water color; given that many of the effects of high-tDOM water are due to its color, this potential change in the color of water with a given tDOM concentration may be important (Weyhenmeyer and others 2014). Mechanistic and phenomenological watershed models can forecast the net effects of these changes, and there is a clear need to continue developing, testing, and integrating these models with climate and vegetation projections (Futter and others 2007; Larsen and others 2011a).

Other regional- or global-scale environmental changes may also have an impact on tDOM loads and surface water browning. Notably, nitrate deposition may continue to affect tDOM loads via both its plant fertilization and soil acidification effects. Land-use and land-cover changes have also been implicated in altering tDOM fluxes (Mattsson and others 2005), and will interact with changing atmospheric deposition and climate conditions to regulate tDOM loading to lakes in a given region (for example, Winterdahl and others 2014).

Overall, specific quantitative or even qualitative predictions about future tDOM loads at relevant regional or lake-level spatial scales are difficult given our current understanding. Nonetheless, it seems likely that tDOM loads will continue to change in coming decades as anthropogenic effects reshape soil organic matter pools and their connections to aquatic systems. Given the potential for these changes to profoundly influence lake ecosystems, there is a concurrent need for aquatic ecologists to consider the potential impacts of changing tDOM loads.

Challenge 2: Complex Interacting Effects

Terrestrial DOM influences lake biota and biogeochemistry directly, and also indirectly via its regulating effects on the physical environment. These features create complex networks of interactions among physics, biology, and chemistry. For simplicity, we consider the effects of tDOM change but not potential interactions with climate or other ongoing environmental changes (Kritzberg and others 2014; Weidman and others 2014). We focus our discussion in this section and those that follow on predicting the effect of increases in tDOM

Table 1. Some Mechanisms By Which Changes in Climate (Temperature, Precipitation, and Hydrology) Have Affected, and May Continue to Affect, Terrestrially Derived Dissolved Organic Matter (tDOM) Loads to Lakes at Time Scales Ranging From Years to Centuries

Driver	Mechanism	Effect on tDOM load	Reference
Years			
Increased temperature	Increased soil decomposition rate, decreased soil OM pool	Decrease	Kirschbaum (2006)
Increased temperature	Increased microbial release of sorbed soil OM	Increase	Freeman and others (2001a), (2001b), von Lutzow and Kogel-Knabner (2009)
Increased temperature	Increased soil oligochaete activity	Increase	Cole and others (2002)
Increased precipitation	Increased GPP of terrestrial vegetation, increased soil OM pool	Increase	Wu and others (2011)
Increased runoff	Increased tDOM transport through catchment	Increase	Tranvik and Jansson (2002), Pastor and others (2003), Erlandsson and others (2008)
Drought	Decreased tDOM transport through catchment	Decrease	Schindler and others (1997)
More flashy runoff	More flashy transport	More flashy	Schindler and others (1997), Hongve and others (2004)
Increased frequency or magnitude of drought-rewetting cycles	Increased aerobic mineralization of peat, coupled with flushing out of soluble tDOM	Increase?	McDonald and others (1991), Mitchell and McDonald (1992), Hughes and others (1998), Clark and others (2005), (2009)
Change in snow cover duration	Soil frost depth, soil solution tDOM concentrations and fluxes	Change	Haei and others (2010)
Decades			
Increased temperature	Terrestrial vegetation assemblage shifts towards species with greater GPP and biomass, increased soil OM pool	Increase	Barichivich and others (2013)
Increased temperature	Melting permafrost, increase or decrease in tDOM load depending on depth of organic soil layer relative to hydrologic flowpaths	Change	Striegl and others (2005), Frey and McClelland (2009)
Increased temperature and altered hydrology	Change in wetland and peatland soil OM stocks	Change	Davidson and Janssens (2006)
Centuries			
Increased temperature and altered geographical distribution of precipitation	Change in wetland and peatland equilibrium states, change in geographical distribution of wetlands	Change	Belyea and Malmer (2004)

GPP, gross primary production; OM, organic matter.

(''browning''), but in general our predictions can be reversed for scenarios of decreasing tDOM.

Lake carbon cycles provide one example of these complex effects. Lakes are hotspots for carbon processing on the landscape, and play a significant role in regional and global carbon cycles (Cole and others 2007; Tranvik and others 2009). In general, tDOM concentration is positively correlated with ecosystem respiration and CO_2 release to the atmosphere(del Giorgio and Peters 1994; Sobek and others 2005; Solomon and others 2013). Yet while that relationship is a powerful heuristic, the complexity of the underlying mechanisms adds considerable noise and limits its utility for predicting the carbon balance implications of changing tDOM inputs. For instance, consider the ways in which tDOM interacts with phytoplankton production, which removes CO_2 from the water via photosynthetic fixation (Figure 4A). Terrestrial DOM reduces light availability at a given depth, which can limit production, although it also absorbs heat and decreases the depth of the mixed layer, constraining epilimnetic phytoplankton to the near-surface zone where light availability is higher than it is at

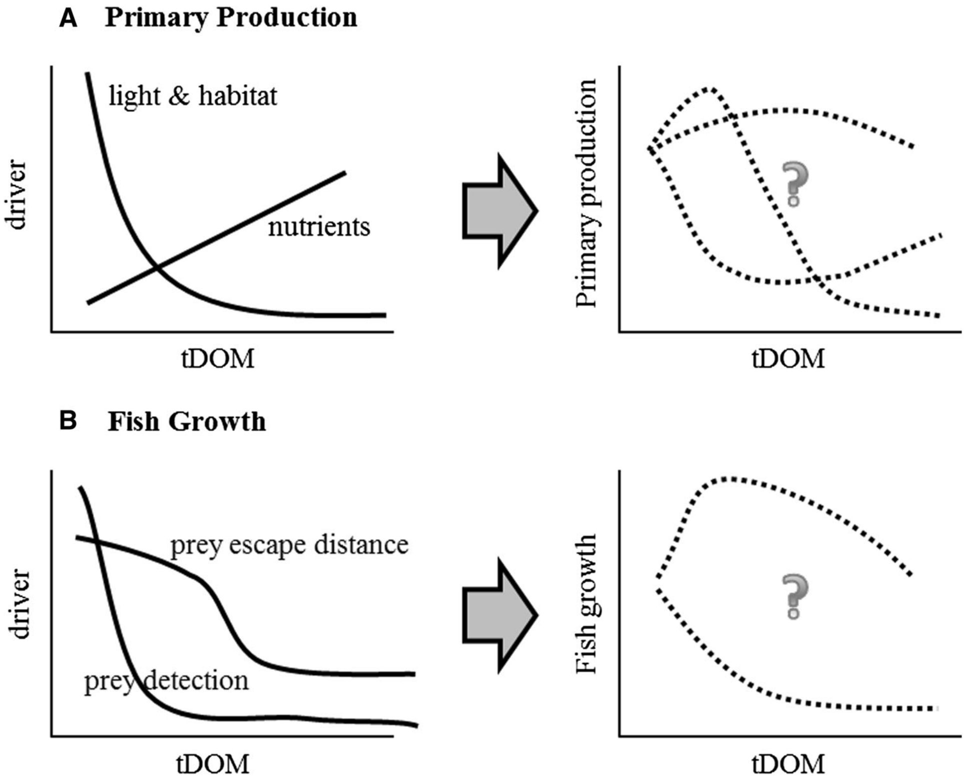

Figure 4. Terrestrial DOM affects lake processes through complex networks of physical, chemical, and biological effects. Predicting the implications of tDOM change, therefore, requires research that is both mechanistic and holistic. Interacting and counteracting effects of tDOM on light, nutrients, and other factors make it difficult to predict how tDOM change will affect ecosystem services like primary production (**A**) and fish growth (**B**).

greater depths (Jones 1992; Carpenter and others 1998). Mineralization of tDOM by heterotrophic bacteria releases nutrients and inorganic carbon, both of which may stimulate phytoplankton production; on the other hand, the bacteria themselves may outcompete phytoplankton for the nutrients that are released, and stronger, shallower stratification limits phytoplankton access to internally recycled nutrients (Jackson and Hecky 1980; Jones 1992; Hessen 1998; Jansson and others 2012). In short, tDOM has a series of cascading and interacting physical, chemical, and biological effects that strongly influence rates of primary production; other carbon cycle processes are similarly influenced, and also interact with each other and with rates of primary production (Brothers and others 2014). These complexities are not unique to the carbon cycle; for instance, tDOM-induced changes in light regime can alter benthic nitrogen sinks by changing the redox conditions that control nitrification and denitrification (Fork and Heffernan 2013).

Behavior adds another layer of complexity in considering tDOM effects on animals such as fishes (Figure 4B). Fish are keystone species in many lakes, and support culturally and economically valuable fisheries. Processes that drive the fitness of an individual fish and the dynamics of fished populations—such as avoiding predators, capturing food, growing, and reproducing—are strongly influenced by tDOM concentrations (Williamson and others 1999; Stasko and others 2012). Dark water reduces the abundance of the zooplankton and zoobenthos that form the base of food chains supporting fishes (Karlsson and others 2009; Jones and others 2012; Kelly and others 2014). It also can drive predator-prey interactions by favoring species adapted to feed in low-light environments. For example, perch feeding on zooplankton are at a competitive disadvantage relative to roach in high-tDOM, low-light conditions (Estlander and others 2010). This effect is exacerbated where the tDOM-driven light limitation reduces the abundance of macrophytes (Sondergaard and others 2013), which provide refuge habitat that normally lowers predation risk and increases invertebrate prey availability for perch (Olin and others 2010). Although warmer surface waters in dark lakes could enhance growth rates of some fish species, the accompanying steeper thermal stratification promotes hypolimnetic hypoxia, decreasing available fish habitat. Spawning habitat availability and suitability similarly depend on temperature and dissolved oxygen. Fish behavior responds to all of these forces, as individuals try to maximize fitness by allocating activities like foraging in time and space, triggering cascading effects on the abundance or behavior of lower trophic levels which in turn feed back to fish.

Challenge 3: Non-Linear Relationships and Context Dependence

Many processes in lakes are non-linearly related to tDOM concentration. This has two important implications. First, a given change in tDOM load will have different effects depending on the initial context. Second, identifying the shapes of relationships between lake processes and tDOM, and the position of threshold or inflection points in those relationships, is an important research goal.

Changes in light availability and thermal structure in response to differences in tDOM concentrations (for example, Figure 2) are one important example of a non-linear effect. A given change in tDOM concentration alters the heat distribution and stratification strength considerably in a lake that was initially low-tDOM but only slightly in a lake that was initially high-tDOM (Snucins and Gunn 2000). Similarly, Read and Rose (2013) modeled lakes across a DOC concentration gradient and found striking non-linearity in thermal responses to climate, with clearer lakes being increasingly sensitive to climate variability and DOC perturbations. The power-law relationship between light attenuation and tDOM concentration (Morris and others 1995) structures these non-linear physical patterns. These effects are likely stronger in small lakes than in large ones, because wind-driven mixing and basin-scale hydrodynamics become more important in larger lakes, reducing the relative importance of water clarity as a control on thermal structure (Fee and others 1996; Read and others 2012). The non-linear effects of light and heat propagate up the food web to control biomass production at trophic levels ranging from primary producers to top consumers, including benthic algae, zoobenthos, zooplankton, and fishes (Ask and others 2009; Karlsson and others 2009; Finstad and others 2014; Kelly and others 2014). Many of these food web studies suggest a threshold DOC concentration of roughly 10 to 14 mg l^{-1} above which consumer production is severely reduced, and a recent experimental pond study that found little effect on zoobenthos as a result of raising DOC concentrations to 10 mg l^{-1} lends further credence to this idea (Jonsson and others 2015). Yet the existence of such a threshold and the DOC concentration at which it occurs has not been explicitly investigated.

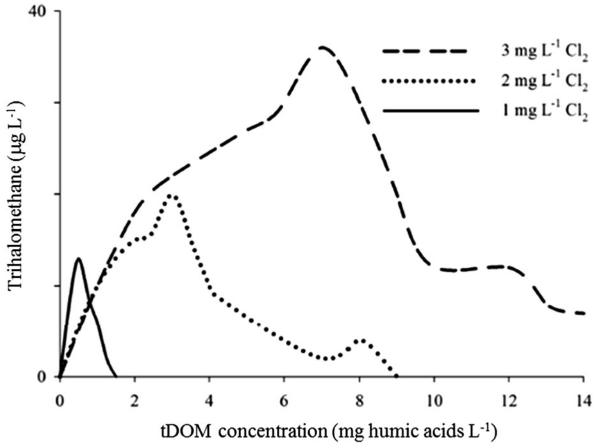

Figure 5. Terrestrial DOM concentrations are non-linearly related to many important ecosystem processes. Describing the shape of these relationships, including critical thresholds of tDOM, is therefore an important objective. The production of carcinogenic trihalomethanes during drinking water purification varies non-linearly with tDOM concentration, and with other factors such as dosage of chlorine (Cl_2). Redrawn from Adin and others (1991), copyright 1991, with permission from Elsevier.

The effects of changing tDOM loads on drinking water supplies will also be context-dependent (Figure 5). Lakes and other surface waters provide drinking water for a substantial portion of the world population, including, for instance, 56% of the United States population (Kenny and others 2009). Elevated tDOM concentrations can increase treatment costs and reduce quality of drinking water in several ways, as they can cause color, taste, and odor problems; transport heavy metals and organic pollutants; promote the growth of bacteria; and produce chlorination byproducts called trihalomethanes, which may be carcinogenic (Matilainen and others 2010; Ledesma and others 2012). In general, trihalomethane production increases with DOC concentration, but the mechanism is complex and depends on chlorine dosage, bromine concentration, pH, and temperature (Adin and others 1991; Krasner and others 1994). These concerns are motivating modified treatment strategies such as coagulation, magnetic ion exchange, and adsorbents, typically increasing costs for utilities and consumers (Matilainen and Sillanpaa 2010).

Challenge 4: Substituting Space for Time

Surveys of lakes that differ in tDOM concentration have been instrumental in developing understanding of tDOM effects (Karlsson and others 2009; Lapierre and others 2013). For example,

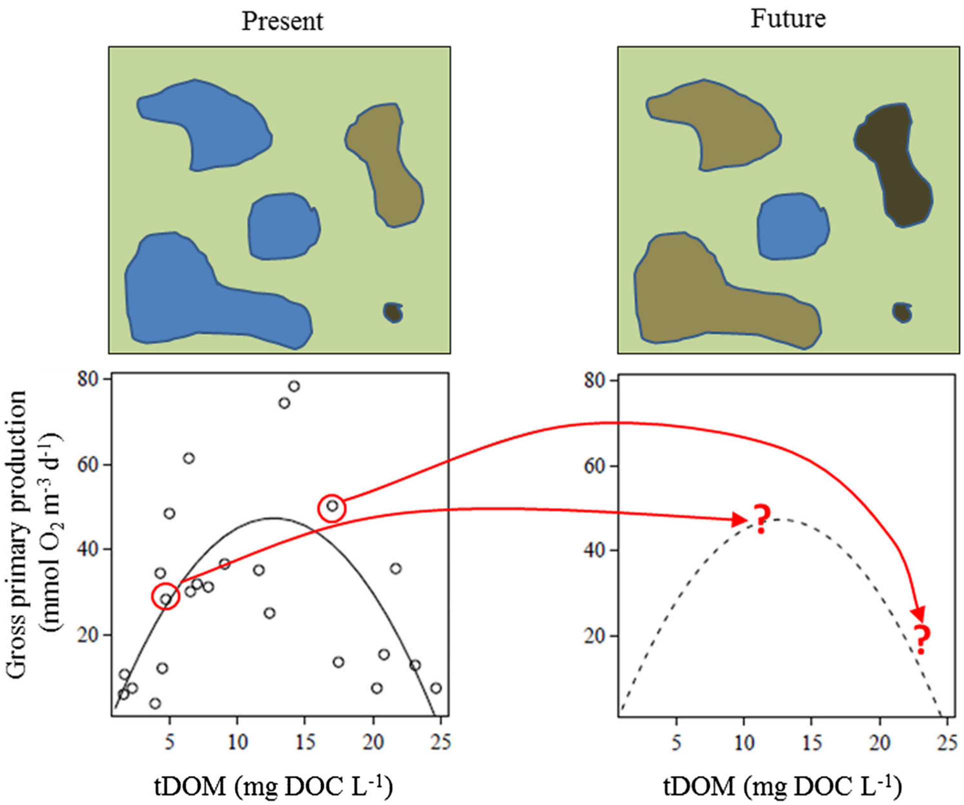

Figure 6. Future changes in tDOM inputs may alter existing relationships on which our understanding of tDOM effects is built. *Left* Present understanding of the relationship between tDOM and phytoplankton gross primary production is built on spatial surveys across existing gradients on the landscape (data from Hanson and others 2003; copyright 2003 by the American Society of Limnology and Oceanography, Inc. and modified by permission of Wiley). *Right* It is unclear whether future changes in tDOM concentration will shift phytoplankton gross primary production along the relationship observed in spatial surveys, or whether those changes will alter the mechanisms that produced the spatial patterns, yielding new relationships.

phytoplankton primary production per unit area shows a hump-shaped relationship with tDOM concentration, with peak rates at intermediate tDOM concentrations (Hanson and others 2003; Figure 6). This pattern seems to occur because hydrologic inputs bring nutrients as well as tDOM, so intermediate tDOM lakes have enough nutrients to support phytoplankton productivity and little enough tDOM that the shading effect on phytoplankton is not strong. Clearer lakes have plenty of light but are nutrient limited, whereas darker lakes have plenty of nutrients but are light limited.

Yet although surveys across space can help develop understanding of mechanisms, they may fail as predictive tools if change across time alters those mechanisms or invokes new ones (Clark and others 2010). For instance, the cross-lake relationship between tDOM and phytoplankton production depends in part on cross-lake correlation between tDOM concentrations and nutrient loads, which may be altered by the changes in soils and hydrology that would drive temporal change in tDOM within a given lake. The relationship may also depend in part on static lake properties like morphometry that would not change with changing tDOM loads.

Understanding the implications of temporal changes in tDOM inputs will also require that we pay attention to dynamic eco-evolutionary and community assembly processes that have not been apparent given the more static worldview of spatial surveys. Given the many strong effects of tDOM on lake ecosystems, it seems almost certain that changes in tDOM concentrations will impose selective pressures that favor some phenotypes over others. Alternatively, higher tDOM might confer an advantage to fish species that are less reliant on visual feeding, altering community structure over time (Stasko and others 2012). Transient responses like these will likely occur at decadal time scales for fishes, and much more rapidly for invertebrates and microbes with shorter generations and faster dispersal, and may significantly modify ecological responses to changing tDOM loads.

Synthesis and Implications

Because of the central role that tDOM plays in structuring lake ecosystems and important ecosystem services, resource managers and policymakers need to understand the implications of ongoing and future changes in tDOM inputs to surface waters (Stanley and others 2012). Although aquatic scientists know a great deal about the role of tDOM, new research and new kinds of research are needed to bring our understanding to bear on policy and management.

Quantitative predictions of future tDOM loads and concentrations for particular regions and watersheds will be essential to management decision-making. We know that loads depend on an interacting set of drivers encompassing atmospheric chemistry, hydrology, soil processes, terrestrial vegetation, and climate, and that concentrations depend on loads and the in-lake processing of those loads (Kohler and others 2013). This is a complex system that crosses traditional disciplinary boundaries; furthermore, there are significant uncertainties about future trends in some of the important driving factors. Improving predictions about future loads will require interdisciplinary integration and a variety of approaches including long-term observation, paleolimnological analyses, better sampling in different biomes, conceptual and mechanistic models, and scenario analyses.

To complement those predictions of future loads, we need better understanding of how changes in loads will influence ecosystem processes and services. The non-linear relationships that we have highlighted here indicate that many lakes may be quite resilient to tDOM load alterations, at least with respect to particular processes. On the other hand, the complexity of tDOM-driven physical-chemical-biological interactions, and our uncertainty about the applicability of space-for-time substitutions, suggests that understanding tDOM-driven changes will require research that is both mechanistic and holistic. Observational surveys have been and will continue to be essential, especially when they can describe important thresholds and non-linear relationships. Increasingly, researchers should use replicated experiments and models that can isolate key mechanisms and integrate complex and interacting effects. Whole-ecosystem experiments, although they sacrifice replication, will be essential for understanding the net results of complex interactions. By integrating impact-oriented research with better predictions of future tDOM loads, aquatic scientists will be able to provide policy-relevant science to help maintain valuable ecosystem services in the face of large-scale change in a major ecosystem driver.

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