Terrestrially Derived Dissolved Organic Matter – Its Influence on Lake Food Webs

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Terrestrially derived dissolved organic matter (DOM) can profoundly influence life in lakes, from the primary producers at the base of the food web all the way up to the fishes. In this article we provide an overview of these influences, based on completed and ongoing research conducted by scientists across the lake-rich regions of the northern hemisphere. We find it to be a fascinating research area, because it incorporates many fundamental principles of lake ecology and because we are learning more about it all the time.

The effects of DOM on lake food webs are diverse and interconnected. The most visually apparent effect is on the penetration of sunlight through the water. Complex molecules common in terrestrially derived DOM absorb solar radiation at particular wavelengths. This gives the water a characteristic brownish tinge, just the way that tea leaves do to a cup of tea (Figure 1). A higher DOM concentration means more light absorption, and less light available at any depth in the water column of the lake. Absorption of sunlight by DOM also warms up the water, increasing surface water temperature and altering stratification patterns. DOM also has chemical and biological effects. For instance, it includes weak organic acids that can reduce pH, nutrients like nitrogen and phosphorus that benefit algae, and organic carbon compounds that can provide a source of energy to bacteria.

The base of the food web

When DOM reduces light penetration, the effects on algae – the primary producers at the base of the food web – can be profound. Consider first what reduced light penetration means for the benthic algae that live on the mud, rocks, and other surfaces at the bottom of the lake. While a tree in a forest might grow from the shade to reach the sun, these benthic algae are stuck in place, doing the best they can with the light they can capture. A reduction in light availability limits their ability to photosynthesize, reducing their productivity. If light levels are low enough, benthic algae may not be able to capture enough energy to keep ahead of their maintenance costs. Thus their total productivity across the lake as a whole decreases as both their productivity at any depth, and the range of depths over which they can persist, decrease.

For the pelagic (open water) algae that float in the water, the effects of DOM on productivity are more complex. These pelagic algae (also known as phytoplankton) experience the same reduction in light availability at a given depth that the benthic algae do. But they are also subjected to two counterbalancing effects of DOM that are unique to the pelagic habitat.

Figure 1. Samples from lakes spanning a gradient of terrestrial dissolved organic matter (DOM) concentrations.

The first of these counterbalancing effects is an increase in nutrient availability: Higher DOM concentrations are generally associated with higher concentrations of the nutrients that algae need for growth, like phosphorus and nitrogen. This matters for phytoplankton living in the water column, but is less important for benthic algae that can access nutrients oozing upward from rich lake sediments.

The second counterbalancing effect is a little harder to understand, but boils down to an interaction between light, heat, and mixing. Recall that higher DOM concentrations mean lower light availability at any depth, because DOM molecules absorb solar radiation. Like a black shirt on a sunny day, darker water not only absorbs light, but heats up in the process. In a high-DOM lake, therefore, the vertical distribution of heat tends to be weighted towards the surface – the epilimnion (upper water layer) is warm and thin, the thermocline (zone of temperature transition) is fairly shallow and sharp, and the hypolimnion (bottom layer) is cold and thick. For phytoplankton circulating throughout the epilimnion, the shallow extent of this layer can actually be good news: even though they experience less light at any given depth, the range of depths they are circulating over has been reduced. Under the right conditions, this may even mean that the average amount of light that they "see" in a day may not be much different than it would be in a lower-DOM lake (Figure 2).

What does this all mean for pelagic primary productivity? Recent research

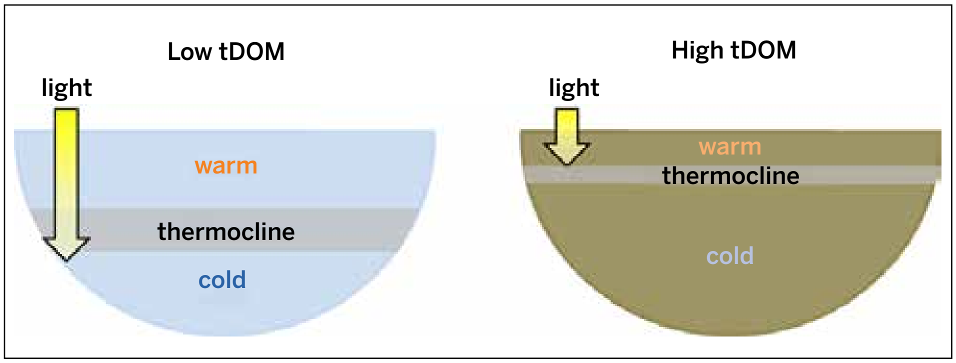

Figure 2. Contrasting depths of stratification in a clear (low tDOM) and brown (high tDOM) lake.

suggests that it follows a hump-shaped relationship with DOM concentration (Kelly et al. 2018; Figure 3). When DOM concentrations are very low there's plenty of light available in the water column, but nutrients are limiting and so primary productivity is low. At the other extreme, when DOM concentrations are very high there's very little light available, so primary productivity is low even though nutrients are plentiful. Somewhere in the middle there's a switch point where primary productivity is maximized. The DOM concentration at which this switch occurs is predicted to depend on the molecular characteristics of the DOM, which influence how much light it absorbs and how nutrient-rich it is. Lake size is also important, because in a large lake the depth of the thermocline is driven primarily by the wind, rather than by the effects of DOM on heat absorption.

Moving up the food web

The effects of DOM on light, heat, and the productivity at the base of the food web also influence organisms at higher trophic levels, like benthic invertebrates, zooplankton, and fishes. Several studies have documented relationships between DOM concentrations and the productivity, biomass, or individual growth of these groups.

These patterns presumably arise in large part from bottom-up limitation: control of primary productivity by DOM in turn limits the potential productivity of the organisms further up the food web that depend on that primary productivity. The bottom-up effects are strong enough to overwhelm the modest positive effects of DOM on food web productivity which occur when bacteria consume DOM and are in turn consumed by animals like zooplankton. There is even some evidence that the hump-shaped relationship between DOM concentration and pelagic primary production can be mirrored by the organisms that rely on that primary production. For instance, in one whole-lake experiment where a modest increase in DOM concentration led to an increase in pelagic primary productivity, the productivity of zooplankton increased as well (Kelly et al. 2016).

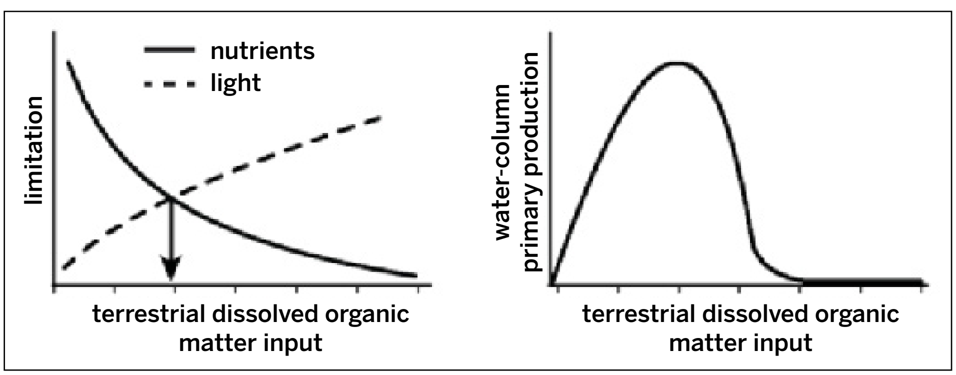

Figure 3. With low DOM input nutrient availability can be limiting and therefore productivity is low. At high DOM input levels light is severely limiting and productivity is also low. We expect the highest productivity at intermediate DOM input levels because neither nutrients nor light are extremely limiting. (Figure after Kelly et al. 2018.)

Other forces beside bottom-up limitation are also clearly at work in the relationship between DOM and animal populations in lakes. One study of benthic invertebrates from ten lakes that spanned a wide range of DOM concentrations showed that it was the effects of DOM on heat, rather than on primary production, that seemed to be most important for controlling productivity of this important group of lake organisms (Craig et al. 2015). Lakes with high DOM concentrations had shallower thermoclines and thus less of the warm, well-oxygenated bottom habitat that supports fast growth of benthic invertebrates. Other studies have demonstrated the ways in which DOM alters predation rates of fish on their prey via changes in the visible light environment (Jönsson et al. 2013), and the ways in which it alters rates of cellular damage in zooplankton via changes in the ultraviolet light environment (Wolf et al. 2016).

As these examples make clear, differences in DOM concentrations can impose strong differences on the environment and ecological interactions that organisms experience in lakes – the kinds of differences that might be expected to impose selective pressure on the traits of those organisms. One interesting new thread of research has begun to explore the potential for these sorts of eco-evolutionary dynamics. Reductions in the availability of benthic prey for fishes in high DOM lakes has been shown in several studies to drive a shift to higher use of pelagic prey. One such study documented systematic changes in the body shape of Eurasian perch inhabiting high DOM lakes when compared to those from low DOM lakes, including increased eye size and loss of habitat-specific morphologies (Bartels et al. 2016). Another study revealed that the time to maturity and investment in reproduction by bluegill sunfish changed dramatically across a set of lakes spanning a DOM concentration gradient, such that lifetime reproductive output of fish residing in high DOM lakes was significantly less than fish in low DOM lakes (Craig et al. 2017).

What does this mean for my lake?

Watershed inputs of DOM vary significantly from lake to lake and on a regional basis as a result of differences in land cover and climate. Depending on the amount of forest and wetlands surrounding a lake, as well as the size of a lake's watershed relative to its volume, the DOM concentration of lakes can vary over more than a factor of ten. However, most lakes, especially those that tend to have shoreline residential development, are low in DOM concentration and have relatively high water clarity unless excess nutrient inputs have resulted in eutrophication. Low DOM concentrations and high water clarity mean that supply of non-DOM-associated nutrients from a lake's watershed, often from human sources like fertilizer, dictate algal growth and growth of consumers, including fish. In contrast, lakes that have high DOM concentrations and low light availability are expected to have low food web productivity regardless of the level of nutrient supply.

Inputs of DOM can also vary across time. Inter-annual differences in precipitation can cause year-to-year differences in lake DOM concentrations, but many lakes across the northern hemisphere have shown long-term increases in DOM concentrations over the past four decades, a process referred to as lake browning (Monteith et al. 2007). Lake browning is thought to be driven by recovery of lake watersheds from acidification and because of changes in climate and land use. As a result, in regions historically impacted by acidification essentially all lakes are gradually increasing in their DOM concentrations, but regions with limited past effects of acidification have shown more heterogeneous long-term trends in lake DOM concentrations (Meyer-Jacob et al. 2019).

Although the diverse and important effects of DOM on lakes have been recognized for over a century, our current, synthetic understanding of how physical, chemical, and biological responses combine to impact lake food webs has only emerged recently as a result of a renewed focus on DOM in lakes driven by observations of global lake browning. The most important implication of recent work is that how a lake food web responds to increased DOM concentrations will depend on its current DOM concentration, as well as its size and shape. Lakes low in DOM are expected to see moderate increases in growth of phytoplankton and consumers that are able to make use of pelagic prey with increased DOM inputs. These increases will result from fertilization effects of nutrients associated with DOM. In contrast, lakes that are already high in DOM are more likely to see reductions in food web productivity both in the water column and benthic habitat because these systems are predominantly light-limited, rather than limited by nutrients, and more DOM means even less light availability.

Like many ongoing global changes, the causes of browning are diffuse and non-local. As a result, discrete, local actions are unlikely to alter long-term trends in inputs of DOM to lakes. Further, increases in DOM input to lakes in areas recovering from acidification actually represent a return to a less human-impacted state. This clouds the judgement of browning as a good or bad environmental change. Rather aquatic scientists and managers should focus on the implications of a new, browner world for the future use and management of aquatic resources, such as drinking water and fisheries.

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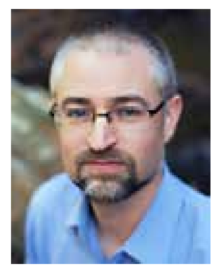

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