Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm

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Abstract

The primary interpretive paradigm used to study lakes is their trophic status. Oligotrophic lakes have low nutrient loading and low productivity, while eutrophic lakes have high nutrients and high productivity. The strong empirical relationship between nutrient loading and productivity is a valuable tool for teaching, for research, and for management of lakes. In order to incorporate the variety of other known anthropogenic impacts on lakes, however, lake characterization needs to extend beyond the nutrient-productivity paradigm. For example, acid precipitation, heavy metal and toxic organic contaminants, increases in UV radiation, and global warming are all recognized threats to lake ecosystems. One of the key characteristics of lakes that determines how they respond to disturbances such as these is their concentration of colored dissolved organic carbon (CDOC). Here we argue that a paradigm that includes CDOC (using the absorption coefficient at 320 nm as a proxy) as well as nutrients will be useful in predicting and understanding the response of lake ecosystems to multiple stressors. We propose to resurrect the CDOC axis that was proposed by investigators earlier this century and to extend it by adding some operational definitions to permit placing some of the major lake types on the axes in a way that will help us to better understand the structure, function, and response to disturbance of lake ecosystems that are subject to natural and anthropogenic environmental changes at the local, regional, and global scales. Data from a few diverse lakes and a successional sequence in Glacier Bay, Alaska, are used to illustrate the potential utility of the 2-axis model in separating lake types.

The most commonly used paradigm for studying lake ecosystems defines lakes in terms of their trophic status. Lakes with low nutrients and low organic production are considered oligotrophic, while those with high nutrient inputs and organic productivity are eutrophic (Wetzel 1983). This paradigm has been adopted by the general ecological community as well as limnologists and is in general use in introductory ecology and limnology textbooks. The trophic status paradigm is supported by a particularly strong empirical relationship between chlorophyll and phosphorus (Vollenweider 1968; Dillon and Rigler 1974; McCauley et al. 1989), by comparative studies and whole-lake experiments that have clearly demonstrated the role of nutrients and grazers in eutrophication (Schindler 1974; Pace 1984; Carpenter et al. 1991), and by the widespread success of remediation of human-accelerated eutrophication of lakes through nutrient reduction (Edmondson 1991).

In spite of the utility of this trophic paradigm in assessing and remediating eutrophicated lake ecosystems, it is focused largely on just one of many characteristics of lake ecosystems: nutrient limitation of productivity. There is increasing recognition that a wide variety of anthropogenic stressors influence lakes in addition to nutrient loading. These multiple stressors include acid precipitation, contamination by mercury and toxic organics, increased UV radiation (UVR), and global warming to name just a few. Interestingly, colored dissolved organic carbon (CDOC) seems to play a central role in mediating the impact of many of these anthropogenic stressors. Here we argue that a paradigm that includes CDOC as well as nutrients is required to understand the response of lake ecosystems to natural and anthropogenic environmental changes at the local, regional, and global scales.

Recognition of the potential importance of DOC in lakes is not a new discovery, neither is its incorporation into the trophic paradigm for studying lakes. The concept of lake trophy and the terms oligotrophic and eutrophic were first proposed in 1907 by Weber; and as early as 1921 Theinemann added the term "dystrophic" in referring to high DOC lakes (Rodhe 1969). Around the same time Birge and Juday (1927), in some of the earliest systematic chemical studies of lakes, carried out more than 500 DOC analyses and cat-

egorized lakes according to their quantity and source of DOC. High DOC lakes were divided into two types: allotrophic—those that receive their DOC largely from marshes, and autotrophic—those that derive a substantial portion of their carbon from within the lake. Rodhe (1969) later formalized this concept of viewing lakes according to their sources and amounts of organic carbon with a graphical scheme with four lake types along two axes: an axis of autotrophy where lakes went from oligotrophic to eutrophic, an axis of allotrophy where lakes went from oligotrophy to dystrophy, and a diagonal to "mixotrophic" lakes that were high on both axes. Likens (1972*a*) modified this scheme to explicitly include nutrients and to develop it as a tool for understanding eutrophication. During this same period, however, indeed in the same volumes in which Rodhe and Likens published their papers, the role of DOC in lakes was largely eclipsed by an emphasis on the recently discovered strong relationship between phosphorus and chlorophyll (Natl. Acad. Sci. 1969; Likens 1972*b*).

Thus the chlorophyll-phosphorus relationship has been a central focus and major interpretive paradigm in limnological research and teaching in recent decades, with little recognition of the potential role of DOC. Notable exceptions to this include the detailed treatment of DOC in Wetzel's limnology text (Wetzel 1983) and studies in Finland where high DOC lakes are common and DOC has been a major focus of studies since the 1930s (Salonen et al. 1992). In the past few years there has been a resurgence of interest in DOC, and it is becoming increasingly clear that DOC plays a central role in many ecosystem processes, particularly those involving human disturbance. Here we provide a brief overview of some of these findings and propose a simple conceptual model to resurrect the DOC axis in the interpretive paradigm for limnological studies. Our purpose is not to provide an exhaustive review, but rather to provide a brief overview of some of the key roles that DOC plays in mediating the response of freshwater ecosystems to both natural and anthropogenic stressors.

Dissolved organic carbon is a heterogeneous mix of yellow to brown or even black organic carbon compounds found in all natural waters in varying concentrations and referred to by various names including dissolved organic matter (DOM), natural organic matter (NOM), gilvin, gelbstoff, yellow substance, humic matter, and humus. The source of DOC may be either in-lake processes (autochthonous, macrophytes and phytoplankton) or from the surrounding watershed (allochthonous). Generally allochthonous DOC is composed of more recalcitrant and highly colored humic and fulvic acids, while autochthonous DOC generated by phytoplankton or macrophytes is more labile and less highly colored (Wetzel 1983). DOC concentrations can range from <1 mg liter^{-1} in the most transparent lakes to 50 mg liter^{-1} or more.

DOC has a variety of effects on lake ecosystems, which might be broken down into four major types (Table 1). The strong and selective absorption of solar radiation by DOC is responsible for many of its ecosystem level effects (Kirk 1994*a*). Absorption increases exponentially with decreasing wavelength, so that the short wavelength visible and especially UVR is most highly attenuated (Kirk 1994*b*). DOC

concentration alone predicts the attenuation of UVR in lakes with an r^2 value in excess of 0.8 based on recent empirical models (Scully and Lean 1994; Morris et al. 1995; Laurion et al. 1997). At low DOC concentrations (<1–2 mg liter^{-1}), small variations in DOC can, in turn, play a striking role in modifying the depth to which damaging UVR penetrates (Williamson et al. 1996). When these empirical relationships are used to estimate attenuation depths in different lake regions of North America, we find that in some regions the UV-B attenuation depths (1% of surface irradiance, 320 nm) may exceed 4 m in many lakes, while in other regions median attenuation depths are <0.5 m (Williamson et al. 1996). By reducing UVR attenuation depths, DOC will also reduce UVR damage to phytoplankton (Moeller 1994; Karentz et al. 1994), zooplankton (Williamson et al. 1994), and fish (Williamson 1996; Williamson et al. 1997, 1999).

At higher DOC concentrations the light attenuating properties of DOC may modify the longer wavelength solar radiation as well, with consequent effects on the structure and function of lake ecosystems. For example, at higher DOC concentrations mixing depths are reduced (Christensen et al. 1996; Fee et al. 1996), primary productivity is reduced (Jones 1992; Christensen et al. 1996; Carpenter et al. 1998), and phytoplankton and zooplankton community structure and distribution altered (Wall and Briand 1979; Arvola et al. 1992; Salonen and Lehtovaara 1992). One of the clearest examples of these multiple responses of lake ecosystems comes from a study in which one of two experimentally separated lake basins showed pronounced increases in DOC over a period of just a few years, and thus permitted documentation of DOC-related changes (Christensen et al. 1996). Within 2 yr of separating the east basin of Long Lake, Wisconsin, DOC concentration almost doubled from 7.5 to 14.1 mg liter^{-1}, water color (absorption coefficient at 440 nm) tripled, the 1% attenuation depth of photosynthetically active radiation (PAR) decreased, the maximum depth of oxygenation (1 mg liter^{-1}) decreased, and the proportion of the phytoplankton community (chlorophyll) in the epilimnion vs. the rest of the water column increased in comparison to the reference basin. These changes suppressed increases in primary production and algal biomass when the lake was experimentally enriched with N and P. Based on an analysis of these enrichment experiments, Carpenter et al. (1998) have estimated that an increase in refractory DOC concentration from 5 to 17 mg liter^{-1} will have effects on chlorophyll and primary production comparable to a reduction in P input rate from 5 to 0.5 mg m^{-2} d^{-1}.

The concentration of DOC in lakes also provides signals of watershed characteristics, as well as local, regional, and global disturbance (Table 1). The watershed catchment surrounding a lake, and the wetland and littoral areas in particular, is the primary source of DOC in most lakes (Wetzel 1992). The quantity and quality of DOC in a lake is dependent upon the vegetation type, season, climate, hydrology, and disturbance in the surrounding watershed (Engstrom 1987; Cronan 1990; Vincent and Pienitz 1997). Coniferous forests may provide a greater DOC input to adjacent lakes than hardwoods, and seasonal patterns may consist of reduced DOC concentrations in watershed soils during winter (Cronan and Aiken 1985) and increased DOC concentrations

Table 1.   Examples of processes influenced by DOC in freshwater ecosystems.

1. Increases attenuation of solar radiation	
Increases attenuation of photosynthetically active radiation, which:	Kirk 1994*b*; Morris et al. 1995
• reduces primary productivity	Jackson and Hecky 1980; Carpenter et al. 1998
• decreases mixing depth in small lakes (S.A.< 500 ha)	Christensen et al. 1996; Fee et al. 1996
• alters depth distribution of phytoplankton and zooplankton	Arvola et al. 1992; Salonen and Lehtovaara 1992; Christensen et al. 1996
• alters water color	Engstrom 1987; Rasmussen et al. 1989; Christensen et al. 1996; Carpenter et al. 1998
Primary factor controlling variation in attenuation of UVR among lakes. Empirical relationships show $r^2 = 0.8+$	Scully and Lean 1994; Morris et al. 1995; Laurion et al. 1997
Reduces UVR damage to zooplankton and fish	Siebeck et al. 1994; Williamson 1996; Williamson et al. 1994, 1997, 1999
2. Provides signals of watershed characteristics and local, regional, and global processes	
• type and extent of vegetation in littoral and terrestrial watershed	Cronan and Aiken 1985; Engstrom 1987; Cronan 1990; Wetzel 1992; Vincent and Pienitz 1997
• watershed drainage ratio and slope	Engstrom 1987; Rasmussen et al. 1989
• watershed hydrology and precipitation	Engstrom 1987; Cronan 1990; Forsberg 1992; Hornberger et al. 1994
• drought decreases DOC	Schindler et al. 1992
• forest fires increase DOC	Schindler et al. 1992
• acidification decreases DOC, increases transparency	Yan et al. 1996; Schindler et al. 1996; Williamson et al. 1996
• global warming will alter DOC in lakes	Forsberg 1992; Schindler et al. 1996
3. Alters contaminant toxicity and nutrient availability	
• increases acidity (lowers pH)	Wetzel 1983; Driscoll et al. 1989
• reduces metal toxicity (Al and Cu) in fish	Driscoll et al. 1980; Welsh et al. 1993
• ameliorates negative effects of low pH on biota	Collier et al. 1990; Nelson and Magnuson 1992
• binds methylmercury(II), reducing accumulation in fish	Hintelmann et al. 1997
• reduces toxicity of polycyclic aromatic hydrocarbons	Oris et al. 1990; Gensemer et al. 1999
• reduces the bioavailability of PCBs	Knulst 1992
• alters availability of P, Fe, and C of different molecular weights and thus C cycle, energy supply, productivity, and eutrophication	Stewart and Wetzel 1982; Francko 1986; Hessen 1992; Hobbie 1992; De Haan 1993; Herndl et al. 1993; Lindell and Rai 1994
4. Interferes with drinking water purification	
• use of strong oxidants such as chlorine and ozone produce toxic disinfection by-products (DBPs) such as trihalomethanes (THMs)	Edzwald et al. 1985; Krasner et al. 1989; Reckhow and Singer 1990
• ozonation produces aldehydes such as formaldehyde	Nawrocki and Kalkowska 1995; Krasner et al. 1989
• reacts with oxidizing disinfectants to reduce their effectiveness	Harrington et al. 1996

in rivers in late winter and early spring (Hornberger et al. 1994). Watershed drainage and slope are important in determining the degree of inundation of the soils, which in turn contributes to DOC generation within the watershed (Engstrom 1987; Rasmussen et al. 1989). Forest fires may increase DOC inputs (Schindler et al. 1992), while anthropogenic acidification may decrease DOC (Yan et al. 1996; Schindler et al. 1996; Williamson et al. 1996). Periods of drought related to regional changes in climate may either increase DOC concentrations in lakes (Forsberg 1992) or reduce them (Yan et al. 1996; Schindler et al. 1996). Stratospheric ozone depletion may increase incident UV-B radiation, but UVR is effectively attenuated by high concentrations of DOC in the water column (Kirk 1994*b*; Scully and Lean 1994; Morris et al. 1995). In low to moderate DOC lakes, however, attenuation depths (1% of surface irradiance) for damaging UVR may exceed several meters (Morris et al. 1995; Williamson et al. 1996). Photobleaching by the UVR may lead to springtime increases in UV penetration that peak

just following summer solstice (Morris and Hargreaves 1997).

DOC is an important carbon source for microbial plankton communities and is the major driver dominating material and energy flux in freshwater ecosystems (Hessen 1992; Hobbie 1992; Wetzel 1995). With regard to UV radiation, DOC may on the one hand enhance growth in microbial communities by mitigating the potential for UV damage and by generating the release of more labile organic compounds during photobleaching (Kieber et al. 1989; De Haan 1993). On the other hand, in low DOC environments UVR may directly damage microbial populations (Herndl et al. 1993). Photodamage may be aggravated by the loss of the UV absorption potential of DOC during photobleaching which leads to an increase in the depth to which damaging UVR penetrates the water column (Morris and Hargreaves 1997).

DOC also alters nutrient cycling and contaminant toxicity (Table 1). Nutrient cycles are altered in fundamental ways by the DOC-induced changes in light attenuation, thermal

stratification, and depth distribution of the phytoplankton and zooplankton discussed above. DOC concentration may also influence the rate of oxygen depletion in lakes through photochemical oxidation (Lindell and Rai 1994), as well as the availability of critical nutrients such as iron (Jackson and Hecky 1980) and phosphorus (Stewart and Wetzel 1982; Francko 1986).

The toxicity of a variety of contaminants and heavy metals may be reduced by high concentrations of DOC. Laboratory experiments with aquatic organisms ranging from duckweed to *Daphnia* and fish have demonstrated that humic substances can reduce the toxicity of polycyclic aromatic hydrocarbons such as anthracene (Oris et al. 1990; Gensemer et al. 1999). DOC reduces the bioavailability of PCBs during acidification (Knulst 1992), and also reduces the toxicity of aluminum and copper to fish (Driscoll et al. 1980; Welsh et al. 1993). DOC alters the cycling and toxicity of mercury either directly by decreasing the rates of net methylation (Miskimmin et al. 1992) or binding with methylmercury (MeHg), making this toxic form of mercury less available for biological uptake (Hintelmann et al. 1997), or indirectly by reducing solar radiation in the water column. Sunlight mediates both photodegradation of methylmercury in lakes (Sellers et al. 1996) and photoproduction of dissolved gaseous mercury (Amyot et al. 1994). Humic substances can also initiate the reduction of inorganic mercury (Hg^{2+}) to elemental mercury (Hg^0), which, due to its low solubility, is more subject to volatilization and loss to the ecosystem than is MeHg (Alberts et al. 1974). Methylmercury concentration is positively correlated with wetland surface area within a watershed and is not associated with particulates, suggesting that DOC-bound Hg is the primary mechanism of transport of high Hg concentrations from wetlands to rivers (Hurley et al. 1995).

Both organic and anthropogenic mineral acids may decrease the pH of freshwater ecosystems and reduce their acid neutralizing capacity (Driscoll et al. 1989). Results of whole-lake liming and whole-lake acidification experiments have demonstrated decreases in DOC with decreasing pH (Bukaveckas and Driscoll 1991; Schindler et al. 1991, 1997). In some large rivers during periods of peak flow associated with spring snowmelt, DOC concentrations may be elevated as pH declines (Campbell et al. 1992). As with toxicants, DOC may ameliorate the negative effects of pH on biota. For example, yellow perch from acidic, high DOC lakes do not experience the same level of physiological disturbance observed in perch in anthropogenically acidified lakes (Nelson and Magnuson 1992). Both fish and benthic invertebrates can tolerate a lower pH in naturally acidic high DOC systems than they can in clear anthropogenically acidified systems, although DOC concentrations >20 mg liter^{-1} may be toxic (Collier et al. 1990). In acidified lakes organisms are subjected to multiple stresses in addition to pH (Frost et al. 1999), and DOC and pH have interactive effects on the toxicity of contaminants (Knulst 1992; Miskimmin et al. 1992; Welsh et al. 1993).

DOC is also important in the production of toxic byproducts of drinking water treatment (Table 1). A variety of strong oxidants is used to disinfect or reduce odors in drinking water, most notably chlorine and ozone, but also UVR and hydrogen peroxide (Krasner et al. 1989). The negative effects of DOC on the disinfection process are twofold. DOC reacts with these strong oxidants, making them less effective disinfectants (Harrington et al. 1996). In addition, these reactions with DOC produce a variety of disinfection by-products (DBPs) in drinking water, including several potential carcinogens and mutagens such as trihalomethanes (THMs, primarily chloroform), haloacetic acids (e.g., trichloroacetic acid), and aldehydes (e.g., formaldehyde) (Krasner et al. 1989; Reckhow and Singer 1990; Nawrocki and Kalkowska 1995). Humic acids tend to consume more chlorine and produce more toxic organic halides than fulvic acids (Reckhow et al. 1990). The concentration of THMs in the final drinking water is a function of the DOC in the raw supply water, which can in turn be predicted by the UV absorption of the supply water (Edzwald et al. 1985).

These multiple and varied effects of DOC on freshwater and its usage suggest a need to resurrect the paradigm that includes DOC as well as nutrients in analyses of lake ecosystems. To consider this need in the context of lakes, the graphical model developed by Rodhe (1969) is a useful starting point. We suggest that providing this model with axes that can be operationally defined and applied will improve its utility. The most logical x-axis is total phosphorus (TP, μg liter^{-1}) as it will continue to be a strong predictor and diagnostic tool for human disturbance in lake ecosystems. The light-attenuating properties of DOC are central to many of its effects on ecosystems, and this attenuation increases with decreasing wavelength. Although the optical quality of DOC (i.e., absorptivity) varies with its source and composition, water color is closely related to DOC concentration with coefficients of determination that exceed 0.8 (Cuthbert and del Giorgio 1992; Morris et al. 1995; McKnight et al. 1997). This makes the absorption coefficient (a) as estimated from absorbance in a laboratory spectrophotometer (D) a convenient and dependable option for the y-axis. The absorption coefficient for a given wavelength can be estimated from D by dividing by the optical pathlength (r) and using a factor to convert from 10 to base e (Kirk 1994a):

$$a = 2.303D/r. \tag{1}$$

This axis can serve as a measure of the colored fraction of DOC (CDOC).

The absorption coefficient at 440 nm has been suggested as a standard measure of color in aquatic ecosystems in the past (Cuthbert and del Giorgio 1992). On the other hand, UV absorbance at 254 nm has been used effectively to determine concentrations of organic carbon in drinking water supplies for the purpose of monitoring DBP precursors (Edzwald et al. 1985). Because no solar radiation <290 nm reaches the earth's surface, use of UV-C (200–280 nm) or shorter wavelength UV-B radiation would make it difficult to relate inherent optical properties of water such as the absorption coefficient obtained in the laboratory to apparent optical properties such as attenuation coefficients (K_d) obtained in the field with submersible instruments (Kirk et al. 1994). Short wavelength UV-B is also attenuated so rapidly in high CDOC lakes (in a few centimeters) that field measurements are extremely difficult. Longer wavelengths in the visible light range (400 + nm) on the other hand are too insensitive to the low levels of CDOC in extremely trans-
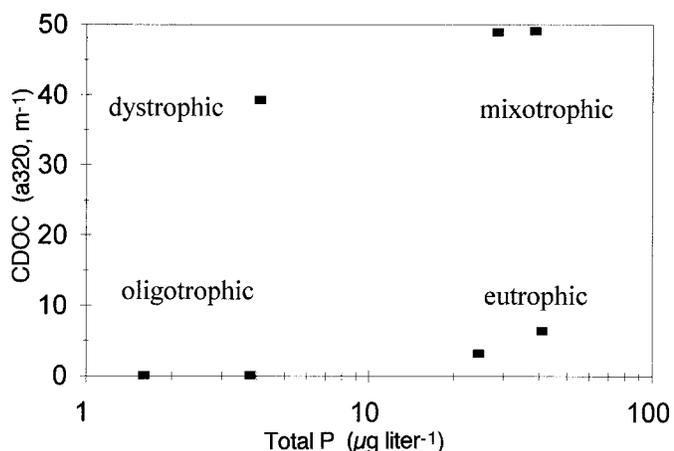
Fig. 1. Location of several lakes on the proposed 2-axis model that incorporates colored DOC (CDOC, as absorption coefficient at 320 nm, *see Eq. 1*) into the current trophic status (total phosphorus, TP) paradigm. The lakes were selected to demonstrate the differences that exist among lakes along these two axes. Table 2 gives lake names, locations, and related optical and chemical data.
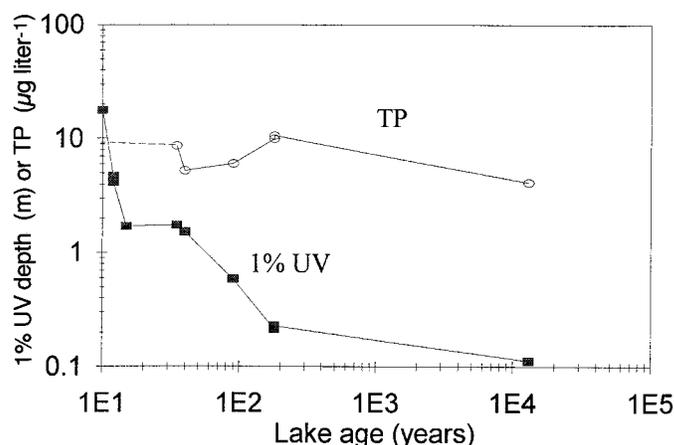

Fig. 2. Attenuation depths (1% of surface irradiance at 320 nm) and total phosphorus data for the lakes in the deglaciation chronosequence in Glacier Bay, Alaska. Note the decrease in the 320-nm attenuation depth with lake age, while the TP levels stay relatively constant over time in this highly pristine environment. The UV data for attenuation depths were collected with the 320-nm band of a Biospherical Instruments Inc. PUV-501 during summer 1996. (The TP data are from Olson et al. 1995.) Because TP data were not available for the youngest lakes, data from a lake (Plateau) of the same age in the same region were used (dashed line).

parent lakes. Here we propose to use the absorption coefficient at 320 nm (a_{320}, the boundary between UV-B and UV-A radiation) as a metric of CDOC in natural waters. As with TP or any other limnological characteristic, caution must be used in extrapolating a single value from a lake since the optical properties of lakes, including the absorption coefficient at 320 nm can vary seasonally and with depth (Morris and Hargreaves 1997). For more general use, epilimnetic a_{320} values during midsummer (at or soon after summer solstice) might be appropriate, but more detailed resolution can be obtained within a lake by comparing a_{320} values for different depths or times of year. We have used the TP and a_{320} axes to plot several lakes as examples to show how these metrics permit a useful separation of a variety of lakes (Fig. 1). It is clear from looking at these plots that if these lakes were plotted on a single trophic axis, important differences in the structure and function of the high and low CDOC systems would not be apparent. Dystrophic lakes would not be separable from oligotrophic lakes, and mixotrophic lakes would not be separable from eutrophic lakes.

The roots of this trophic-DOC paradigm are in studies of succession using the sediments of peat bogs in Germany (von Post 1916 [1991]; Rodhe 1969). Studies of lake succession are usually limited to paleolimnological studies. Rarely does one have the opportunity to study lakes of different ages in the same region. In Glacier Bay, Alaska, however, a pronounced deglaciation chronosequence has left behind lakes that vary in age from 10 or so years to over 10,000 yr (Engstrom and Fritz 1990). These lakes occur in a pristine environment where anthropogenic impacts are minimal, and lake productivity is extremely low. The younger lakes have only sparse vegetation in their watersheds, are largely fed by groundwater, and consequently have extremely low CDOC. As the lakes increase in age, the terrestrial vegetation in the surrounding watershed goes from

sparse herbaceous plants to alder thickets, to mature coniferous or mixed coniferous-deciduous forests or muskegs. The growth of peat combined with paludification leads to a watershed catchment that often generates high quantities of CDOC in the older lakes (Engstrom and Fritz 1990).

We have collected light and UVR profiles on a subset of the 32 Alaskan lakes studied by Engstrom and Fritz (1990) and have found a decrease in the depth to which 320-nm radiation penetrates with increasing lake age (Fig. 2). We have used published data (Olson et al. 1995) to plot the TP in these lakes to permit us to compare changes in CDOC with changes in TP during early lake succession (using a space-for-time substitution model, Fig. 2). The results show that TP is relatively constant over time, while pronounced directional changes occur in CDOC. These differences in CDOC suggest that the younger lakes will be more vulnerable to many of the disturbances discussed above, while these disturbances will be mitigated by high CDOC in the older lakes. Lake ontogeny in Glacier Bay is much more complex than this one graph suggests, and succession may take any of several trajectories depending on the hydrologic and geologic characteristics of the watershed (Engstrom and Fritz 1990). This same point can be extended to other lakes of similar age but differing CDOC in other areas of the world (Fig. 1).

We suggest CDOC here as the secondary axis because of the wide variety of roles that it plays in the physical, chemical, and biological processes in lake ecosystems, particularly with regard to mitigating stressors. Selection of the 320-nm wavelength makes the index more sensitive to CDOC, which strongly absorbs the shorter wavelengths of light. This is in contrast to suspended particulates which are more uniform in the wavelengths of light that they attenuate. In ad-

Table 2. Total phosphorus, absorption coefficient at 320 nm ($=a_{320}$), DOC, and DOC-specific absorbance (a_{320}:DOC) values for the lakes in Fig. 1, demonstrating the value of adding a third axis such as DOC concentration to the 2-axis model. For example, many prairie lakes have high DOC concentrations with low color. Addition of this third axis permits a clear separation of the two eutrophic lakes that differ in their a_{320} and TP by only twofold, but differ in their DOC concentrations by sixfold. In addition, note that the a_{320}:DOC values range across more than an order of magnitude, reinforcing the idea that the quality as well as quantity of DOC may vary among lakes.

Lake name (region)	TP (μg liter^{-1})	a_{320} (m^{-1})	DOC (mg C liter^{-1})	a_{320} : DOC	Lake type
Schmoll (Argentina)	1.6	0.1	0.5	0.20	oligotrophic
Giles (Pennsylvania)	3.8	0.1	1.16	0.09	oligotrophic
Brush (Montana)	41.0	6.4	24.9	0.26	eutrophic
Waynewood (Pennsylvania)	24.6	3.2	4.4	0.74	eutrophic
Pleasant Knob (Alaska)	4.1	39.3	9.16	4.3	dystrophic
Bolger (Michigan)	38.7	49.1	15.1	3.2	mixotrophic
Morris (Michigan)	28.6	48.9	14.4	3.4	mixotrophic

dition to this second axis, however, there are many other dimensions that could be added to provide more information on a lake ecosystem. Regional climate, mixing depth, mean basin depth, and fetch may be important to name just a few. For example, although most of the world's lakes are relatively small and shallow (Wetzel 1990), a substantial proportion of the world's water is contained in the largest lakes where CDOC is less likely to be important in determining the mixing depth (Fee et al. 1996).

The proposed model could be extended to three dimensions with any of these additional axes to provide further refinements. For example, despite the strong correlation between color and DOC concentration, the optical quality of DOC can show strong variation among lakes (Cuthbert and del Giorgio 1992; Morris et al. 1995; McKnight et al. 1997) and even among seasons within a single system (Visser 1984; Morris and Hargreaves 1997). These differences could be resolved by adding a third axis that includes DOC concentration as well as UV absorption. When we do this for the group of lakes presented in Fig. 1, we see a clear separation of the two eutrophic lakes based on DOC concentration (Table 2). The importance of this third axis is also apparent from the a_{320}:DOC ratios, which vary over an order of magnitude. Some of this variation in DOC quality vs. quantity is due to the relative concentrations of humic and fulvic acids, which can be separated to some extent with more detailed analysis of their absorption or fluorescence spectra (McKnight et al. in review). However, these optical separations may be difficult due to the complex composition of compounds that make up DOC (Green and Blough 1994; Blough and Green 1995). Similar approaches to developing a third axis could be taken with regard to refining the relationships between nutrients and productivity by adding an axis to incorporate nutrient limitation or co-limitation by nitrogen or micronutrients (e.g., Wurtsbaugh et al. 1985; Morris and Lewis 1988; Elser et al. 1990).

Local and regional problems with nutrient enhancement and subsequent anthropogenic eutrophication of lakes are likely to be continuing problems as human population and development expand. Thus the nutrient-productivity relation-

ship and the trophic concept in lakes will continue to be important and useful conceptual tools. However, there is also a clear need to incorporate DOC into this paradigm. DOC will, in part, determine the degree of autotrophy vs. heterotrophy, the vertical structure of temperature and oxygen, and the potential response to natural and anthropogenic disturbances ranging from nutrient inputs, toxic organics and heavy metals, to forest fires, acid precipitation, climate change, and ozone depletion. Lakes are an integral part of their watershed and airshed (Likens 1984). The signals provided by the quantity and quality of DOC in lakes can provide key information to help us to better understand how lakes will respond to stressors within the lake as well as the watershed and airshed within which they are located. Resurrecting the DOC axis in the nutrient-productivity paradigm will provide a more robust conceptual framework for addressing these concerns.

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