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Biotic, chemical, and morphometric factors contributing to winter anoxia in prairie lakes

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Abstract

To assess how features of lakes and their watersheds influence winter oxygen decay rates and the frequency of anoxia in shallow prairie lakes, we measured lake and watershed characteristics for 21 south-central Alberta lakes and related these to measured oxygen decay rates during 1998–2000. Oxygen decay rates were functions of macrophyte biomass, percentage littoral area, and total phosphorus and ranged from 0.006 to 0.216 mg O_2 m^{-3} d^{-1}. Oxygen decay rates were ~4 times higher in shallow polymictic lakes compared to deep, stratified lakes. Within shallow lakes, those classified as turbid had decay rates ~1.5 times higher than those classified as clear. Chlorophyll *a* was not a predictor of the oxygen decay rate in shallow lakes; however, macrophyte-derived carbon averaged ~150 times more than phytoplankton-derived carbon in the shallow lakes we examined. Reasons that lakes frequently or never become anoxic are related to productivity and morphometry; however, processes explaining occasional anoxia appear not to be related to factors we measured.

Dissolved oxygen (O_2) is a common water quality indicator. Nutrient enrichment enhances primary production, increases O_2 depletion rates, and leads to decreased water quality (Dillon et al. 1978; Snodgrass and Ng 1985; Lind 1987; Gelda and Auer 1996). When low O_2 concentration results in anoxia, fish die. Fish kills have resulted in a need to predict anoxia to proactively manage lakes with goals of sustaining productive fisheries and maintaining ecosystem stability. Loss of a top predator has consequences to lower trophic levels; hence anoxia can affect community structure. The frequency and extent of fish kills determine the structure of fish assemblages (Tonn and Magnuson 1982; Rahel 1984) with implications to lower trophic levels (Carpenter and Kitchell 1993).

In lakes, winter O_2 budgets are a function of the O_2 mass at freezing, the duration of ice cover, and the balance of processes that produce and consume O_2. Winter O_2 depletion rates depend on the particulate organic matter (POM) mass decomposing in the lake (Lasenby 1975; Welch et al. 1976; Cornett and Rigler 1980; Mathias and Barica 1980; Jackson and Lasenby 1982), which is composed of senesced aquatic macrophytes and phytoplankton produced during the previous summer. Microbial decomposition of POM and chemical oxidation of reduced inorganic chemical species results in biological O_2 demand (BOD) and chemical O_2 demand (COD). Oxygen consumption in the water and sediments is primarily a function of lake productivity, since BOD and COD are proportional to the supply of oxidizeable material (Lasenby 1975; Charlton 1980; Cornett and Rigler 1980, 1987; Mathias and Barica 1980; Jackson and Lasenby 1982). As lake productivity increases, organic loading increases (Hargrave 1975), resulting in elevated rates of O_2 consumption via BOD (Rosa and Burns 1987). Hence the probability of anoxia and fish kills increases with nutrient enrichment.

Problems associated with anoxia are not restricted to shifts in lake structure and include shifts in lake functioning. When O_2 concentrations at the sediment–water interface fall below 1 mg L^{-1}, there is a shift from aerobic to anaerobic respiration (Nürnberg 1995). Changes in processes such as sulfate reduction, denitrification, and methanogenesis occur. As chemical products of organic matter decay are released to the water, they rapidly oxidize, causing O_2 depletion from the overlying water (Stumm and Morgan 1981). Once all available O_2 has been consumed, alternate electron donors are selected, and respiration occurs anaerobically. Anaerobic respiration causes increased nutrient cycling and regeneration and release of toxic compounds such as methane (CH_4) and hydrogen sulfide (H_2S).

Models have been developed that predict rates of hypolimnetic O_2 consumption in lakes as a function of morphometry, chlorophyll *a* (Chl *a*), temperature, and/or phosphorus (Lasenby 1975; Cornett and Rigler 1979; Walker 1979; Charlton 1980; Trimbee and Prepas 1988; Cornett 1989). These models accurately predict O_2 depletion in large deep lakes that rarely become anoxic and small shallow lakes that frequently become anoxic, but fail in lakes that experience anoxia once every ~5 to 10 yr (Mathias and Barica 1980; Barica et al. 1983). Stefan and Fang (1994) suggested this failure was due to the dynamic nature of shallow lakes that results from high sensitivity to environmental change. Shallow lakes are sensitive to nutrient loading changes because they have relatively small volumes and respond quickly to climate change because their relatively large surface areas, small volumes, and shallow depths buffer less against temperature change (Schindler et al. 1996).

Many prairie lakes experience occasional anoxia (Barica and Mathias 1979; Trimbee and Prepas 1988). Poor predic-

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Table 1. Study lakes are located in south central Alberta and cover a range of watershed types. SA is surface area and z_{max} is the maximum depth. The lakes are classified as either clear (C) or turbid (T) based on turbidity. Dimictic lakes are classified as deep (D), and polymictic lakes are classified as shallow (S). Lakes classified as experiencing occasional anoxia become anoxic roughly every 5–10 yr.

Region	Lake	Location (°N, °W)	SA (ha)	z_{max} (m)	Macrophyte biomass (kg m^{-2})	Mean summer Chl *a* (μg L^{-1})	State (C/T)	Depth (S/D)	Anoxic frequency
Calgary	Bonavista	50 56, 114 03	20.1	7.8	1.71	2.61	C	D	Never
	Midnapore	50 55, 114 03	11.3	8.0	2.21	0.46	C	D	Never
	Sundance	50 54, 114 02	12.5	13.0	1.96	0.6	C	D	Never
Caroline	Birch	52 01, 114 51	24.3	9.9	0.09	2.09	C	D	Occasional
	Cow	52 17, 115 01	821.8	1.6	0.26	2.69	T	S	Occasional
	Crimson	52 27, 115 02	331.9	2.0	0.87	4.71	T	S	Occasional
	Horseshoe	52 00, 114 49	5.8	8.5	1.45	1.38	C	D	Occasional
	Ironside	52 15, 115 00	3.9	13.0	0.33	1.25	C	D	Frequent
	Mitchell	52 13, 115 01	14.9	7.3	1.18	3.01	C	D	Occasional
	Phyllis	52 06, 114 58	17.5	6.7	2.34	1.44	C	D	Occasional
	Yellowhead	52 57, 114 48	21.3	13.0	0.85	1.95	C	D	Occasional
Kananaskis	Gap	51 03, 115 14	28.6	3.0	6.98	0.13	C	S	Never
	Sibbald	51 03, 114 53	3.2	3.5	2.11	0.71	C	S	Frequent
Strathmore	Barnett	51 04, 113 14	26.8	2.1	9.70	4.75	C	S	Frequent
	Dawson	51 08, 113 20	32.2	1.7	2.17	8.41	T	S	Frequent
	East	51 03, 113 11	3.2	1.4	1.97	8.93	C	S	Frequent
	Golf Course	51 03, 113 24	11.1	1.0	1.05	15.31	T	S	Frequent
	Long	51 03, 113 11	9.7	1.6	0.93	3.07	C	S	Frequent
	Mushroom	51 06, 113 24	12.0	1.3	0.60	25.66	T	S	Frequent
	Picnic	51 02, 113 23	2.2	3.3	0.89	8.87	T	S	Occasional
	West	51 03, 113 11	3.5	1.8	0.15	15.63	T	S	Frequent

tive power may be due to ignoring macrophytes as a major source of POM (Chambers 1994). Senescing macrophytes should play an important role in winter O_2 depletion, and estimating POM via only Chl *a* may lead to a gross underestimation of potential O_2 demand. Macrophytes can cover entire lake bottoms, reach high densities and biomass, and generate high POM loading. Eutrophication, in response to some agricultural practices, translates into increased productivity. Consequently, macrophytes have become problematic in prairie lakes experiencing human disturbance (Chambers 1994; Smith and Barko 1990). Increased POM loading from macrophytes should have an impact on rates of O_2 depletion.

The purpose of this study was to test the hypothesis that in shallow prairie lakes, winter O_2 decay is proportional to macrophyte biomass of the previous summer. We also consider relationships between winter O_2 decay rates and lake and watershed features (morphometry, nutrients, phytoplankton biomass) to seek general patterns between O_2 decay rates and lake attributes.

Methods

Study area—We sampled 21 lakes from four regions of south-central Alberta between 1998 and 2000: Kananaskis ($n = 2$), Caroline ($n = 8$), Strathmore ($n = 8$), and Calgary ($n = 3$) (Table 1). The study lakes were selected because their watersheds range in size, land-use practices (farming, ranching, recreational, urban), nutrient inputs, Chl *a*, and macrophyte biomass. These lakes have historically experienced varying frequencies of anoxia and fish kills, from anoxia almost yearly, to once every 5–10 yr, to never anoxic.

Kananaskis lakes are located in the foothills of the Rocky Mountains west of Calgary and have high watershed relief. The watersheds are densely vegetated with white spruce (*Picea glauca* (Moench) Voss), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). Caroline region lakes are also in the Rocky Mountain foothills but have less watershed relief, and the surrounding vegetation consists primarily of trembling aspen and balsam poplar. Cattle ranching is the main land use, and there is a small amount of crop farming. Several Caroline lakes are stocked with rainbow trout (*Oncorhynchus mykiss*) or brook trout (*Salvelinus fontinalis*) and are angled all year. Strathmore lakes, approximately 40 km east of Calgary, have the lowest watershed relief and are the shallowest of our study lakes. Agriculture consists largely of grain farming, but there are several cattle feedlots in the vicinity. The Calgary lakes are located within the city and are surrounded by housing developments; their main use is recreation.

Field methods—Macrophytes and water chemistry (total phosphorous, Chl *a*, Secchi depth, turbidity) were sampled during July and August of 1998 and 1999, when macrophytes were at their maximum seasonal biomass. Macrophytes were harvested from 6 to 15 sites with four quadrats (1,000 cm^2) per site depending on lake size. Quadrats were placed on the lake bottom and the macrophytes within harvested. Macrophytes were stored in plastic freezer bags on ice in coolers for transport back to the lab, where they were washed, spun dry in a lettuce spinner, separated, identified to species, and fresh mass measured. Watershed character-

Table 2. Oxygen depletion rates for the 23 study lakes after initial removal of initial O_2 data to correct for O_2 inputs after freezing. O_2 depletion rates for each lake and year were calculated using a one-pool single exponential decay model ($O_2 = Ae^{-kt}$ where A is the initial $[O_2]$ at freezing, k is the decay rate, t is time, e is the base of the natural logarithm, and n is the number of data in the regression). Lakes were considered anoxic when the O_2 concentration fell below 1 mg L^{-1}.

Lake	Winter	Points removed	n	A (g m^{-3})	k (g m^{-3} d^{-1})	F value	p	Anoxic (Y/N)
Barnett	1998–1999	0	5	174,044	0.216	241.59	0.0005	Y
Birch	1999–2000	2	4	28.299	0.018	3,868.12	0.0003	N
Bonavista	1999–2000	1	4	20.815	0.016	3,410.92	0.0003	N
Cow	1998–1999	0	5	23.323	0.023	370.09	0.0003	N
Crimson	1998–1999	0	6	24.779	0.028	183.10	0.0001	Y
Dawson	1998–1999	0	4	6,953.3	0.143	1,433.19	0.0007	Y
East	1999–2000	1	7	390.9	0.120	1,020.01	<0.0001	Y
Gap	1998–1999	0	5	10.226	0.000	140.60	0.0011	N
Golf Course	1998–1999	0	5	14.402	0.057	377.79	0.0002	Y
Horseshoe	1999–2000	1	5	24.180	0.031	1,931.24	<0.0001	Y
Ironside	1999–2000	0	7	8.555	0.019	127.49	<0.0001	Y
Long	1999–2000	1	6	56.500	0.043	138.15	0.0002	Y
Midnapore	1999–2000	1	4	11.580	0.008	556.18	0.018	N
Mitchell	1998–1999	0	5	16.738	0.026	708.24	<0.0001	Y
Mitchell	1999–2000	3	5	29.124	0.019	1,676.18	<0.0001	N
Mushroom	1998–1999	0	4	14.407	0.077	8,313.96	0.0001	Y
Phyllis	1998–1999	0	6	15.666	0.014	1,230.42	<0.0001	N
Phyllis	1999–2000	1	5	16.164	0.008	2,867.67	<0.0001	N
Picnic	1998–1999	0	3	55.341	0.064	158.56	0.0561	Y
Sibbald	1998–1999	0	4	14.407	0.071	19,727.20	<0.0001	Y
Sundance	1999–2000	1	4	10.721	0.006	1,814.94	0.0006	N
West	1999–2000	2	5	100.0	0.038	239.70	0.0005	N
Yellowhead	1999–2000	3	6	21.231	0.019	2,674.43	<0.0001	N

istics (relief, catchment area, and land cover) were determined from satellite images of the study sites using Geographic Information System (GIS) and 1:20,000 or 1:50,000 topographic maps. If lake bathymetry was unavailable, we mapped it during early summer, 1999 and 2000, when macrophyte biomass was low.

During January to April of 1999, dissolved O_2 (mg L^{-1}) in 11 of the 21 study lakes was measured every 2 weeks with an ORION Model 842 dissolved oxygen meter and probe that was calibrated to 100% O_2 saturated water at 22°C. The remaining 10 lakes plus two repeats (Mitchell Lake and Phyllis Lake) were sampled similarly from November 1999 until April 2000. A minimum of three sites per lake were sampled, and dissolved O_2 was measured at 0.5-m depth intervals, with 0 m taken at the hydrostatic water level through holes drilled in the ice. Dissolved O_2 and temperature profiles, ice thickness, and snow thickness were measured at each site. One sample site was at the lake's location of maximum depth. If a lake did not appear to have homogeneous O_2 concentrations or was larger than 3 km^2, then more than three sample sites were chosen. For example, Cow Lake (surface area [SA] ~ 8 km^2) was sampled at 7–8 sites per sample day.

Winter O_2 concentrations were calculated using O_2 concentration depth profiles and lake bathymetry. The mass of O_2 was calculated for each 1.0-m depth stratum by averaging the O_2 concentrations measured within a stratum (e.g., for 1- to 2-m depth: averaged O_2 concentrations for 1.0-, 1.5-, and 2.0-m depths) and multiplying by the volume of water in the stratum. The 0-m O_2 concentration for each profile was excluded from calculations since this value may have been contaminated with O_2 introduced via mixing during hole drilling. Hence, the 0- to 1-m depth O_2 concentration was assumed to be the average of the 0.5- and 1.0-m O_2 concentrations. We corrected the O_2 mass for the 0- to 1-m stratum by subtracting the volume of ice present and estimating the O_2 mass in the remaining volume of water. Oxygen masses of each stratum were summed to yield a total lake O_2 mass for each sample day. We estimated volumetric O_2 concentrations (g m^{-3}) by dividing the total lake O_2 mass by lake volume.

Water for Chl *a* analyses was taken at each profile location just below the ice–water interface by inverting 1-liter Nalgene bottles. Samples were transported to the lab in coolers to prevent freezing. Thirty to 100 ml were filtered through 25-mm Whatman glass microfiber (GF/C) filters that were then frozen until extraction. Chlorophyll *a* concentrations (μg L^{-1}) were measured fluorometrically following extraction into acetone (Watson et al. 1992) and were corrected for phaeopigments.

Modeling and analysis—Winter oxygen decay rates were calculated with a nonlinear, single exponential decay model ($O_2 = Ae^{-kt}$; where O_2 is the dissolved oxygen concentration, A is the initial $[O_2]$ at freezing, e is the base of the natural logarithm, k is the decay rate, and t is time), which we previously deemed most appropriate for similar shallow lakes (Meding and Jackson 2001). We evaluated model fits by vi-

Table 3. Pearson correlation matrix for lake and watershed characteristics of study lakes located in south central Alberta (n = 20; Gap Lake not included).

Variable	k	Volume	SA	SA : vol	z_{max}	z_{mean}	Macrophyte biomass	Chl a	TP	Turbidity	DOC	% littoral cover	Total C
Decay rate (k) (g m^{-3} d^{-1})	1.000												
Volume (m^3)	−0.169	1.00											
Surface area (SA) (ha)	−0.124	0.996*	1.000										
SA : vol (m^{-1})	0.513*	0.064	0.125	1.000									
Maximum depth (z_{max}) (m)	−0.559*	−0.216	−0.268	−0.813*	1.000								
Mean depth (z_{mean}) (m)	−0.552*	−0.075	−0.140	−0.821*	0.924*	1.000							
Macrophyte wet biomass (kg m^{-2})	0.709*	−0.176	−0.167	0.053	−0.152	−0.135	1.000						
Summer Chl a (μg L^{-1})	0.340	−0.147	0.105	0.806*	−0.587*	−0.6024*	−0.145	1.000					
Total phosphorus (TP) (μg L^{-1})	0.459*	−0.107	−0.082	0.353	−0.344	−0.357	−0.002	0.508*	1.000				
Turbidity (NTU)	0.171	0.248	0.282	0.710*	−0.648*	−0.612*	−0.334	0.814*	0.554*	1.000			
DOC (μg L^{-1})	0.381	−0.161	−0.117	0.474*	−0.544*	−0.557*	−0.003	0.523*	0.268	0.313	1.000		
Percentage littoral cover	0.458*	0.264	0.307	0.756*	−0.797*	−0.688*	0.123	0.508*	0.020	0.444*	0.528*	1.000	
Total carbon (kg)	0.382	0.661*	0.657*	0.188	−0.395	−0.277	0.455*	−0.089	−0.001	0.141	−0.040	0.417	1.000

* Significant (α = 0.05).

sual examination of the residuals and summary statistics (e.g., F value). For all lakes, the independent variable, time, began with day 0 at freezing. To attempt to correct for O_2 inputs during the initial period after freezing, initial O_2 concentration data were consecutively removed, and the model was refit to the remainder of the O_2 data as outlined in Meding and Jackson (2001). Data were no longer removed once the highest F value was achieved. No data were removed if the complete set of O_2 concentrations yielded the highest F value. In some cases there were relatively few observations; the highest F value did not yield the best visual fit of the residuals; and we therefore combined the next highest F value with the best visual fit to determine the best model fit. These analyses were performed with proc NLIN in SAS (v. 8.0).

An estimate of the initial O_2 at freezing was not obtained for lakes sampled during January to April of 1999. For three lakes (Golf Course, Mushroom, and Sibbald), O_2 concentrations were extremely low at first measurement in January of 1999, making it difficult to fit the single exponential decay model. We assumed that water froze at 0°C, had 100% O_2 saturation, and had a barometric pressure of 670 mm Hg, and we used Mortimer's Nomograph (Mortimer 1981) to estimate the concentration of O_2 at freezing to be 14.4 mg L^{-1} and refit the model for these three lakes. Oxygen decay rates calculated for Mitchell and Phyllis Lakes were assumed to be independent from one year to the next. In total, 23 O_2 'lake-year' decay rates were calculated.

To examine general patterns between winter O_2 decay rates (k) and lake and watershed characteristics, we performed general linear, nonlinear, and backward multiple regression. The lakes were categorized according to state (clear vs. turbid), depth (shallow vs. deep), and frequency of anoxia (frequent, occasional, never) to examine whether or not general patterns were related to such functional categorizations. Lakes with turbidities <3–4 Nephelometric Turbidity Units (NTU) were classified as clear, and lakes with turbidities >3–4 NTU were classified as turbid (Jackson 2003). Shallow lakes are polymictic during summer (z_{max} < 5 m), while deep lakes stratify and are dimictic (z_{max} > 5 m). Analysis of covariance (ANCOVA; α = 0.05) was performed to test for different relationships based on classes (state, depth, anoxic frequency). Total phosphorus (TP) and Chl a were $\log_{10}$ transformed to better meet the assumptions of multivariate regression analysis.

The masses of total summer phytoplankton-derived and total summer macrophyte-derived carbon were calculated and summed to yield a total lake carbon-loading estimate due to autochthonous production. Phytoplankton-derived carbon was estimated from chlorophyll with the carbon : Chl a relationship of Banse (1977). We assumed phytoplankton growth occurred throughout the entire water column because the volumes of water below 5 m were small compared to volumes in the upper 5 m of our study lakes. The greatest mean depth (z_{mean}) was 5.4 m, and lakes stratified if the maximum depth was >5 m. We assumed that 90% of fresh macrophyte mass was water (Hutchinson 1975) and that carbon was 38% of dry macrophyte mass (Duarte 1992). Total lake macrophyte carbon (kg) was the product of the mean macrophyte carbon mass per square meter and the area of the

Table 4. Lake and watershed variables of 20 south central Alberta lakes (Gap Lake not included) correlated with O_2 decay rates (k) and turbidity for the entire set of lakes, and when grouped according to depth (polymictic/stratified) and state (clear/turbid) ($\alpha = 0.05$). No lake and watershed correlated with decay rates for deep lakes.

Group	Dependent variable	Independent variables	Parameter estimate	Partial r^2	df	F value	r^2	$p > F$
Entire lake set	Decay rate (k) ($g\ m^{-3}\ d^{-1}$)	Intercept	−0.073	—	21	47.22	0.869	<0.0001
		Macrophyte biomass ($kg\ m^{-2}$)	0.018	0.50				
		$\log_{10}$ total phosphorus ($\mu g\ L^{-1}$)	0.050	0.33				
		Percentage littoral cover	0.0003	0.06				
Entire lake set	Turbidity (NTU)	Intercept	0.478	—	21	31.32	0.839	<0.0001
		$\log_{10}$ Chl a ($\mu g\ L^{-1}$)	0.412	0.62				
		Macrophyte biomass ($kg\ m^{-2}$)	−0.090	0.16				
		Maximum depth (m)	−0.030	0.05				
Clear lakes	Decay rate (k) ($g\ m^{-3}\ d^{-1}$)	Intercept	−0.117	—	14	182.89	0.975	<0.0001
		Total carbon (kg)	0.000	0.71				
		Percentage littoral area	0.001	0.06				
		$\log_{10}$ total phosphorus ($\mu g\ L^{-1}$)	0.099	0.03				
Turbid lakes	Decay rate (k) ($g\ m^{-3}\ d^{-1}$)	Intercept	−0.047	—	6	74.94	0.961	0.0007
		$\log_{10}$ total phosphorus ($\mu g\ L^{-1}$)	0.070	0.84				
		Algal carbon ($g\ m^{-3}$)	−0.041	0.13				
Shallow lakes (<5.0 m)	Decay rate (k) ($g\ m^{-3}\ d^{-1}$)	Intercept	−0.020	—	10	46.5	0.901	<0.0001
		Macrophyte biomass ($kg\ m^{-2}$)	0.019	0.77				
		$\log_{10}$ total phosphorus ($\mu g\ L^{-1}$)	0.037	0.15				

lake <3 m in depth—the maximum depth at which we observed macrophyte colonization. Macrophyte-derived carbon, expressed volumetrically, was determined by dividing total macrophyte carbon by the lake volume.

Results

O_2 decay, anoxia, and lake and watershed variability—To attempt to estimate only the O_2 decay processes and not O_2 inputs via freeze-out of gases and photosynthesis after freezing, initial O_2 concentrations were removed from 11 of the 23 lake O_2 time series prior to determining the O_2 decay rates (Table 2). Significant nonlinear regressions were fit for all lakes. Throughout winter, lake ice was generally black; hence, little O_2 was lost via slushing and white ice formation. Oxygen decay rates ranged from 0.006 to 0.216 g O_2 m^{-3} d^{-1}, with the exception of Gap Lake. This lake did not completely freeze over during the winter of 1998–1999, had an O_2 decay rate of 0 g O_2 m^{-3} d^{-1}, and was therefore excluded from subsequent analyses. Oxygen concentrations fell below 1 mg L^{-1} for 12 of the 23 lakes, indicating that functional anoxia was reached. Mitchell Lake was anoxic the first year sampled but only dropped to 1.88 mg L^{-1} the following winter (1999–2000), slightly higher than our 1 mg L^{-1} operational definition of anoxia.

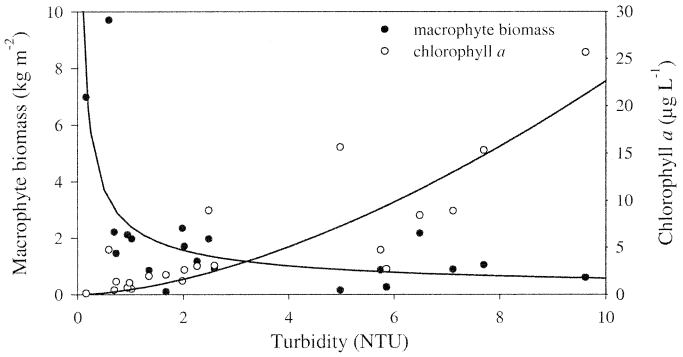

Fig. 1. Relationship between turbidity, total macrophyte-derived carbon, and total phytoplankton-derived carbon and Chl a concentration.

Strong, significant correlations were found between O_2 decay and macrophyte biomass per unit area, TP concentration, and percentage littoral cover (Table 3), which together explained 87% of the variation in decay rates when combined in a multiple regression model (Table 4). Decay rates correlated most strongly with macrophyte biomass. Turbidity correlated negatively with macrophyte biomass and positively with $\log_{10}$ Chl a (Table 4). Nonlinear exponential lines of best fit ($y = ax^b$) indicate a stronger relationship between Chl a and turbidity ($F_{22} = 50.83$, $p < 0.0001$) than macrophyte biomass and turbidity ($F_{22} = 23.94$, $p < 0.0001$) although both relationships were highly significant (Fig. 1).

Clear and turbid lakes—Decay rates were generally higher in turbid (average turbidity = 6.8 NTU) than clear (average turbidity = 1.6 NTU) lakes and four times higher in shallow than deep lakes (Table 5). Clear lakes had higher average macrophyte biomass per unit area and significantly lower Chl a and TP concentrations than turbid lakes (t-test, df = 21, $p < 0.001$). In general, the mass of macrophyte-derived carbon decreased and the mass of phytoplankton-derived carbon increased with turbidity (Fig. 1). Log_{10} Chl a concentration explained 62% of the variability in turbidity for all lakes; however, when classified by state, depth, or anoxic frequency, Chl a failed to significantly explain any variability in k (Table 4). Variation in O_2 decay rate ex-

Table 5. Means (SE) of lake and watershed variables for study lakes (Gap Lake not included) located in south central Alberta, grouped according to state, depth, and anoxic frequency. Macrophyte wet biomass is the biomass per unit area at depths less than 3 m since plants were not observed at greater depths.

Variable	Entire lake set (n = 22)	Clear state (n = 15)	Turbid state (n = 7)	Shallow (<5.0 m) (n = 11)
Decay rate (k) (g m^{-3} d^{-1})	0.048 (0.011)	0.042 (0.015)	0.061 (0.015)	0.080 (0.017)
Volume (m^3)	1,013,000 (516,000)	383,000 (65,000)	2,362,000 (1,569,000)	1,553,000 (1,027,000)
Surface area (SA) (ha)	64.6 (38.9)	13.8 (2.0)	173.5 (117.1)	114.3 (76.5)
SA : Volume (m^{-1})	0.591 (0.068)	0.460 (0.061)	0.864 (0.117)	0.837 (0.081)
Maximum depth (z_{max}) (m)	5.57 (0.89)	7.32 (1.01)	1.81 (0.28)	1.93 (0.24)
Mean depth (z_{mean}) (m)	2.27 (0.31)	2.81 (0.37)	1.11 (0.15)	1.14 (0.13)
Macrophyte wet biomass (kg m^{-2})	1.65 (0.41)	2.02 (0.58)	0.85 (0.25)	1.88 (0.81)
Summer Chl a (μg L^{-1})	5.36 (1.35)	2.45 (0.55)	11.61 (2.98)	8.98 (2.22)
Total phosphorus (TP) (μg L^{-1})	90.64 (46.94)	18.81 (2.82)	244.57 (135.68)	166.20 (90.06)
Turbidity (NTU)	3.23 (0.57)	1.57 (0.81)	6.79 (0.58)	4.92 (0.88)
DOC (μg L^{-1})	18.67 (3.0)	14.9 (2.3)	26.7 (7.6)	27.1 (4.8)
Percentage littoral cover	57.3 (8.3)	44.7 (9.6)	84.3 (10.7)	90.0 (7.0)
Total autochthonous carbon (kg)	17,900 (7,060)	11,000 (6,370)	32,500 (17,100)	31,400 (13,100)
Total phytoplankton carbon (kg)	182 (90)	42 (8)	486 (256)	321 (173)
Total macrophyte carbon (kg)	17,700 (6,990)	10,960 (6,360)	32,100 (16,900)	31,100 (13,000)
Phytoplankton carbon (g m^{-3})	0.30 (0.07o)	0.1 (0.0)	0.6 (0.2)	0.5 (0.1)
Macrophyte carbon (g m^{-3})	42.5 (15.8)	49.4 (22.9)	27.7 (8.2)	74.1 (29.0)
Total phytoplankton : Macrophyte carbon	0.025 (0.008)	0.016 (0.005)	0.044 (0.022)	0.029 (0.015)

plained by lake characteristics that classify lakes by state yielded a significant overall model (ANCOVA, df = 21, r^2 = 0.972, $p < 0.0001$); however, a significant interaction between state and lake variables indicates that clear and turbid lakes have a different relationship between O_2 decay rates and the lake variables we measured. When lake variables were regressed on k for clear and turbid lakes separately, total carbon explained 71% of the variation in k in clear lakes, and total phosphorus explained 84% of the variation in turbid lakes (Table 4).

Shallow and deep lakes—Deep lakes averaged 9.2 m, while shallow lakes averaged 1.9-m maximum depth (Table 5). In addition to the large difference in O_2 decay rates between these classifications, the mean TP concentration was 11 times greater, and total carbon loading was ~4 times greater in shallow lakes compared to deep lakes. Oxygen decay rates in shallow lakes correlated with macrophyte biomass and $\log_{10}$ TP (Table 4), but in deep lakes k did not correlate with any of the morphometric and biological lake and watershed variables we measured. Hence, it was not possible to further separate deep and shallow lakes via analysis of covariance.

Deep lakes were relatively clear, but shallow lakes were either clear or turbid (Fig. 2). Shallow, clear lakes had low phytoplankton : macrophyte carbon ratios, and deep clear lakes had high ratios (Fig. 2). The ratio of phytoplankton : macrophyte-derived carbon increased significantly with turbidity in shallow lakes (F_{10} = 21.34, $p < 0.01$), but no significant relationship was found for deep lakes (Fig. 2).

Frequency of anoxia—Our study lakes included nine lakes that are frequently anoxic, eight that are occasionally anoxic, and three that are never anoxic (Gap Lake excluded) (Table 1). Eight of the nine lakes classified as frequently anoxic were anoxic during the winters we sampled (Table 2). The three lakes classified as never anoxic had O_2 concentrations >3 mg L^{-1} when the ice broke up. Of the eight lakes that occasionally experience anoxia, four became anoxic. These four had the highest O_2 decay rates of all the lakes that occasionally become anoxic. Two of these existed in a clear state and the other two in a turbid state. Frequently anoxic lakes had much higher TP, DOC, and summer Chl a concentrations, were the shallowest of all the lakes, and had the highest percentage littoral cover of all our study lakes. These lakes also had the highest mean decay rates of all our study lakes (four times higher than lakes that are occasionally anoxic and eight times higher than lakes that are never anoxic). Lakes that never experience anoxia had the lowest mean decay rates.

Clear lakes experience all three categories of anoxic frequency (Fig. 3a). Turbid lakes either frequently or occasionally experience anoxia. When depth is considered, three classes of lakes appear: (1) deep, clear lakes that never become anoxic; (2) shallow turbid, and deep clear lakes that occasionally reach anoxia; and (3) shallow turbid, and shallow clear lakes that frequently reach anoxia (Fig. 3b).

Discussion

The geochemical definition of anoxia is 0 mg L^{-1}. However, processes that are relevant to lake functioning shift from aerobic to anaerobic at O_2 concentrations below ~1 mg L^{-1} (Greenbank 1945; Nürnberg 1995), and minimum critical tolerance levels for fish can be as high as 3 to 4 mg L^{-1} O_2 (Greenbank 1945). For this study, we considered a lake to be functionally anoxic if its O_2 concentration fell below 1 mg L^{-1}.

Table 5. Extended.

Variable	Deep (>5.0 m) (n = 11)	Frequent (n = 9)	Occasional (n = 10)	Never (n = 3)
Decay rate (k) (g m^{-3} d^{-1})	0.017 (0.002)	0.087 (0.021)	0.025 (0.005)	0.010 (0.003)
Volume (m^3)	473,000 (68,000)	147,000 (47,000)	1,893,000 (1,095,000)	675,000 (70,000)
Surface area (SA) (ha)	14.9 (1.9)	11.7 (3.6)	127.2 (83.4)	14.7 (2.7)
SA : Volume (m^{-1})	0.345 (0.033)	0.846 (0.106)	0.466 (0.044)	0.224 (0.072)
Maximum depth (z_{max}) (m)	9.20 (0.78)	3.04 (1.27)	6.63 (1.12)	9.60 (1.70)
Mean depth (z_{mean}) (m)	3.41 (0.34)	1.78 (0.24)	2.73 (0.39)	4.03 (0.68)
Macrophyte wet biomass (kg m^{-2})	1.42 (0.24)	2.11 (0.98)	1.14 (0.24)	1.96 (0.15)
Summer Chl a (μg L^{-1})	1.75 (0.26)	9.30 (2.75)	3.06 (0.72)	1.22 (0.69)
Total phosphorus (TP) (μg L^{-1})	15.09 (1.45)	192.61 (109.04)	22.65 (6.04)	11.38 (2.55)
Turbidity (NTU)	1.54 (0.18)	4.04 (1.10)	3.10 (0.71)	1.24 (0.40)
Dissolved organic carbon (DOC) ($\mu g \cdot L^{-1}$)	10.2 (0.5)	29.0 (5.7)	12.1 (1.4)	9.6 (1.5)
% littoral cover	24.56 (5.1)	83.3 (11.1)	41.0 (11.5)	33.3 (10.1)
Total autochthonous carbon (kg)	4,290 (1,200)	16,900 (10,600)	22,800 (12,500)	4,000 (2,530)
Total phytoplankton carbon (kg)	45 (9)	65 (23)	331 (191)	42 (19)
Total macrophyte carbon (kg)	4,250 (1,200)	16,870 (10,600)	22,500 (12,300)	3,950 (2,500)
Phytoplankton carbon (g m^{-3})	0.1 (0.0)	0.5 (0.2)	0.2 (0.0)	0.1 (0.0)
Macrophyte carbon (g m^{-3})	10.9 (3.2)	85.6 (34.6)	14.4 (3.2)	6.7 (4.7)
Total phytoplankton : Macrophyte carbon	0.020 (0.007)	0.032 (0.018)	0.022 (0.008)	0.014 (0.003)

O_2 decay, anoxia, and lake and watershed variability—Lakes historically used to develop O_2 depletion models were located in the Arctic, on the Canadian Shield of central and northern Ontario, or in northern Alberta (Welch 1974; Lasenby 1975; Welch et al. 1976; Charlton 1980; Cornett and Rigler 1980, 1984; Jackson and Lasenby 1982; Babin and Prepas 1985; Trimbee and Prepas 1988). They were typically deep (average z_{max} = 26 ± 22 m, z_{max} range = 3–88 m), stratified lakes with limestone or granite basins and low nutrient loading.

The lakes included in our study differ from those traditionally used to model winter oxygen dynamics, with the exception of the Manitoba prairie lakes studied by Barica and Mathias (1979). Unfortunately, they did not measure phosphorus concentrations or macrophyte biomass. Typical oxygen depletion models have considered only phytoplankton as the source of autochthonous organic matter for decomposition. Such rates may not be appropriate for much shallower prairie lakes that harbor large, dense stands of macrophytes and may grossly underestimate winter O_2 decay rates in shallow prairie lakes. We found that macrophyte biomass is an important predictor of O_2 decay rates (k) in shallow prairie lakes and explained 50% of the variation in k. Our study lakes are relatively productive, shallow (average z_{max} = 5 ± 4 m, z_{max} range = 1–13 m), wind-mixed lakes. Many do not have permanent outflows, and inputs occur via rainfall and catchment runoff.

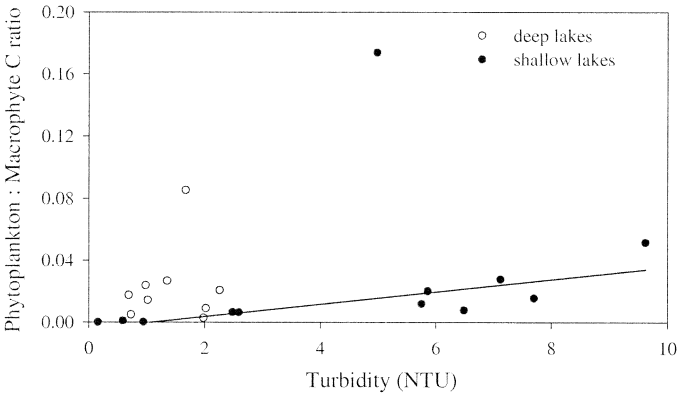

Fig. 2. The ratio of phytoplankton : macrophyte-derived carbon increases with turbidity in shallow lakes, but no relationship is evident for deep lakes.

That Chl a was *not* a predictor of k in shallow prairie lakes was a surprising finding. Even in lakes with high turbidities, Chl a failed to correlate with k. Numerous prairie lakes are shallow and polymictic, and the entire lake is typically colonized by phytoplankton. However, in the shallow prairie lakes we examined, macrophyte-derived carbon inputs are likely so large that phytoplankton inputs do not significantly influence decay rates. Estimates of macrophyte and phytoplankton-derived carbon support this hypothesis. On average, the mass of macrophyte-derived carbon was ~150 times greater than phytoplankton-derived carbon and comprised ~98% of total autochthonous loading. However, phytoplankton communities do influence lake characteristics and processes such as nutrient retention and cycling, turbidity, and Secchi depth.

Macrophytes are the primary contributors of POM in shallow prairie lakes. Oxygen decay rates are a function of POM loading; hence, macrophyte biomass is an important predictor of k in these lakes. The percentage of the lake bottom that supports macrophyte growth also correlates positively with O_2 decay rates, further indicating the importance of macrophytes in determining O_2 decay rates. The average depth of our study lakes was 2.3 m, with an average percent

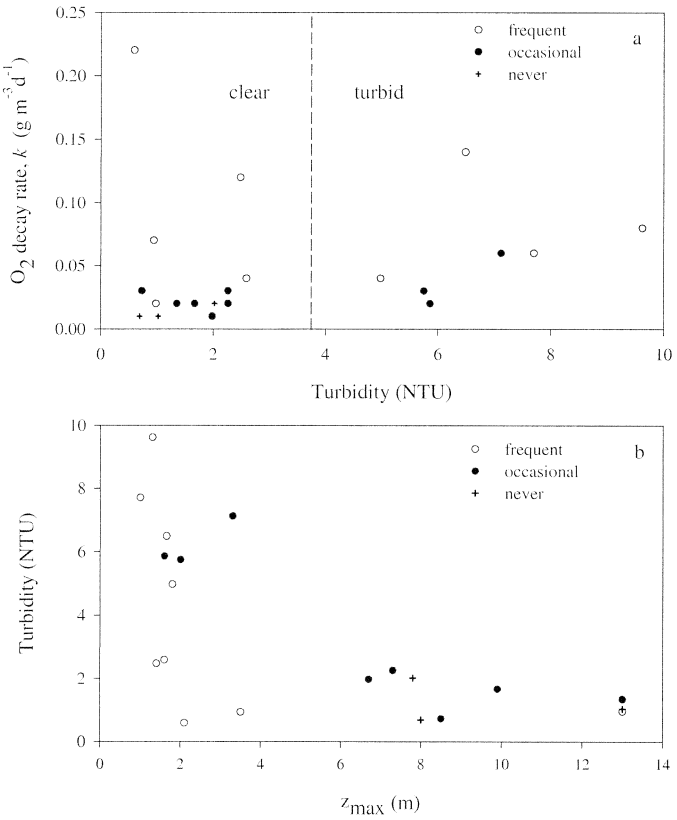

Fig. 3. (a) When grouped according to turbidity and anoxic frequency, clear lakes reach anoxia at all three frequencies and turbid lakes reach anoxia either frequently or occasionally. (b) When depth is factored in, the lakes separate into distinct groups.

plant cover of 60%. Several lake bottoms were entirely covered by macrophytes ($n = 10$).

To search for patterns in functional relationships between O_2 decay rates and lake and watershed characteristics, we separated our study lakes into (1) clear and turbid lakes, (2) shallow and deep lakes, and (3) frequency of anoxia (never, occasional [once every 5–10 yr], and frequent [once every 1–2 yr]).

Clear and turbid lakes—Total phosphorus concentrations are tightly coupled with productivity in aquatic systems (Dillon and Rigler 1974). At extreme levels of nutrient loading, shallow lakes may exist in phytoplankton-dominated or macrophyte-dominated states (Jeppesen et al. 1998). Both conditions are characterized by high organic matter loading and high O_2 demand under ice during winter. We observed both clear and turbid lakes, but macrophytes appeared to be the primary source of decaying POM, even in turbid lakes where phytoplankton are abundant.

Total phosphorus was a strong predictor of O_2 decay rates in turbid lakes and a weak predictor in clear lakes (Table 4). Clear lakes had much lower water column TP concentrations, implying they might be less productive; however, the mean macrophyte biomass per unit area was ~2.5× higher than in turbid lakes (Table 5). Water column TP concentrations do not necessarily indicate the concentration of phosphorus available to rooted macrophytes because they acquire phosphorus primarily from the sediments (Barko and Smart 1980; Cariganan and Kalff 1980). We did not measure sediment phosphorus, but it is unlikely that sediment phosphorus limits macrophyte growth because nutrient loading from the watershed is high in these shallow prairie lakes (Allan et al. 1980). Water column total phosphorus concentrations were low in clear state lakes likely because phosphorus was bound up in macrophyte tissues that have long turnover times (the entire growing season). Nutrient turnover is more rapid in phytoplankton-dominated lakes because phytoplankton lifespans are generally on the order of days to weeks.

Total carbon is the strongest predictor of O_2 decay in clear lakes and is comprised primarily of macrophyte-derived carbon. The extent to which macrophytes control lake function in clear lakes (i.e., O_2 decay) is proportional to their abundance (Gasith and Hoyer 1998). Biomass and percentage littoral cover are different measures of macrophyte abundance. The significance of percentage littoral cover suggests that not only is macrophyte carbon loading an important correlate of k in clear lakes, but also the distribution of macrophytes across the lake bottom is important.

Turbid lakes were phytoplankton dominated relative to clear lakes, but macrophytes remained the primary contributors of POM and hence the principal correlate of O_2 decay. Even though macrophyte biomass per unit area was lower in turbid than clear lakes, percentage littoral cover was higher (Table 5). High turbidities caused by phytoplankton shading (Spence 1982) and resuspension of sediments from wind mixing (James and Barko 1990) likely cause light limitation and reduce or inhibit macrophyte growth, resulting in lower macrophyte biomass per unit area. Chlorophyll *a* concentrations and phytoplankton carbon loading were greater in turbid lakes compared to clear lakes, and phytoplankton contributed to a larger proportion of total carbon loading as exhibited by the phytoplankton : macrophyte-derived carbon ratios.

Shallow and deep lakes—Lake and watershed characteristics of deep and shallow prairie lakes differ greatly (Table 5). Shallow lakes were more productive than deep lakes and had high TP concentrations that are consistent with intensive agriculture in the surrounding watersheds. These lakes support high abundances of blue-green algae, an observation that is consistent with empirical patterns (Downing et al. 2001) and the high concentrations of phosphorus (Jackson 2003). It has been suggested that in shallow clear lakes, macrophytes induce N limitation of phytoplankton, which further promotes water clarity (Van Donk et al. 1993; Van Donk and Gulati 1995). The deeper lakes are located in the Caroline region in the foothills of the Rocky Mountains where watershed relief is greater and much of the watershed is vegetated, consisting primarily of deciduous species. Nutrient loading via runoff is likely lower because the undisturbed watersheds retain nutrients. Nutrient cycling within the watershed occurs over a longer time (decades) than in the prairie landscape where soil erosion is high, and regular cultivation and turnover of crops occurs every year or two according to farming practices.

Deep lakes have lower TP concentrations, are less pro-

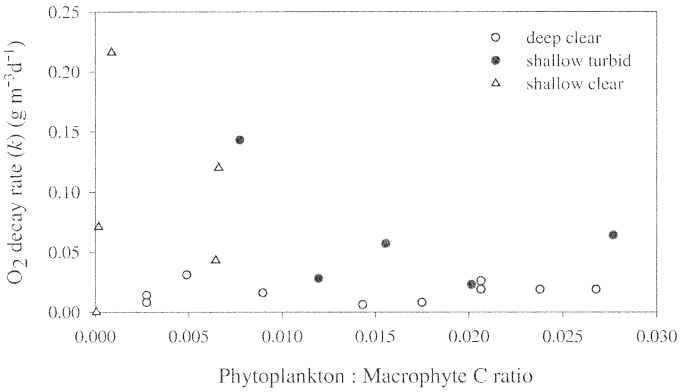

Fig. 4. Shallow clear lakes have low phytoplankton : macrophyte carbon ratios and high O_2 decay rates (k). Shallow turbid lakes have high phytoplankton : macrophyte carbon ratios and high O_2 decay rates. Finally, deep clear lakes also have high phytoplankton : macrophyte carbon ratios; however, they have low O_2 decay rates.

ductive, and have smaller SA : volume ratios than shallow lakes (Table 5). Oxygen decay rates are lower in deep lakes because total autochthonous carbon loading is lower, and less of the water volume is in contact with the sediments where O_2 demand is great (Table 5). That O_2 decay rates do not correlate with any lake and watershed characteristics measured for deep lakes was surprising. Lakes classified as deep in this study more closely resemble lakes upon which previous models have been based, yet earlier developed models do not seem to fit our study lakes. Autochthonous carbon inputs should drive O_2 consumption, but they do not account for significant variation in k. For the deep lakes, watershed loading may be important; however DOC, a measure of dissolved carbon inputs from overland flow, failed to correlate with k. Because these lakes are surrounded by vegetated watersheds, perhaps direct input of coarse POM plays an important role in O_2 decay (e.g., leaves and woody debris), although we did not measure allochthonous carbon loading.

Shallow clear lakes were dominated by macrophytes, and phytoplankton-derived carbon contributed a very small proportion of total autochthonous carbon inputs that drive O_2 decay (Fig. 4). The low phytoplankton : macrophyte carbon ratio in shallow clear lakes is consistent with the suggestion that macrophytes maintain a clear state by stabilizing the sediments with their roots and decrease water circulation and sediment resuspension (James and Barko 1990). Macrophytes may also release toxic, allelopathic chemicals that inhibit phytoplankton growth (Wium-Andersen et al. 1982; Gross et al. 1996).

Deep, stratified lakes were always clear. They had smaller surface areas and greater depths, yielding only a small littoral area suitable for macrophyte colonization. Chlorophyll *a* concentrations were low, but unlike macrophytes, phytoplankton colonize a larger proportion of the lake. Consequently, in deep lakes, phytoplankton contributed a higher proportion of the total autochthonous carbon than in shallow clear lakes, as exhibited by the high phytoplankton : macrophyte carbon ratio (Fig. 4), and should be an important carbon source.

Frequency of anoxia—Classifying a lake as clear or turbid alone does not predict anoxic frequency (Fig. 3a) because lakes that experience frequent and occasional anoxia existed in both states. Our hypothesis that occasionally anoxic lakes would exist in a clear, macrophyte-dominated state was not supported. The reasons that lakes never reach anoxia and frequently reach anoxia are straightforward and are related directly to nutrient levels, productivity, and morphometry (Lasenby 1975; Welch et al. 1976; Barica and Mathias 1979; Cornett and Rigler 1979, 1980; Charlton 1980; Mathias and Barica 1980; Babin and Prepas 1985; Cornett 1989). Phytoplankton and macrophytes are important sources of carbon, and morphometry determines the mass of O_2 stored at freezing as well as the area of the sediments in contact with the water column. Frequently anoxic lakes were generally different from lakes that occasionally experience anoxia and lakes that never experience anoxia, neither of which differed significantly from each other for any lake and watershed characteristics we measured. There are two distinct types of lakes that experience occasional anoxia: shallow turbid, and deep clear. Likely, different mechanisms and processes determine whether a lake will experience anoxia.

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