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Seasonal and diel changes of dissolved oxygen in a hypertrophic prairie lake

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Abstract

Humboldt Lake, a hypertrophic prairie lake typical of many found on the Great Plains of North America, is usually ice-covered from early November to about mid-May. The lake is an important recreational fishery, now mainly stocked with walleye. It has a high potential risk of experiencing fish kills because of the very large cyanobacterial blooms that develop in it, the high rates of algal and bacterial production and the high concentrations of ammonia (NH_3-N) and dissolved organic matter. Following the collapse of cyanobacterial blooms, shallow prairie lakes are known to undergo periods of anoxia that can lead to summer fish kills. In some of the lakes, anoxia forms during the long period of ice cover, causing winter fish kills. Two years of seasonal and diel data (total phosphorus, dissolved oxygen (DO), NH_3-N and chlorophyll-*a* concentrations, and bacterial production) were analysed in this study to assess why significant fish kills did not occur during this period or during the ≈ 30 years of records from Saskatchewan Environment. Humboldt Lake did not become anaerobic, either following the collapse of the cyanobacterial bloom or under ice cover, indicating that the oxygen (O_2) influx (strong mixing) and production processes were greater than the microbial and chemical O_2 demands, both over seasonal and diel time scales. Several published risk threshold criteria to predict the probability of summer and/or winter fish kills were applied in this study. The threshold criteria of maximum summer chlorophyll and maximum winter NH_3-N concentrations indicated that a summer fish kill was unlikely to occur in this hypertrophic prairie lake, provided its water quality remained similar to that during this study. Similarly, the threshold criteria of initial DO storage before ice cover and the rate of O_2 depletion under ice cover also indicated a winter fish kill was unlikely. However, recent development in the watershed might have resulted in significant water quality deterioration and the winter fish kill that occurred in 2005.

Key words

bacterial production, cyanobacterial blooms, dissolved oxygen, fish kills.

INTRODUCTION

Millions of water bodies of different sizes are scattered across the Canadian prairies, ranging from small farm dugouts, marshes and 'pothole' lakes to large reservoirs, meltwater channel lakes and large lakes (> 30 000 km^2); examples of the latter being lakes Winnipeg and Manitoba (Barica 1987). These water bodies range from freshwater to hypersaline and cover the trophic spectrum.

Most prairie lakes are naturally eutrophic because of their high nutrient loading, high solar input, shallowness, internal nutrient regeneration and extended freeze-up (Barica 1987). They also exhibit extreme fluctuations in dissolved oxygen (DO) concentrations. Dense blooms of algae, usually cyanobacteria, are often the dominant primary producers (Barica 1987). Thus, the recreational quality of these lakes can be reduced by nuisance algal blooms and the associated risks of summer and winter fish kills. Summer fish kills occur through a variety of mechanisms, including oxygen (O_2) depletion, toxins released by cyanobacteria and/or ammonia (NH_3-N) build-up, while winter fish kills may result from NH_3-N build-up and/or O_2 depletion.

Much of the limnological research conducted on Saskatchewan prairie lakes has been conducted by Hammer, who characterized their basic physical and chemical features (Hammer 1978, 1986; Hammer & Haynes 1978; Hammer *et al.* 1983). One of the more remarkable lakes in this region is Humboldt Lake (52°09′N, 105°06′W), located in

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south-central Saskatchewan. This lake is hypertrophic, with a surface area of 17.2 km^2 and a maximum depth of ≈ 8 m (mean depth = 4.8 m), and is slightly saline (total dissolved solids = 3.3 g L^{-1}; Hammer 1978). It is a long (12.4 km) and narrow (0.5–2.0 km) lake orientated along an east–west direction and lying in a gently rolling prairie landscape (Evans *et al.* 1995). This long fetch and low relief, combined with strong prairie winds, promotes vertical mixing of the lake's water column. Sulphate is the dominant anion (72.3%) and magnesium is the dominant cation (60.7%), with concentrations of 16 084 µmol and 12 754 µmol, respectively (Arts *et al.* 1992). With a salinity of ≈ 3.9 g L^{-1} (Hammer 1978), its water is denser (1.0032) than more typical freshwater lakes, thereby being somewhat more resilient to vertical mixing. Ice cover typically forms in early November, attaining a maximum thickness of 1.0–1.5 m by January (Arts *et al.* 1992). The ice-free period usually starts in early May. The lake's chemistry and ice cover chronology are typical of a large number of eutrophic to hypertrophic, small to medium-sized, lakes on the Great Plains of North America (cf. Hammer 1986; Barica 1987). Historically, the common fish species in the lake were walleye (*Sander vitreus*; formerly *Stizostedion vitreum*), northern pike (*Esox lucius*), yellow perch (*Perca flavescens*) and brook stickleback (*Culaea inconstans*). However, the lake is now mainly stocked with sport fish, predominantly walleye (Evans *et al.* 1995). These species are typical for prairie lakes.

Relatively few studies have focused on developing models that can be used to make predictions regarding prerequisite conditions that can lead to fish kills in shallow, prairie lakes. The most detailed work has been conducted by Barica (e.g. 1975, 1984). He reasoned that there was a major increase in bacterial numbers and activity following the collapse of summer cyanobacterial blooms in prairie lakes, which depleted the water column of O_2, leading to the build-up of high NH_3-N concentrations under winter ice-cover. He advocated the use of simple risk threshold criteria (Table 1) to predict the risk level of summer fish kills due to water column deoxygenation. Based on the maximum winter NH_3-N concentrations and maximum summer chlorophyll-*a* concentrations, Barica (1975, 1984) predicted summer fish kills in 57 prairie lakes with > 90% accuracy. This approach to predicting fish kills has been successfully applied to other lakes outside the prairies, such as Laguna de Bay in the Philippines (J. Barica, pers. comm., 2005).

As noted above, Humboldt Lake is ice-covered from November to early May. Prairie lakes can develop mid-winter anoxia resulting in major fish mortalities, which Barica and Mathias (1979) attributed to the microbial decomposition of organic matter (dissolved and particulate) when O_2 influxes, due to primary production and mixing, are reduced because of snow and ice cover. They developed a nomogram, using initial O_2 storage and rate of O_2 depletion, to determine the critical time to reach total anoxia in a lake, thereby predicting the occurrence of a winter fish kill (Table 1).

There are several reasons why eutrophic prairie lakes in general, and Humboldt Lake in particular, might be at high risk for summer and/or winter fish kills. First, Humboldt Lake has a maximum summer chlorophyll-*a* concentration of > 200 µg L^{-1} (Robarts *et al.* 1992). According to Barica (1987), this places the lake in a high-to-very-high risk category for summer fish kills (Table 1). Second, primary production and, consequently, bacterial production in Humboldt Lake are in the upper range measured for freshwater systems (Robarts *et al.* 1994). Third, Humboldt Lake has high NH_3-N concentrations in summer (277 µg L^{-1}) and winter (518 µg L^{-1}), which approach Canadian water quality guidelines limits for aquatic life (Canadian Council of Ministers of the Environment 2000). Fourth, the lake has high concentrations of dissolved organic matter (DOM), ranging from 19.9–27.9 mg L^{-1} (0 = 22.7 mg L^{-1}) as dissolved

Table 1. The threshold risk criteria developed by Barica (1975, 1987) to predict the risk of summer and winter fish kills in prairie lakes

Model use	Parameter	Lower limit for high risk
Summer fish kill	Maximum summer chlorophyll-*a* concentration	100 µg L^{-1}
Summer fish kill	Maximum summer chlorophyll-*a* concentration	100 µg L^{-1}
	Mean summer conductivity	≈ 3000 µS cm^{-1}
Summer fish kill	Maximum summer chlorophyll-*a* concentration	100 µg L^{-1}
	Minimum Secchi disc transparency	0.3 m for non-*Aphanizomenon* blooms
		0.4 m for *Aphanizomenon* blooms
Summer fish kill	Maximum summer chlorophyll-*a* concentration	100 µg L^{-1}
	Maximum winter ammonia concentration	1000 µg L^{-1}
Winter fish kill	Initial O_2 storage before ice cover	Variable depending upon initial
	Rate of O_2 depletion under ice cover	storage and depletion rate

organic carbon (Robarts *et al.* 1994), another typical feature of prairie lakes (Arts *et al.* 2000). With such high microbial production rates and DOM concentrations, it might be expected that summer and/or winter fish kills, concomitant with periods of anoxia, will occur. Despite the hypertrophic nature of this lake, however, fish kills have been reported only sporadically (J. Merkowsky, pers. comm., 2004).

This article focused on two annual cycles (including total phosphorus (TP) and phytoplankton biomass) and diel changes in DO, NH_3-N and chlorophyll-*a*, and bacterial numbers and production in Humboldt Lake, to explain the absence of fish kills for ≈ 30 years. It had three objectives, the first being to determine whether or not Humboldt Lake experienced sustained periods of anoxia, either following the summer cyanobacterial bloom collapse or under ice cover. The second was to ascertain if the lake might have short periods of anoxia over a diel cycle due to increased bacterial production, which has not been reported in previous studies of fish kill lakes, during or immediately following summer cyanobacterial blooms. The third objective was to apply a suite of risk threshold criteria (Table 1) to determine if they were in agreement with the seasonal and diel biological and chemical data from Humboldt Lake. Although these criteria are still being used by fish-farming and provincial organizations in Manitoba and Saskatchewan, examples highlighting the application of their work remain unpublished (J. Barica, pers. comm., 2005). Conclusions were then drawn about the suitability of the various risk criteria to hypertrophic Humboldt Lake, which is a prairie lake generally at the upper range, in terms of its physical characteristics, compared to the lakes studied by Barica and colleagues, but is still typical of many lakes on the prairies. Although Barica (1987) noted that his chlorophyll and NH_3-N threshold criteria (Table 1) were designed for lakes sufficiently shallow to undergo winter anoxia (i.e. those with a mean depth < 4 m), it was hypothesized that they could be applied to deeper lakes, such as Humboldt Lake.

MATERIALS AND METHODS

Water sample collection

Water samples were collected with an 8-L water sampler (internal diameter = 7 cm, length = 71.5 cm; General Oceanics, Miami, FL, USA) from a central, deep-water station. The sampler was operated horizontally to avoid sampling bias due to marked variations in phytoplankton biomass with depth. Water was collected from the surface and at 3-m and 6-m (bottom) depths. However, data are presented only for the surface and 6-m depths as there was usually little variation over the water column for all parameters except chlorophyll (Fig. 1). Temporal sampling intervals for the seasonal study in 1989–1991 were: (i) biweekly during May–June 1989; (ii) weekly during July–September 1989; (iii) biweekly to mid-October 1989; (iv) monthly during ice cover in January, February and March 1990 (water samples were collected from the surface, just beneath the ice, and 6-m depth); (v) monthly during May–October 1990; and (vi) only in January 1991 (bacterial production data was lost because water in the incubation containers froze). Dangerous ice conditions prevented sampling in the intervening months.

In highly productive waters, DO concentrations might show significant diel changes, with the concentrations declining markedly during night-time hours (Wetzel 2001). To investigate this phenomenon, water samples were collected from the surface, 3-m and 6-m depths, depending upon the parameter measured, in two diel studies in July and August 1990. Sampling began at 10.00 hours, being repeated at 4-h intervals throughout, and including, 10.00 hours the next day.

Physical and chemical parameters

The water temperature was measured with a thermistor (Cole Palmer, Vernon Hills, IL, USA). Water samples taken from the surface and 6-m depths were analysed for NH_3-N, TP and chlorophyll-*a* (Robarts *et al.* 1992). For O_2 analyses, water from the sampling bottle was slowly drained into glass bottles and allowed to overflow for several minutes. Winkler reagents were then added, and the bottles were closed with glass stoppers and placed in a cool box for transport to the laboratory for colourimetric analysis using a spectrophotometer (Perkin Elmer, Wellsley, MA, USA).

Biological parameters

Water samples (10 mL) collected for bacterial numbers were placed in sterile glass tubes and preserved with Lugol's iodine solution. Bacteria were counted, using an epifluorescence microscope and DAPI stain, as described by Tumber *et al.* (1993). Bacterial production was measured as the rate of incorporation of [methyl-^{3}H] thymidine (TdR) into bacterial DNA. Three 10-mL water samples were incubated *in situ* in sterile glass tubes (two live and one control), after being injected with TdR (Robarts *et al.* 1994). Humboldt Lake is one of only two prairie lakes in which detailed measurements of bacterial production have been made. Although Barica (1987) proposed increased bacterial activity following a cyanobacterial bloom collapse as the mechanism for deoxygenation in prairie lakes, this parameter was not measured.

The phytoplankton biomass (wet weight) was determined from the measured length and width determinations of individual species, which were then converted to volume and wet weight using previously derived formulae (Evans *et al.* 1995).

The correlations between the chemical and biological parameters were tested using Spearman Rank Correlation Analysis.

RESULTS

Seasonal cycles

The TP concentration was generally > 250 μg L^{-1} for most of the study period, and exceeded 400 μg L^{-1} during the summer. The TP concentrations were high even under ice cover, exceeding 150 μg L^{-1} and demonstrating the hypertrophic character of this lake (Fig. 1). From June to late August in 1989, cyanobacteria (*Aphanizomenon flos-aquae*) were the dominant (99%) phytoplankton species in Humboldt Lake (Arts *et al*. 1992). Large centric diatoms, mainly *Stephanodiscus niagarae*, dominated the biomass in autumn, while the dominant groups under the ice were the species of Chlorophyta, Chrysophyta and Cryptophyta. During the summer of 1990, *A. flos-aquae* was replaced as the dominant species by *Gleothece rupestris*, a non-bloom-forming cyanobacterium, although *Aphanizomenon* was still present in high numbers (Robarts *et al*. 1992). Thus, although the dominant species were different in the two summers, the phytoplankton dynamics in Humboldt Lake were generally characteristic of eutrophic to hypertrophic lakes, with summer populations dominated by cyanobacteria (Fig. 1). This characteristic dates back to at least 1961 in this lake (Hammer *et al*. 1983; Arts *et al*. 1992). The large

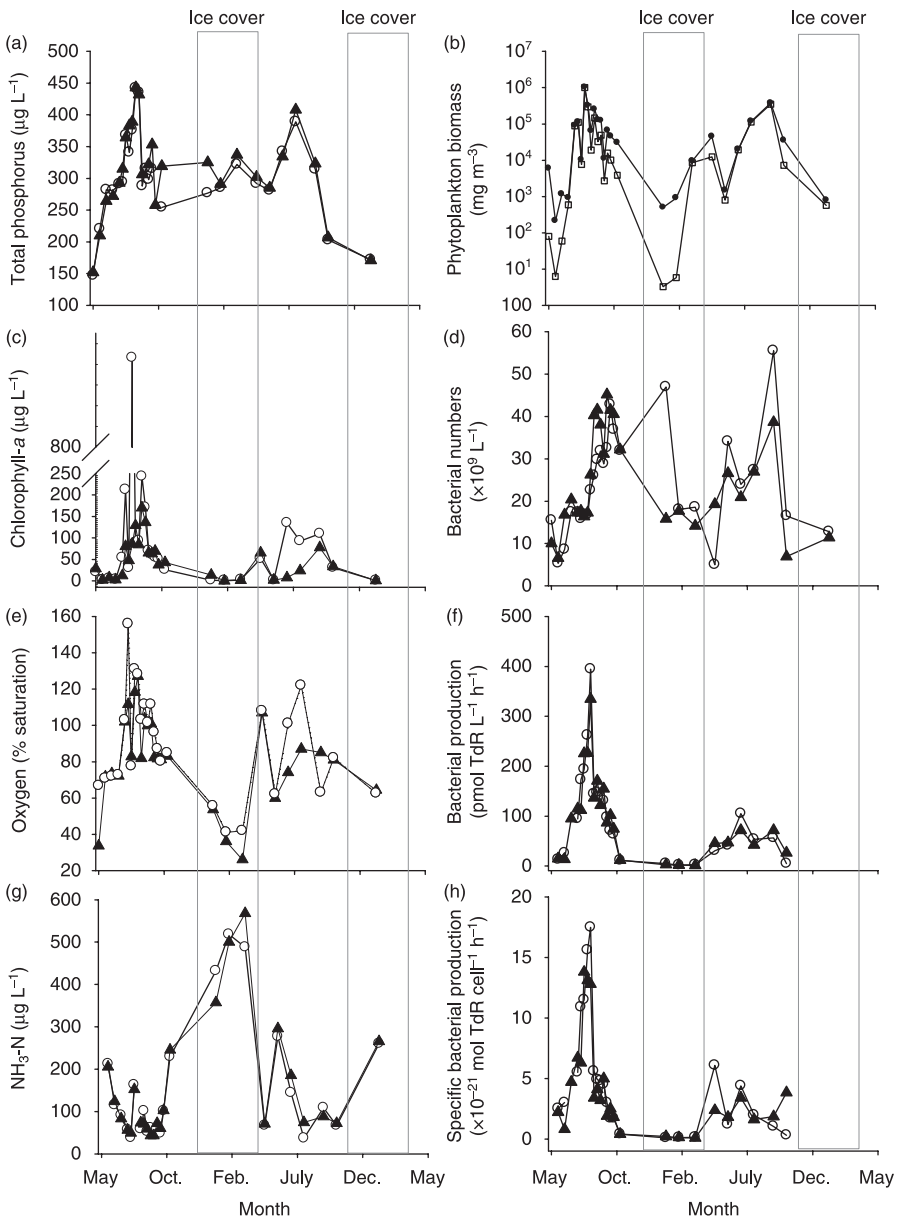

Fig. 1. Seasonal changes in Humboldt Lake. (a) total phosphorus concentration, (b) phytoplankton biomass, (c) chlorophyll-*a*, (d) bacterial numbers, (e) oxygen saturation, (f) bacterial production, (g) ammonia (NH_3-N), and (h) specific bacterial production. (a), (c)–(h): ○, at the surface; ▲, 6-m depth (≈ 0.5 m above the sampling station bottom). (b): □, cyanobacterial biomass; ■, total biomass. Week zero is May 1989 and week 85 is January 1991.

populations of summer cyanobacteria were accompanied by high levels of chlorophyll-*a*, which reached a maximum of 839 μg L^{-1} in August 1989 (Fig. 1). Although the total phytoplankton chlorophyll-*a* concentration in 1990 was not as great as in the previous year (i.e. chlorophyll levels > 100 μg L^{-1} only occurred between early July and mid-September), the cyanobacterial biomass was similar in both years (Fig. 1).

According to Barica (1978), a cyanobacterial bloom collapse occurs when the chlorophyll-*a* concentration in a lake changes by > 70 μg L^{-1} $week^{-1}$. In Humboldt Lake, the *Aphanizomenon* bloom collapsed twice in 1989: by 183 μg L^{-1} $week^{-1}$ in late July and by > 700 μg L^{-1} $week^{-1}$ (by ≈ 100 μg L^{-1} $week^{-1}$ at deeper depths; Robarts *et al.* 1992) in early August (Fig. 1). However, these were only partial bloom collapses, according to Barica's (1978) definitions, as deoxygenation did not occur (Fig. 1).

Humboldt Lake was generally well-mixed due to the long fetch and almost daily strong winds characteristic of the region (Robarts *et al.* 1994). The O_2 concentrations varied between 3.6 and 13.4 mg L^{-1} (O_2 = 8.8 mg L^{-1} ± 0.29 mg L^{-1} SE), the lowest value being recorded at the 6-m depth at the end of March under the ice. At higher depths in the water column, the O_2 concentrations were close to twice this lowest value. However, there was usually a small difference between the surface and bottom waters during the ice-free season (Fig. 1). The O_2 saturation averaged 85.5% (range = 26–156%). The highest saturation occurred with the summer chlorophyll peaks, dropping sharply after the lake froze (Fig. 1). Both the O_2 concentration (r = 0.70, P < 0.001) and O_2 saturation (r = 0.81, P < 0.001) were correlated with the chlorophyll-*a* concentrations. Generally, the NH_3-N concentration followed a reverse pattern, compared to both the O_2 concentration (r = −0.67, P < 0.001) and O_2 saturation (r = −0.82, P < 0.001), with the highest concentrations (> 500 μg L^{-1}) occurring under the ice and the lowest oncentrations (≈ 50 μg L^{-1}) occurring in the summer (Fig. 1).

Although the bacterial numbers were generally highest in summer, there was a large seasonal variation (Fig. 1). The bacterial numbers were only weakly and positively correlated to changes in the chlorophyll-*a* concentrations (r = 0.34, P = 0.02). Both bacterial production and specific bacterial production were highest in the summer and lowest in the spring, autumn and winter (Fig. 1), being correlated to changes in O_2 concentration (r = 0.50, P < 0.001) and O_2 saturation (r = 0.73, P < 0.001). These positive correlations indicate that the bacterial production was not sufficiently high to exert a major demand on the O_2 concentration, relative to the O_2 production and influx processes. If the bacterial production was able to exert a large, significant demand on the O_2 concentrations, inverse correlations would have been expected in the lake. Even under the ice, which can attain a thickness of 1.0–1.5 m (Arts *et al.* 1992), the bacterial O_2 consumption was not sufficiently high to produce anoxic conditions. In the autumn of 1989–March 1990 period, the O_2 concentration decreased at an average of 0.048 mg L^{-1} day^{-1}. This simple calculation suggests that it would have taken about another 80 days to consume all the O_2 (3.6 mg L^{-1}) at the 6-m depth recorded in late March. As the lake became ice-free by mid-May, it is unlikely that Humboldt Lake would have become anaerobic, even in late winter, assuming the O_2 consumption rate remained constant. Furthermore, as the snow melts in April, the light penetration through the ice would increase, thereby also stimulating an increase in algal production. However, Babin and Prepas (1985) suggested that O_2 consumption under ice cover is not constant, being greatest during the first three months of ice cover, which implies that our simple calculation probably overestimated O_2 consumption (see Discussion). The O_2 concentration was 6.1 mg L^{-1} just beneath the ice in March. Thus, the upper water column was even less likely than the deeper depths to become anaerobic. The dominant factor previously shown to be correlated with bacterial production in Humboldt Lake was the water temperature, followed by the chlorophyll-*a* concentration (Robarts *et al.* 1994).

July and August diel studies

The impact of wind-mixing on the physicochemical limnology of Humboldt Lake can be seen in the diel study data. The water temperature in July varied between 18.5 and 19.5°C over the whole water column, being greatest at 14.00 hours (Fig. 2). The chlorophyll-*a* concentration was greatest in late afternoon, coinciding with the peak in O_2 saturation. The O_2 saturation decreased overnight, increasing thereafter at the surface and 3-m depth (to ≈ 6.0 mg L^{-1}) as the sun came up. It then continued to decrease at the 6-m depth to its starting value on the previous day (5.2 mg L^{-1}). For most of the diel cycle, however, there was little difference between the surface and bottom O_2 concentrations. The chlorophyll concentration followed a similar diel pattern as the DO concentration, while the bacterial numbers were more or less constant over 24 h. The bacterial production was greatest in the afternoon, lowest in late evening, and then increased in the morning, while the specific bacterial production followed a general pattern of being greatest in the morning and lowest at night (Fig. 2).

The water temperature in August was ≈ 1°C warmer than in July (Fig. 3). The temperature at the 6-m depth was lower than at the other depths for only a few hours before the increased wind speed in early evening rendered the

water column isothermal. The DO concentrations also were significantly higher in August, ranging from a low of 8.3 mg L^{-1} at the 6-m depth to a high of 10.2 mg L^{-1} at the surface (data not shown). The per cent O_2 saturation showed a trend similar to that for the water temperature, again demonstrating the effect of wind-mixing on the lake. Unlike in the July study, however, the O_2 saturation did not increase in the morning. The morning of the second day in August was overcast and it began to rain, resulting in a cooler, but well-mixed, water column and a 25% decrease in the O_2 saturation (Fig. 3). The chlorophyll-*a* concentrations were essentially the same over this 24-h period, while the bacterial numbers showed a general decrease. Both the bacterial production and specific bacterial production followed markedly different patterns in August compared to July. They both were greatest during the night in August, decreased by the early morning, and then began to increase as the day progressed (Fig. 3). In both diel studies, the O_2 saturation was at, or near, its greatest values when the bacterial production also was high, again suggesting that

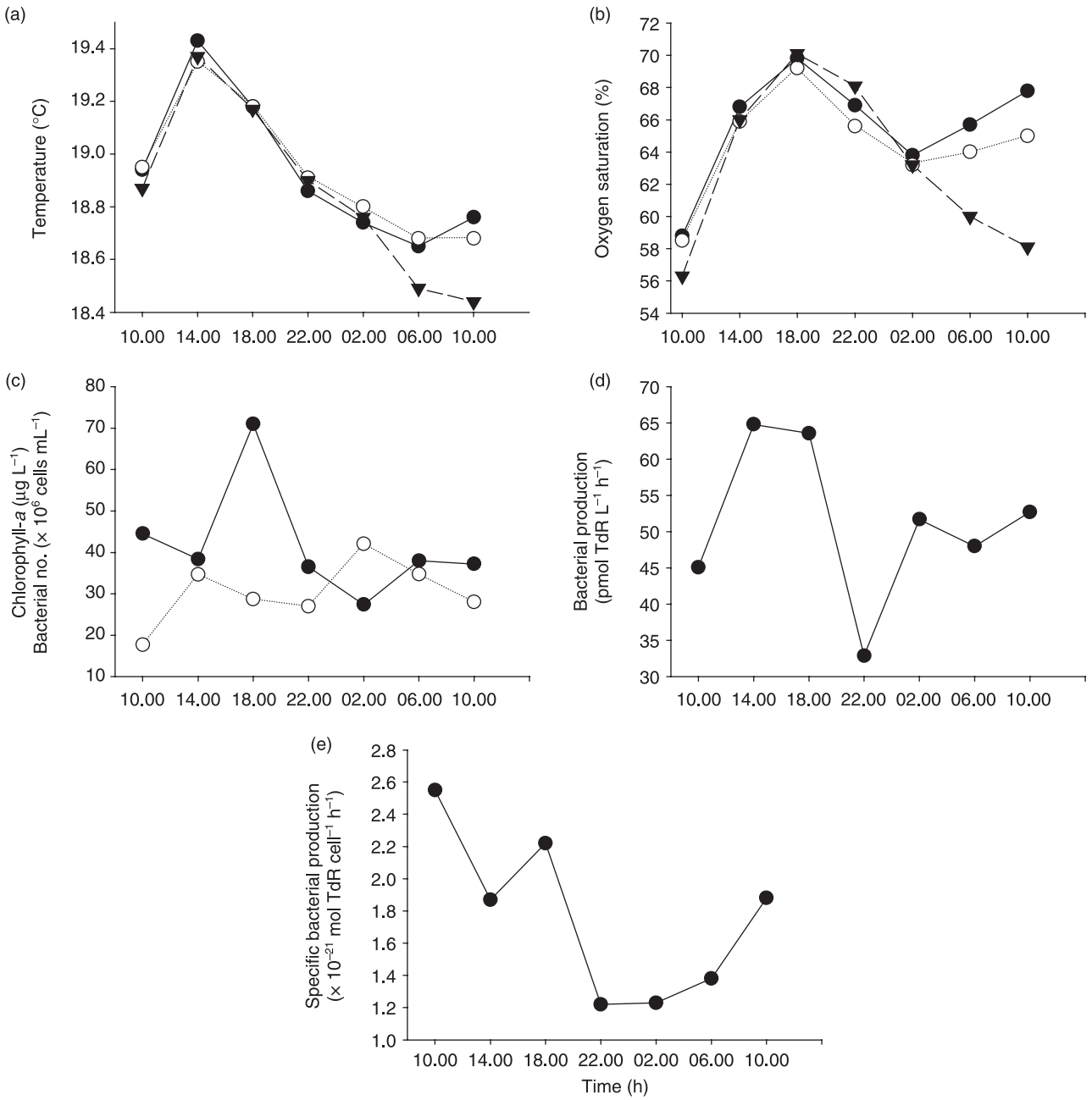

Fig. 2. Diel changes in Humboldt Lake in July 1990. (a) water temperature, (b) oxygen saturation, (c) chlorophyll-*a* concentration (●) and bacterial numbers (○), (d) bacterial production, and (e) specific bacterial production. (a) and (b): ●, surface; ○, 3 m; ▼, 6 m.

the bacterial O_2 consumption was not exceeding the O_2 production and influx processes in Humboldt Lake.

DISCUSSION

Using measurements of microbial processes, it was shown that Humboldt Lake did not become anoxic following cyanobacterial bloom collapses, nor over diel cycles, because O_2 consumption processes in the lake did not exceed production and influx processes. This hypertrophic prairie lake case study showed that the risk threshold criteria previously used to predict fish kills (Table 1) were in agreement with the physicochemical and biological data showing no periods of deoxygenation, and that they can be extended to deeper, larger lakes. This study focused on deoxygenation mainly because low DO is the most common cause of sudden fish kills in prairie lakes (Barica 1987). Other factors, however, including high water temperatures, algal toxins, diseases, pollution and parasites, have been reported as the cause of fish deaths in lakes from many areas of the world (e.g. see Florida Fish and Wildlife Commission,

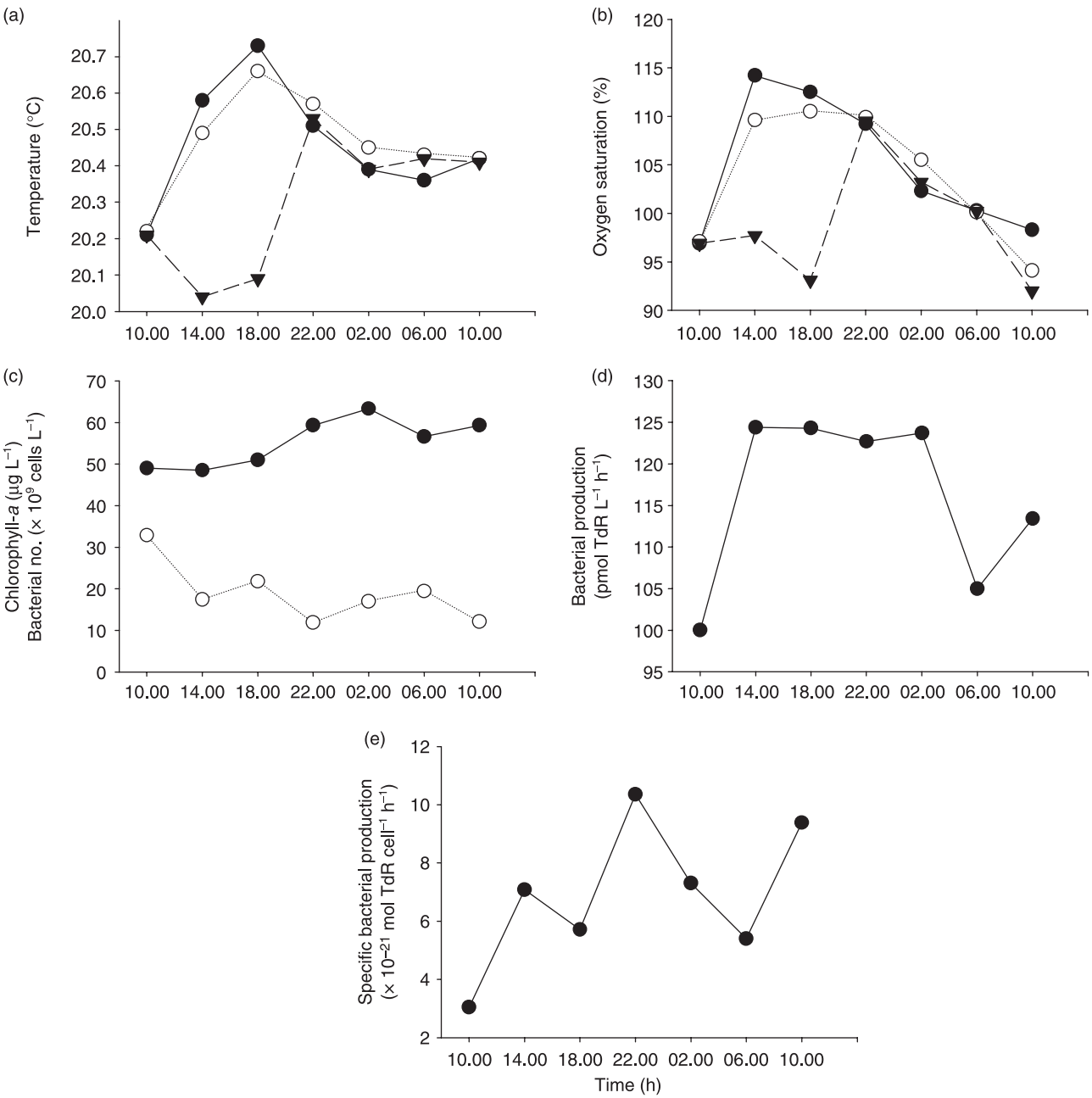

Fig. 3. Diel changes in Humboldt Lake in August 1990. (a) water temperature, (b) oxygen saturation, (c) chlorophyll-*a* concentration (●) and bacterial numbers (○), (d) bacterial production, and (e) specific bacterial production. (a) and (b): ●, surface; ○, 3 m; ▼, 6 m.

Fish and Wildlife Research Institute). Nevertheless, these latter factors appear to be of lesser importance within the Canadian prairie region. Indeed, the high summer NH_3-N concentrations, in combination with a pH of ≈ 9 and a water temperature of between 20°C and 25°C in Humboldt Lake, approached the Canadian water quality guidelines for the protection of aquatic life (Canadian Council of Ministers of the Environment 2000). The cold winter weather characteristic of the Canadian prairies means that lakes that freeze to the bottom generally do not have resident fish populations. Furthermore, the salinity has gradually increased in many lakes of this region, gradually eliminating some fish populations. Algal blooms are a common feature of prairie lakes and can cause fish kills indirectly by the consumption of O_2 when a bloom collapses under the right conditions. This study demonstrated that cyanobacterial blooms can collapse, but that bacterial activity is not always sufficiently large to consume O_2 concentrations down to lethal levels for fish.

According to this study, Humboldt Lake did not experience deoxygenation either seasonally or during two diel periods when the summer cyanobacterial population was high (≈ 50 μg L^{-1} chlorophyll-*a*). In 1989, the *Aphanizomenon* bloom collapsed twice. However, based on Barica's (1978) definition, these were only partial collapses, as there was no deoxygenation of the water column and the chlorophyll-*a* concentration exceeded 20 μg L^{-1} (≈ 100 μg L^{-1} in both July and August 1989; Fig. 1). The per cent O_2 saturation remained near 100% during this period and wind-mixing usually ensured the transfer of O_2 to the bottom of the water column, both seasonally and over the diel cycles. In addition, no evidence of increased bacterial production following these collapses was found. In fact, the bacterial production also decreased sharply with the bloom collapses (Fig. 1).

Others have proposed that additional conditions are required to cause water column deoxygenation with a summer cyanobacterial bloom collapse. Barica (1978) noted that changes in weather conditions (heavy overcast sky, increased wind speeds and decreasing air temperature) were associated with lake deoxygenation, in part by triggering an *Aphanizomenon* bloom collapse. However, Papst *et al.* (1980) suggested this explanation was not satisfactory as cyanobacterial blooms can collapse several days prior to a change in weather conditions and, as was the case in Humboldt Lake, a bloom can collapse without causing anoxia. According to Papst *et al.* (1980), deoxygenation would only occur when a bloom collapse was concomitant with, or followed by, a period of thermal instability, which would entrain low-O_2 water with a high hypolimnetic O_2 demand. Such a scenario, however, is not applicable to Humboldt Lake. Papst *et al.* (1980) did their work at a small (2.4 ha), shallow lake (maximum depth = 2.9 m, mean depth = 1.9 m) surrounded by trees. Humboldt Lake has little protection from the wind, has a much larger surface area, is deeper and, therefore, does not become thermally stratified, although there can be times when the O_2 saturation is slightly lower than at the surface in both summer and winter (Robarts *et al.* 1994; Figs 1–3). Notwithstanding the very large cyanobacterial populations and high rates of bacterial production, the O_2 influx and production processes always exceeded O_2 consumption processes during the study period in this hypertrophic prairie lake.

Phytoplankton production ranged between 0.9 (under ice) and 503 mg C m^{-2} h^{-1} (Robarts *et al.* 1992). The phytoplankton production and bacterial production were correlated in Humboldt Lake and it was estimated that the bacterial production could consume an average of 42–67% of the annual phytoplankton production (Robarts *et al.* 1994), which might account for the fact that bacterial decomposition processes do not have a more marked effect on the lake's O_2 concentrations. The use of the summer maximum chlorophyll-*a* concentration to predict the risk of summer fish kill due to deoxygenation, as proposed by Barica (1975, 1984), was not applicable to Humboldt Lake. This conclusion is based on our seasonal and diel data, suggesting it is unlikely that Humboldt Lake would become anaerobic, even under thick ice cover in winter, as long as the physicochemical characteristics of the lake remain similar to those that existed during the course of this study (but see below).

Although other risk threshold criteria from Barica (1975, 1987) used maximum chlorophyll-*a* concentrations and specific conductance to predict summer fish kills (Table 1), these could not be applied to Humboldt Lake. Both Humboldt Lake and Barica's lakes had high conductance and chlorophyll-*a* values. The chlorophyl *a* concentrations in the lakes that Barica predicted would experience summer fish kills ranged from 100 to 300 μg L^{-1}, with a specific conductivity in the range of 300–3000 μS cm^{-1} (Barica 1987). The specific conductance of Humboldt Lake, however, was about 3900 μS cm^{-1} (Evans *et al.* 1995), therefore being outside the conductivity range for which Barica reported summer fish kills. More data on prairie lakes with specific conductance > 3000 μS cm^{-1} are required to determine if these threshold criteria are applicable to such systems.

Still other risk threshold criteria developed by Barica (1975, 1987) predicted summer fish kills due to deoxygenation, based on minimum Secchi disc transparency and maximum chlorophyll-*a* concentration (Table 1). According to these criteria, a Secchi disc value of 0.4 m and a summer chlorophyll-*a* concentration of 100 L^{-1} represent the lower limits for a high risk of summer fish kill in lakes dominated

by *Aphanizomenon* (Barica 1975). The minimum Secchi disc value in Humboldt Lake was 0.5 m (R. Robarts, unpubl. data, 1990) when the chlorophyll concentration was 234 μg L^{-1}. The greatest observed chlorophyll-*a* peak was 839 μg L^{-1}, accompanied by a Secchi depth of 0.2 m. However, this peak was probably overestimated due to the disruption of the phytoplankton canopy (Robarts *et al.* 1992). Based on these criteria, these data would place Humboldt Lake on the borderline of having a high risk for summer fish kill. As a result of the difficulties (bloom canopies are easily disrupted during measurement leading to large overestimates) in obtaining accurate Secchi disc readings under surface cyanobacterial blooms, such as *Aphanizomenon*, the use of these risk criteria are not recommended.

The NH_3-N concentrations in Humboldt Lake exceeded 500 μg L^{-1} under the ice in March, while the chlorophyll-*a* concentrations reached > 800 μg L^{-1} in the first year of this study and > 100 μg L^{-1} in the second year. When used in conjunction with Barica's (1975, 1984) summer fish kill risk threshold criteria, these data indicated there was no risk. The O_2 concentrations were 6.1 and 3.6 mg L^{-1} just beneath the ice and at the 6-m depth in late March, respectively. Indeed, our simple calculations, using a constant O_2 consumption rate (0.048 mg L^{-1} day^{-1}) for late autumn to March, indicated that anoxia would not have occurred until after May, even if the ice cover had remained on the lake (which it did not).

Barica and Mathias (1979) studied O_2 depletion and fish winter kill risk in small prairie lakes under extended ice cover. They developed risk threshold criteria, based on the initial O_2 storage in a lake just prior to ice formation and the rate of O_2 depletion, to determine the time required to reach total anoxia and, hence, the potential for a winter fish kill. The initial O_2 storage was estimated from the lake volume and surface area. For Humboldt Lake, these values were 81.88×10^6 m^3 and 17.17 km^2, respectively (Hammer & Haynes 1978). The DO concentration in October each year was extrapolated to the time of ice cover in November using the O_2 consumption rate of 0.048 mg L^{-1} day^{-1} calculated above. This calculation gave initial O_2 storage values of 45.8 m^{-2} and 43.3 g m^{-2} in 1989 and 1990, respectively. The rate of O_2 depletion (g m^{-2} day^{-1}) under the ice cover was calculated, using the equation of Barica and Mathias (1979), which correlates this rate to the mean depth. Although this correlation was derived from small (≤ 20 ha) and shallow (mean depth = 4.2 m) pothole lakes, Barica (1984) found it to be applicable to larger lakes in central Canada with mean depths similar to pothole lakes, but not for deeper, stratified lakes. The rate of O_2 depletion in shallow Humboldt Lake (mean depth = 4.8 m) was only 0.44 g m^{-2} day^{-1}.

Babin and Prepas (1985) also developed an equation to calculate winter O_2 depletion rates using the mean summer TP concentration of the euphotic zone and mean depth. They suggested that their equation was more broadly applicable as it was derived from a data set that included lakes ≤ 22 m deep. However, most of the lakes had smaller surface areas and lower TP concentrations than Humboldt Lake. The mean TP = 337 mg m^{-3} in Humboldt Lake for the two years of this study. Inserting these values into Babin and Prepas' (1985) equation gave a winter O_2 depletion rate of 0.80 g O_2 m^{-2} day^{-1} for Humboldt Lake, a value twice as high as that calculated with Barica and Mathias' (1979) equation. Applying both Barica and Mathias' and Babin and Prepas' winter O_2 consumption rates with the initial O_2 storage value indicated it would take > 200 and 100 days, respectively, for Humboldt Lake to become completely anoxic under ice cover in both years. The O_2 consumption rate calculated using Barica and Mathias' equation is in agreement with our *in situ* data, which show no anoxia (Fig. 1), and our calculations indicating that anoxia would not occur before the ice cover left the lake in May. Thus, the risk of winter fish kills in Humboldt Lake is low under conditions (i.e. water levels and quality) similar to those that occurred during our study. However, Babin and Prepas' equation overestimated the winter O_2 consumption rate and predicted anoxia before the ice cover left, which did not occur before our sampling date in March. Consequently, the model of Babin and Prepas was not applicable to Humboldt Lake.

The Provincial Government (Saskatchewan Environment) has records on fish populations in Humboldt Lake dating back to 1962. Winter fish kills were reported in 1966 (≈ 2000 perch), 1969 (≈ 100 000 walleye fry), 1970 (≈ 100 000 walleye fry) and 1974 (205 adult pike; J. Merkowsky, unpubl. data, 2004). A summer fish kill occurred on 29 August 1972 at the mouth of a small creek flowing into the lake, affecting between 2000 and 3000 perch and walleye. The reason for this fish kill was not established. According to Merkowsky, conditions improved in March 1975 with increasing water levels and a lack of snow cover, with no further fish kills being reported up to, and including, the winter of 2003–2004.

Humboldt Lake is located in an area of the Canadian prairies that has experienced precipitation well below normal levels for eight consecutive seasons, from autumn 2000 to summer 2002, after which precipitation levels returned to normal, or above normal, levels (Bonsal & Wheaton 2005). During the drought period, the possibility existed that another winter fish kill could have occurred if the water levels in Humboldt Lake dropped too low. This is because lower water levels would have decreased the

initial O_2 storage, although the daily rate of O_2 depletion also would have decreased due to its relationship with the mean depth (Barica & Mathias 1979). No fish kills, however, were observed during this period.

Of greater concern to fishery managers, however, should be the increasing development in the Humboldt Lake watershed. Over the past few years, housing (including new holiday resorts built on the lake's shore), agricultural and industrial developments have significantly increased. The impacts of this development on the nutrient loads to Humboldt Lake is currently unknown as routine water quality monitoring has not been conducted in recent years due to the lack of funding. Cyanobacterial blooms, however, remain a regular feature in Humboldt Lake during the summer. For example, in August 2004, there was a bloom collapse and DO measurements were taken. The O_2 concentrations decreased to 2 mg L^{-1} during the collapse, the lowest summer O_2 concentrations ever measured (Evans, unpubl. data, 2004). These low O_2 levels suggest that the bloom was larger than previously measured for the lake. Although no summer fish kill was observed, a fish kill did occur during the winter of 2004–2005, affecting pike, perch and walleye. The fish were autopsied, with the cause of death found to be O_2 deprivation. These new observations suggest that there might have been a significant decline in the water quality characteristics of Humboldt Lake in recent years. Therefore, it is now necessary to collect new data to evaluate the risk of winter fish kills (Table 1; see Barica & Mathias 1979 for minimal data requirements). Such measurements are necessary to assess whether or not there is a need for some form of intervention to prevent the occurrence of future fish kills.

CONCLUSIONS

Although Humboldt Lake is a hypertrophic prairie lake, it did not experience periods of deoxygenation following summer cyanobacterial bloom collapses during the early 1990s, as has been reported for many other prairie lakes (Barica 1987). Furthermore, in two summer diel studies, no evidence was found that the water column became anaerobic, nor did the formation of ice cover lead to water column anoxia. For Humboldt Lake, the O_2 influx (wind-induced mixing to the bottom on most days) and production processes were greater than the microbial and chemical O_2 demands, both over seasonal and diel time scales. Of the various risk threshold criteria used to predict summer fish kill, this study found that the use of maximum summer chlorophyll-*a* and maximum winter NH_3-N concentrations (Barica 1975, 1984) were consistent with our limnological data and record of fish kills for Humboldt Lake. Likewise, the winter fish kill risk threshold criteria of Barica and Mathias (1979) seemed equally applicable for use up to 2003. Recent development in the catchment, however, seems to have created new water quality conditions in Humboldt Lake. This conclusion is supported by evidence of a winter fish kill in 2004–2005 and the extremely low O_2 concentrations found following a summer cyanobacterial bloom collapse in 2004. These new conditions point to an urgent need to update the data for predicting the risk of future fish kills in Humboldt Lake and in other lakes on the Great Plains.

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