J. Great Lakes Res. 32:645–652
Internat. Assoc. Great Lakes Res., 2006

NOTE

Occurrence of the Toxin-producing Cyanobacterium *Cylindrospermopsis raciborskii* in Mona and Muskegon Lakes, Michigan

Ying Hong[1], Alan Steinman[1*], Bopaiah Biddanda[1], Richard Rediske,[1] and Gary Fahnenstiel[2]

[1]*Annis Water Resources Institute*
Grand Valley State University
740 West Shoreline Drive
Muskegon, Michigan 49441

[2]*Lake Michigan Field Station*
NOAA Great Lakes Environmental Research Laboratory
1431 Beach Street
Muskegon, Michigan 49441

ABSTRACT. *The bloom-forming and toxin-producing cyanobacterium* Cylindrospermopsis raciborskii *was observed in Muskegon and Mona lakes, drowned river-mouth tributaries of Lake Michigan. Morphological features of the taxon were similar to those described elsewhere. The species was observed only in late summer; elevated bottom water temperature, and perhaps phosphorus concentration, appears to be implicated in its appearance. Maximum abundances at any given site reached 393 and 0.9 trichomes/mL in Mona Lake and Muskegon Lake, respectively. Although these concentrations are low relative to other reports, the presence of this species in these two lakes from adjacent watersheds adds to a growing body of literature that suggests the distribution of* C. raciborskii *is on the increase in northern latitudes.*

INDEX WORDS: *Toxic cyanobacteria,* Cylindrospermopsis raciborskii*, Mona Lake, Muskegon Lake, Lake Michigan.*

INTRODUCTION

Cylindrospermopsis raciborskii is an invasive species (Chapman and Schelske 1997) that has been observed in many tropical, subtropical, and recently, temperate regions. This cyanobacterium is toxin-producing and thrives in eutrophic to hypereutrophic, high-temperature environments. It can tolerate a wide range of both light and temperature by increasing its production of polyunsaturated fatty acids (Varkonyi *et al.* 2000), and can withstand short-term unfavorable conditions by forming resting spores (akinetes; Moore *et al.* 2005). *Cylindrospermopsis* is also able to take up and store phosphorus efficiently (Istvanovics *et al.* 2000) and has the capacity to fix atmospheric nitrogen. These specific features enhance its competitive advantage over other phytoplankton species under variable environmental conditions (Biddanda *et al.* 2006).

Toxin-producing invasive species are one of the greatest threats to global freshwater resources today. *C. raciborskii* is able to produce multiple toxins, and was implicated in one of Australia's worst cases of human poisoning (Falconer 2001). At least three distinct toxins can be produced by *Cylindrospermopsis* (Chorus and Bartram 2004): cylindrospermopsin, which targets primarily the liver and kidneys, and anatoxin-a and saxitoxin, which are both neurotoxins. Because of its potential to produce these toxins and its highly adaptable growth, this genus ranks near the top of the watch list of toxic cyanobacteria for water managers (WHO 1999).

C. raciborskii was recently reported in Canada

*Corresponding author. E-mail: steinmaa@gvsu.edu

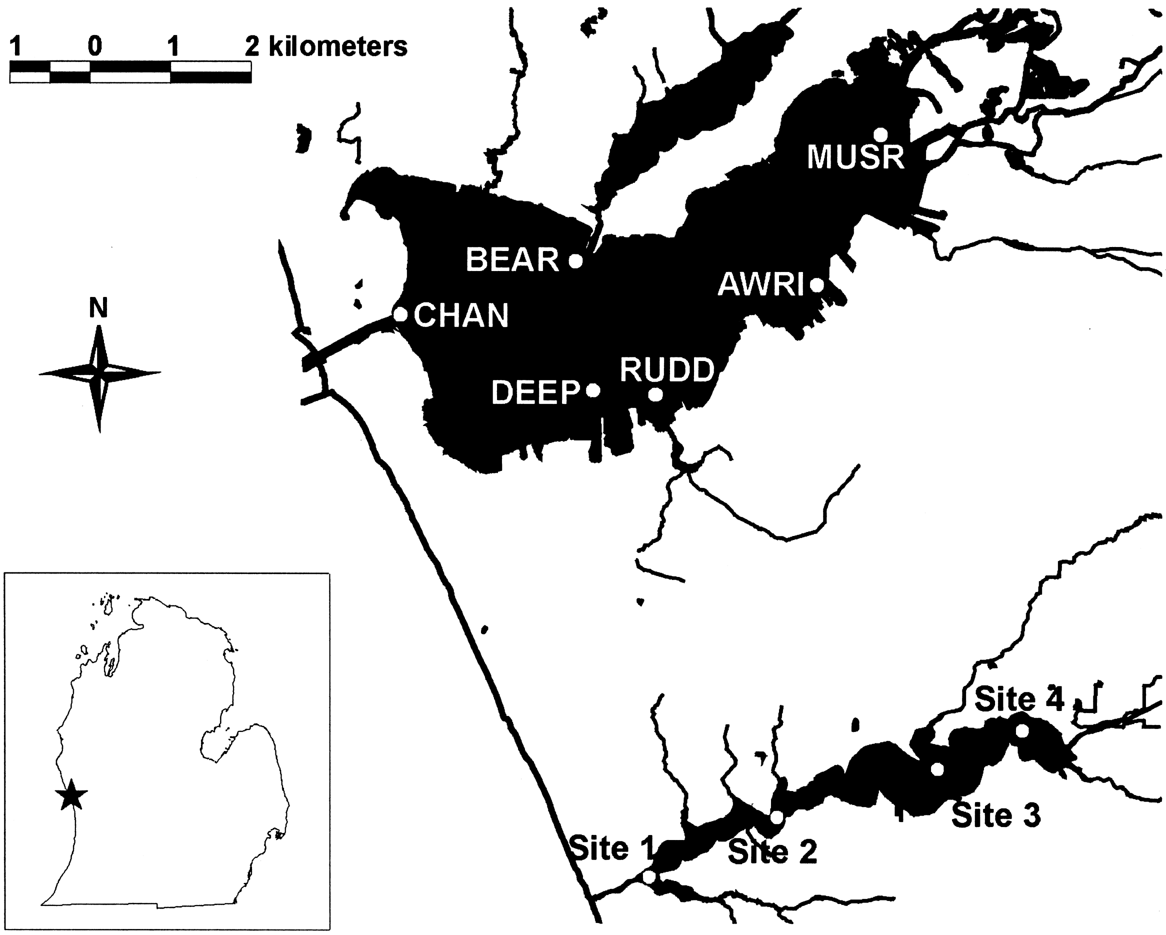

FIG. 1. Inset: Map of the State of Michigan, showing location of Mona Lake and Muskegon Lake. Blow up: Muskegon Lake (top) and Mona Lake (bottom) showing sampling locations and channels draining directly to Lake Michigan.

(Hamilton *et al.* 2005), but documentation of this taxon within the Great Lakes basin has primarily occurred in non-peer reviewed literature (Ann St. Amand, PhycoTech, Inc., pers. comm.). Our report documents the presence of *C. raciborskii* in Muskegon and Mona lakes, drowned river-mouth lakes located in the lower peninsula of Michigan, both of which connect directly to southeastern Lake Michigan. The objective of this study was to document the occurrence and abundance of *Cylindrospermopsis* throughout the ice-free period in these lakes, relate its presence to limnological conditions, and describe its morphological characteristics.

METHODS

Phytoplankton samples were obtained from both Mona and Muskegon lakes, two drowned river mouth systems located in adjacent watersheds in west Michigan (Fig. 1). In Mona Lake, phytoplankton were analyzed from surface samples collected at four sites in May, July, August, and September of 2002 and May, July, and August of 2003. In Muskegon Lake, phytoplankton were analyzed from surface and near-bottom samples collected at six sites in late April/May, July, and September of 2003 and 2005 (Steinman and Ogdahl 2004). Mona and Muskegon lake samples were collected using Van Dorn bottles. Subsamples were fixed with either formalin or Lugol's solution. Phytoplankton species were identified and enumerated utilizing a Nikon Eclipse TE200 inverted microscope (Utermöhl 1958). Most of the identifications were made using magnifications of 450 and 1,000× with phase contrast illumination. In all the samples, 200–300 algal units (cells or filaments) were counted. The

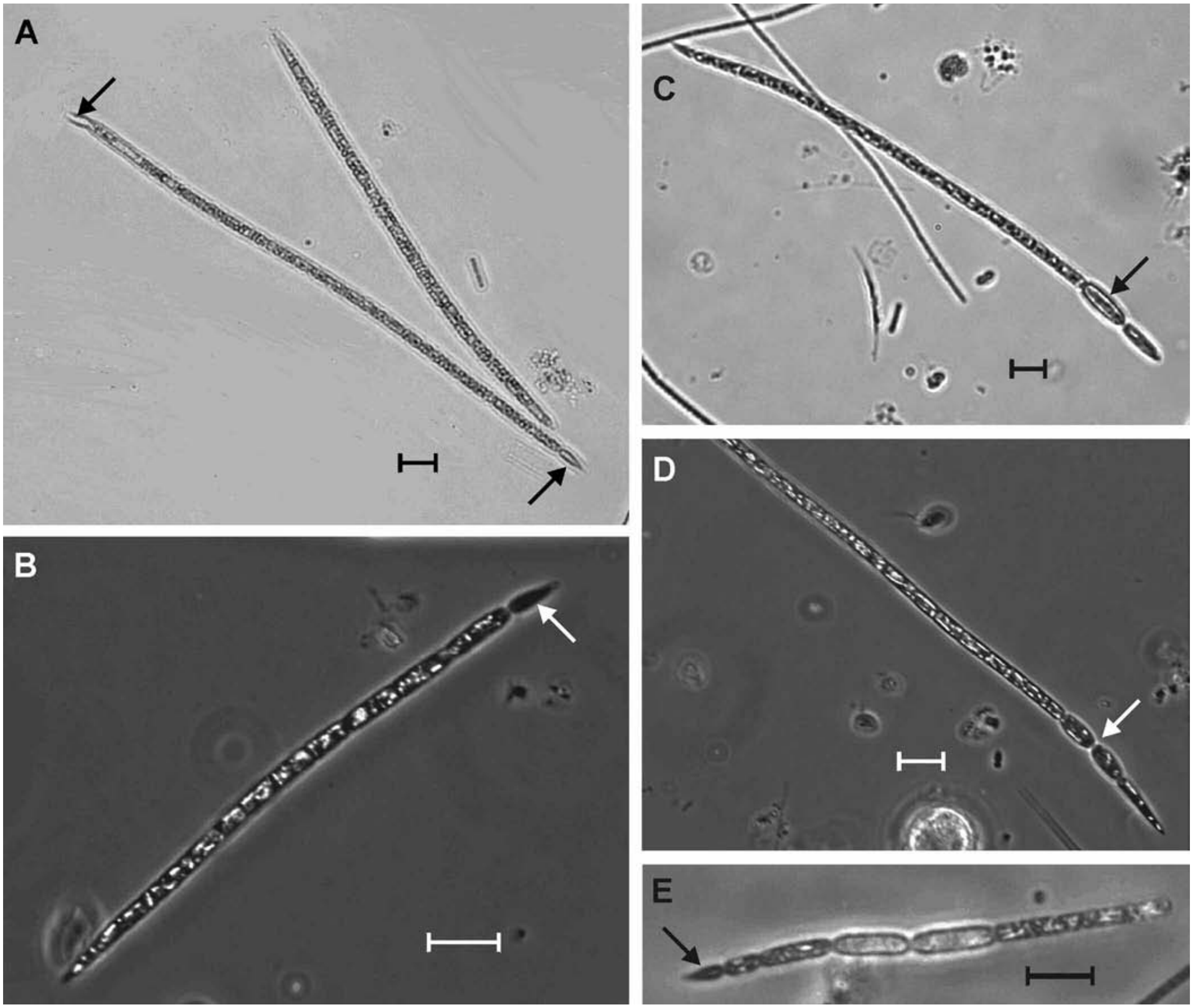

FIG. 2. Photomicrographs showing morphological features of C. raciborskii from Mona Lake. (A) Heterocysts developed from terminal cells at both ends (arrows); (B) Heterocyst developed from one end of trichome (arrow); (C) Solitary akinete (arrow); (D) Akinete pair, adjacent to heterocyst (arrow); (E) Akinete pair formed slightly distant from terminal heterocyst (arrow). Scale bar = 10 µm.

cell volume of each species was calculated by applying the appropriate geometric formulae. Photomicrography was performed using a Spot Insight digital camera, and cell measurements were made from digital image analyses using Image Pro plus software.

At the sampling sites, a Hydrolab DataSonde 4a was used to measure depth, DO, redox, turbidity, pH, temperature, and specific conductance at 1 m below the water surface and 1 m above the sediment surface. In addition, a Secchi disk was used to measure water clarity. Water samples were filtered for chlorophyll *a* analysis and analyzed according to Steinman and Lamberti (1996). Water samples for nutrient analysis were collected 1 m below the water surface and approximately 1 m from the lake bottom with a Van Dorn bottle, stored in acid-washed bottles, and put on ice until delivery to the laboratory, always within 5 hr of collection. Soluble reactive phosphorus (SRP) and total phosphorus (TP) were analyzed on a BRAN+LUEBBE Autoanalyzer (U.S. EPA 1983).

TABLE 1. List of the characteristic features of several* C. raciborskii *populations from different locations.

	Mona Lake This study	Peri Lagoon Hindak 1988	Paranoa Reservoir Branco and Senna 1991	Hungary Slovakia Komarek and Horecka 1979	Cuban Lakes Komarek 1984	Indian Lakes Singh 1962
Shape of filament	Straight	Straight to irregularly bent	Straight to slightly curved	Straight	Straight	Straight to spirally curved
Length of filament (μm)	51–311	42.4–430	100–300	60–250	95–160	90–100
Width of filament (μm)	1.7–4.2	1.2–4.4	1.7–3.0	1.8–4.0	1.7–3.8	2.6–3.0
Length of heterocyst (μm)	5–11.1	4.8–16.0	4.5–7.5	3.4–14	4.5–11.5	3.4–4.5
Width of heterocyst (μm)	1.5–4.6	1.2–4.5	1.5–3.3	1.8–4.0	1.8–3.2	1.8–3.0
Length of akinete (μm)	7.5–16.8	9.6–14.8	11–14	4.5–22	3.8–13	4.5–6.4
Width of akinete (μm)	2–4.9	2.4–5.0	2.5–3.5	2.4–5.5	3.5–3.8	2.8–3.8
Position of akinete	Joined to heterocyst, or separated by a few cells	Joined to heterocyst, or separated by 1 cell	Separated by 2–4 vegetative cells from the apex	Separated by 1–3 vegetative cells from heterocyst	Subapical, separated by 2-4 cells from the apex	Separated by 1 cell, or sub-terminal

One way analysis of variance (ANOVA) was used to determine if there were significant differences between sampling dates. We assumed that sampling events were independent of one another given that hydrologic retention times were shorter than the time intervals of sampling. If data were not normally distributed (as determined by the Kolmogorov-Smirnov test), the Kruskal-Wallis test was used. If the ANOVA was significant, either the Tukey (for equal sample sizes) or Dunn (for unequal sample sizes) test was employed to make pairwise comparisons.

RESULTS AND DISCUSSION

Morphology

Trichomes of *Cylindrospermopsis raciborskii* found in Mona Lake were solitary, straight, or only slightly curved (Fig. 2A) with a length of 51–311 μm (mean ± SD: 123 ± 10.5; n = 41). The trichomes were not finely constricted at the cross walls, and the cross walls were not clearly visible. Trichomes without terminal heterocysts were attenuated to the ends (Fig. 2B) with pointed terminal cells. The individual cells were cylindrical, with a width of 1.7-4.2 μm (mean ± SD: 2.9 ± 0.1; n = 41), exhibiting randomly distributed gas vesicle clusters. Solitary heterocysts were developed from terminal cells at one or both ends of trichomes (Figs. 2A, B) and were conical, pointed to rounded at the ends, and 5–11 (mean ± SD: 8.2 ± 3.8; n = 12) × 1.5–4.6 (mean ± SD: 2.7 ± 0.9; n = 12) μm in length and width, respectively. Akinetes were long and cylindrical to slightly oval-shaped and 7.5–16 (mean ± SD: 12 ± 4.4; n = 19) × 2–4.9 (mean ± SD: 4.1 ± 0.9; n = 19) μm in length and width, respectively. Akinetes were solitary or in pairs (Figs. 2C, D), occurred adjacent to or slightly distant from heterocysts (Fig. 2E), and generally formed near the end of trichomes. In young and sometimes in mature trichomes, akinetes and heterocysts were not developed.

The dimensions of cells, heterocysts, and akinetes of *C. raciborskii* in Mona Lake were similar to those reported from Peri lagoon (Hindak 1988) and eastern Europe (Komárek and Hauer 2004) (Table 1). The formation of phenotypes within *C. raciborskii* has been reported (Chonudomkul *et al.* 2004); cell size and shape might not be under tight genetic control (Saker *et al.* 1999) because they are able to reflect the environmental conditions to some degree.

Environmental Conditions

In Mona Lake, *C. raciborskii* was not observed prior to August in either 2002 or 2003 (Table 2). Environmental conditions that showed statistically significant increases between May and September included surface and bottom temperature, and bottom TP, whereas conductivity significantly declined over that time period (Table 2). Chlorophyll *a*, pH, and Secchi depth varied over time; the chlorophyll data were confounded by algicide treatments in July

TABLE 2. Limnological parameters and biovolume of* C. raciborskii *collected from Mona and Muskegon lakes. Data are surface samples unless otherwise noted. Mona Lake data are means (± SD) from four sites collected in 2002 and 2003 (September data from 2002 only). Muskegon Lake data are means (± SD) from six sites collected in 2003 and 2005. Different letters within a row indicate statistical significance. Mona Lake data are pooled across years because there were no significant differences between 2002 and 2003.

	May	July	August	September
		Mona Lake		
C. raciborskii biovolume ($\mu m^3 \times 10^4$)	0^A	0^A	2002: 10.4 ± 3.7^B 2003: 6.3 ± 3.0^B	2002: 2.4 ± 1.8^B
Surface Temp. (°C)	14.3 ± 1.6^A	24.8 ± 1.2^B	25.7 ± 0.6^B	$23.7 \pm 0.6^{A,B}$
Bottom Temp. (°C)	13.4 ± 1.4^A	19.5 ± 2.9^B	21.7 ± 2.2^B	21.8 ± 0.9^B
Surface SRP (µg/L)	6 ± 2^A	9 ± 5^A	13 ± 12^A	11 ± 8^A
Bottom SRP (µg/L)	5 ± 0^A	121 ± 81^B	114 ± 90^B	60 ± 39^B
Surface TP (µg/L)	58 ± 24^A	$65 \pm 13^{A,B}$	89 ± 20^B	$70 \pm 29^{A,B}$
Bottom TP (µg/L)	56 ± 23^A	208 ± 93^B	244 ± 135^B	$132 \pm 56^{A,B}$
Chl. *a* (µg/L)	33.8 ± 10.1^A	11.8 ± 4.8^B	10.4 ± 4.7^B	28.0 ± 2.6^A
pH	$8.9 \pm 0.1^{A,B}$	$9.0 \pm 0.3^{A,B}$	9.2 ± 0.2^B	8.4 ± 0.4^A
Conductivity (µS/cm)	442 ± 22^B	422 ± 10^B	396 ± 3^A	$407 \pm 5^{A,B}$
Secchi Depth (m)	0.66 ± 0.15^A	0.63 ± 0.17^A	0.52 ± 0.08^A	0.73 ± 0.23^A
		Muskegon Lake		
C. raciborskii biovolume ($\mu m^3 \times 10^4$)	0^A	0^A	ND	2003: 0^A 2005: 0.009 ± 0.013^A
Surface Temp. (°C)	2003: 11.8 ± 0.3^A 2005: 12.8 ± 0.2^A	2003: 23.1 ± 0.4^C 2005: 25.7 ± 0.6^C	ND	2003: 22.2 ± 0.5^B 2005: 21.7 ± 0.2^B
Botttom Temp. (°C)	2003: 11.1 ± 0.5^A 2005: 12.7 ± 0.4^A	2003: 21.0 ± 3.5^B 2005: 17.1 ± 6.7^A	ND	2003: 17.9 ± 4.9^B 2005: 18.9 ± 3.6^A
Surface SRP (µg/L)*	2003: 5^A 2005: 5^A	2003: 5^A 2005: 5^A	ND	2003: 5^A 2005: 5^A
Bottom SRP (µg/L)	2003: 5^A 2005: 5^A	2003: 21.5 ± 25.6^A 2005: 5^A	ND	2003: 17.5 ± 15.1^A 2005: 9.7 ± 10.9^A
Surface TP (µg/L)	2003: 20.8 ± 12.8^A 2005: 20.8 ± 12.8^B	2003: 31.7 ± 4.1^A 2005: 31.7 ± 4.1^A	ND	2003: 25.0 ± 5.5^A 2005: 25 ± 5.5^B
Bottom TP (µg/L)	2003: 15.0 ± 5.5^A 2005: 20.0 ± 0^A	2003: 36.7 ± 18.6^B 2005: 20.0 ± 12.6^A	ND	2003: 36.7 ± 12.1^B 2005: 23.3 ± 10.3^A
Chl. *a* (µg/L)	2003: 10.8 ± 3.1^B 2005: ND	2003: 4.1 ± 1.2^A 2005: ND	ND	2003: 5.7 ± 1.80^A 2005: ND
pH	2003: 8.1 ± 0.5^A 2005: 8.1 ± 0.1^A	2003: $8.4 \pm 0.2^{A,B}$ 2005: 8.7 ± 0.1^C	ND	2003: 8.6 ± 0.1^B 2005: 8.5 ± 0.1^B
Conductivity (µS/cm)	2003: 422 ± 4^B 2005: 309 ± 1^A	2003: 403 ± 3^A 2005: 372 ± 11^B	ND	2003: 421 ± 17^B 2005: 389 ± 11^C
Secchi Depth (m)	2003: 2.3 ± 0.6^A 2005: 2.8 ± 0.6^B	2003: 2.1 ± 0.3^A 2005: 2.3 ± 0.2^A	ND	2003: 2.8 ± 1.0^A 2005: 2.0 ± 0.2^A

*All surface SRP values were at or below the detection limit and arbitrarily assigned the DL value of 5 µg/L.

and August. Mona Lake's eutrophic status, with its combination of high nutrient, moderate transparency, and warm temperature in late summer, provided a suitable habitat for *C. raciborskii.*

In Muskegon Lake, *C. raciborskii* was observed in 2005 (albeit at very low numbers) but not in 2003. As was the case in Mona Lake, *C. raciborskii* was seen only in late summer (Table 2). The only environmental factor that differed significantly between years was specific conductance, which was lower in 2005 on all three sampling dates. Surface and bottom temperatures increased from May to September in both years but the average bottom temperatures never exceeded 19°C (Table 2). Bottom TP concentrations increased significantly over time in 2003 but not in 2005, although levels were

TABLE 3. Comparison of **Cylindrospermopsis** *abundance with reports from other locations.*

	Mona Lake[1]	Muskegon Lake[1]	Newnans Lake[2]	Lake Dora[2]	Lake Eustis[2]	Lake Wauberg[2]	Lake Balaton[3]
Abundance (trichomes/ml)	0.07–0.29 $\times 10^3$	$< 0.001 \times 10^3$	8.8×10^4 – 1.76×10^5	8.50×10^3	7.20×10^4	9.39×10^4	8.37×10^4
% of total phytoplankton (units)	6	< 1	80	23	84	60	30

[1]This study
[2]Chapman and Schelske (1997)
[3]Toth and Padisak (1986)

approximately 3 to 8 times lower in Muskegon Lake than Mona Lake. Internal P loading has been implicated as a promoter of cyanobacterial blooms (Johnston and Jacoby 2003, Wang *et al.* 2005) although to date it has not been explicitly linked to *Cylindrospermopsis*. In addition, our data show relatively high hypolimnetic TP concentrations in Mona Lake in July, when *C. raciborskii* was not yet present. This suggests that TP alone is not controlling its abundance.

We hypothesize that the absence of *C. raciborskii* during spring and early to mid summer was because of unsuitable water temperature. This variable is considered the most important factor influencing the appearance and development of this species (Briand *et al.* 2004). Padisak (2003) reported that optimal temperatures for germination of *Cylindrospermopsis* akinetes were 22–24°C. Hamilton *et al.* (2005) reported that blooms corresponded to high epilimnetic temperatures, and no blooms of *Cylindrospermopsis* occurred when water temperature was < 22°C. The August and September appearances of *C. raciborskii* in Mona Lake corresponded to months when mean bottom water temperatures approached 22°C (Table 2). Bottom water temperatures in Muskegon Lake, even in late summer, may have been too cool to induce significant akinete germination into motile cells (Hamilton *et al.* 2005).

Alternatively, if *Cylindrospermopsis* is a very recent introduction to Mona and Muskegon lakes, the populations may take several years to reach some type of steady state. In this case, robust relationships with environmental factors may be difficult to discern soon after invasion. Experimental manipulations with bottom sediments are needed to more fully determine the relationship between environmental factors, especially temperature, and the distribution of *C. raciborskii* in these lakes.

Abundance and Community Structure

The abundance of *C. raciborskii* (trichomes/ml) in Mona Lake during 2002 and 2003 varied from 0.01–0.39 × 10^3 trichomes/mL, while in Muskegon Lake abundance during 2005 (the first year it was observed) was < 0.001 trichomes/mL (Table 3). These concentrations are very low compared to other studies, where values range from 8.5 × 10^3 to 1.76 × 10^5 (Table 3). *Cylindrospermopsis* accounted for only 6% of the total phytoplankton abundance in Mona Lake and < 1% in Muskegon Lake (Table 3). In samples collected from 23 lakes in the Orlando, FL area, five of the lakes had concentrations of *Cylindrospermopsis* that exceeded 4 × 10^3 trichomes/mL and four other lakes had concentrations that ranged from 1 × 10^3 to 4 × 10^3 trichomes/mL (Phlips 2001). The relatively low abundance of trichomes in Mona and Muskegon lakes may be a result of temperature (Bouvy *et al.* 2000; Briand *et al.* 2004). A shift to dominance of *Cylindrospermopsis* needed only a few degrees rise in temperature in Constance Lake (Hamilton *et al.* 2005). In the Keszthely basin of Lake Balaton, warmer water temperatures in 2000 resulted in an abrupt population increase of *C. raciborskii* (Padisak 2003).

IMPLICATIONS AND CONCLUSIONS

Cylindrospermopsis has been reported to be subtropical and tropical in origin (Padisak 2003), but has gradually spread to temperate areas. In North America, *C. raciborskii* was first recorded from Wooster Lake, Kansas in 1955. Since then, it has been reported in some lakes near Minneapolis, Lake Erie, Constance Lake in Canada (Hamilton *et al.*

2005), and Ball Lake in northeastern Indiana. Over 125 reports of *C. raciborskii* have been mapped in the continental USA outside of Florida as of October 2005 (St. Amand 2002; pers. comm.). Although it is unknown how *Cylindrospermopsis* spread to Mona and Muskegon lakes, possible transfer mechanisms include human activities, such as shipping transport and boating, or waterfowl and wind carriage (cf. Charalambidou and Santamaría 2005).

Given that *C. raciborskii* is extremely adaptable, and that Mona and Muskegon lakes connect directly to Lake Michigan, the potential exists for this species to spread to other parts of the Great Lakes, as well as inland lakes. It will be critical to know if its occurrence was an ephemeral event or if *C. raciborskii* has been able to establish itself in these drowned river-mouth systems, from which it can spread to other bodies of water in the region. Continued monitoring of this taxon's occurrence, abundance, and toxicity is strongly recommended.

ACKNOWLEDGMENTS

Funding for this work was provided by The Community Foundation for Muskegon County through grants from the C.S. Mott Foundation and from the Muskegon Lake Research Endowment Fund. We are grateful to Paul Hamilton, Hedy Kling, and Claire Schelske for their help in confirmation of the species, and to Ann St. Amand for helpful discussions and sharing data with us. Field and laboratory support were provided by Lori Nemeth, Mary Ogdahl, and Mark Luttenton.

REFERENCES

Biddanda, B.A., Abreu, P., and Odebrecht, C. 2006. *Algal blooms and bacterial interactions*. In *Algal cultures analogues of blooms and applications,* ed. D. V. Subba Rao, pp. 163–188. Enfield, New Hampshire: Science Publishers Inc.

Bouvy, M., Falcao, D., Marinho, M., Pagano, M., and Moura, A. 2000. Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. *Aquat. Microb. Ecol.* 23:13–27.

Branco, C.W.C., and Senna, P.A.C. 1991. The taxonomic elucidation of the Paranoá Lake (Brasilia, Brazil) problem: Cylindrospermopsis raciborskii. *Bulletin du Jardin Botanique National de Belgique* 61:85–91.

Briand, J.F., Leboulanger, C., Humbert, J.F., Bernard, C., and Dufour, P. 2004. *Cylindrospermopsis raciborskii* (Cyanobacteria) invasion at mid-latitudes: Selection, wide physiological tolerance, or global warming? *J. Phycol.* 40:231–238.

Chapman, A.D., and Schelske, C.L. 1997. Recent appearance of *Cylindrospermopsis* (Cyanobacteria) in five hypereutrophic Florida lakes. *J. Phycol.* 33:191–195.

Charalambidou, R., and Santamaría, L. 2005. Field evidence for the potential of waterbirds as dispersers of aquatic organisms. *Wetlands* 25:252–258.

Chonudomkul, D., Yongmanitchai, W., Theeragool, G., Kawachi, M., Kasai, F., Kaya, K., and Watanabe, M.M. 2004. Morphology, genetic diversity, temperature tolerance and toxicity of *Cylindrospermopsis raciborskii* (nostocales, cyanobacteria) strains from Thailand and Japan. *FEMS Micob. Ecol.* 48:345–355.

Chorus, I., and Bartram, J. 2004. *Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management*. London: Taylor and Francis Group.

Falconer, I. 2001. Toxic cyanobacterial bloom problems in Australian waters: risks and impacts on human health. *Phycologia* 40:228–233.

Hamilton, P.B., Ley, L.M., Dean, S., and Pick, F.R. 2005. The occurrence of the cyanobacterium *Cylindrospermopsis raciborskii* in Constance Lake: an exotic cyanoprokaryote new to Canada. *Phycologia* 44:17–25.

Hindak, F. 1988. Plankton species of two related genera *Cylindrospermopsis* and *Anabaenopsis* from Western Slovakia. *Arch. Hydrobiol. 89:283–302.*

Istvanovics, V., Shafik, H.M., Presing, M., and Juhos, S. 2000. Growth and phosphate uptake kinetics of the cyanobacterium, *Cylindrospermopsis raciborskii* (Cyanophyceae) in through flow cultures. *Freshwater Biol.* 43:257–275.

Johnston, B.R., and Jacoby, J.M. 2003. Cyanobacterial toxicity and migration in a mesotrophic lake in western Washington, USA. *Hydrobiologia* 495: 79–91.

Komárek, J., 1984. From Komarek and Hauer (2004).

_____, and Hauer, T. 2004. CyanoDB.cz—On-line database of cyanobacterial genera. http://www.cyanodb.cz

_____, and Horecka, M. 1979. Taxonomic position of three planktonic blue-green algae from the genera Aphanizomenon and Cylindrospermopsis. *Preslia Praha* 51:289–312.

Moore, D., O'Donohue, M., Garnett, C., Critchley, C., and Shaw, G. 2005. Factors affecting akinete differentiation in *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria). *Freshwater Biol.* 50:345–352.

Padisak, J. 2003. Estimation of minimum sedimentary inoculum (akinete) pool of *Cylindrospermopsis raciborskii*: a morphology and life-cycle based method. *Hydrobiologia* 502**:**389–394.

Phlips, E. 2001. The Toxic Algae Threat in Florida. *Florida Lake Watch* 20:1–8.

Saker, M.L., Neilan, B.A., and Griffiths, D.J. 1999. Two morphological forms of *Cylindrospermopsis raci-*

borskii (Cyanobacteria) isolated from Solomon Dam, Palm Island, Queensland. *J. Phycol.* 35:599–606.

Singh, R.N. 1962. Seasonal variants of *Anabaenopsis raciborskii* Wolosz. *Hydrobiologia* 20:87–91.

St. Amand, A. 2002. *Cylindrospermopsis:* an invasive toxic algal. *Lakeline* 22:36–38

Steinman, A.D., and Lamberti, G.A. 1996. Biomass and pigments of benthic algae. In *Methods in Stream Ecology*, eds. F.R. Hauer and G.A. Lamberti, pp. 295–313. New York, New York: Academic Press.

_____, and Ogdahl, M. 2004. An innovative funding mechanism for the Muskegon Lake AOC. *J. Great Lakes Res.* 30:341–343.

Tóth, L.G., and Padisák, J. 1986. Meteorological factors affecting the bloom of *Anabaenopsis raciborskii* Wołosz. (Cyanophyta: Hormogonales) in the shallow Lake Balaton, Hungary. *J. Plank. Res.* 8:353–363.

U.S. EPA. 1983. *Methods for Chemical Analysis of Water and Wastes*. U.S. Environmental Protection Agency, Cincinnati, OH. EPA-600-/4-79-020.

Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton—Methodik. *Verh. Internat. Verein. Limnol.* 9:1–38.

Varkonyi, Z.Z., Farkas, O., Garab, T., and Gombos, Z. 2000. The tolerance of cyanobacterium *Cylindrospermopsis raciborskii* to low-temperature photo-inhibition affected by the induction of polyunsaturated fatty-acid synthesis. *Biochem. Soc. T.* 28:892–894.

Wang, S-H., Dzialowski, A.R., Meyer, J.O., deNoyelles, F., Lim, N-C., Spotts, W.W., and Huggins, D.G. 2005. Relationships between cyanobacterial production and the physical and chemical properties of a Midwestern Reservoir, USA. *Hydrobiologia* 541:29–43.

WHO. 1999. *Toxic Cyanobacteria in Water: A guide to their public health consequences, monitoring and management.* World Health Organization.

Submitted: 29 June 2005
Accepted: 28 April 2006
Editorial handling: Rex L. Lowe