J. Phycol. **34,** 766–771 (1998)

LOCAL EXTIRPATION OF *STEPHANODISCUS NIAGARAE* (BACILLARIOPHYCEAE) IN THE RECENT LIMNOLOGICAL RECORD OF LAKE ONTARIO[1]

Matthew L. Julius[2] *and Eugene F. Stoermer*

Center for Great Lakes and Aquatic Sciences, University of Michigan, Ann Arbor, Michigan 48109-1090

and

Christine M. Taylor and Claire L. Schelske

Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, Florida 32653

ABSTRACT

We investigated microfossil assemblages in recent sediments from nine stations across Lake Ontario. Stephanodiscus niagarae *was not present in any of these sediment samples, marking the taxon's extirpation from its type locality. This observation documents the end of a general reduction in size and alteration in valve morphology associated with habitat disturbance.* Stephanodiscus niagarae *may have been directly eliminated from the lake, or sexual reproduction may have been delayed beyond the species' ability to sustain numbers through asexual reproduction.*

Key index words: biodiversity; diatom(s); eutrophication; extirpation; Great Lakes; paleoecology; paleolimnology Stephanodiscus

Ehrenberg (1845) described *Stephanodiscus niagarae* (Figs. 1, 2) from the Niagara Falls. Since its description over 150 years ago, the species has become one of the most studied diatom taxa in the Great Lakes. Taxonomic confusion regarding *S. niagarae* and other *Stephanodiscus* species (Fig. 3) lumped in the invalid *S. astrea* often makes limnological studies involving these species difficult to interpret, but progress has been made toward a greater understanding of *S. niagarae* biology. Paleolimnological studies have reported *S. niagarae* as a major component of siliceous microfossil assemblages in each of the Great Lakes (Stoermer et al. 1985a, b, Wolin et al. 1988, Stoermer et al. 1990, 1996), with relative *S. niagarae* abundance making up over 20% of the microfossil diatom assemblage in some sampling intervals (pre-1850).

This abundance in the limnological record has enabled more detailed biological investigations of the taxon. Stoermer and Yang (1970) found this species in naturally eutrophic areas favoring moderate nutrient enrichment, but they also observed abundance decreasing in areas receiving heavy industrial pollution. Stoermer and Ladewski (1976) identified highest *S. niagarae* abundance at relatively low temperatures (ca. 3°–6° C), with large populations occurring during fall and spring circulation. This allows *S. niagarae* to take advantage of silica supplies made available during isothermal mixing and to avoid effects of maximum silica depletion (Stoermer et al. 1996).

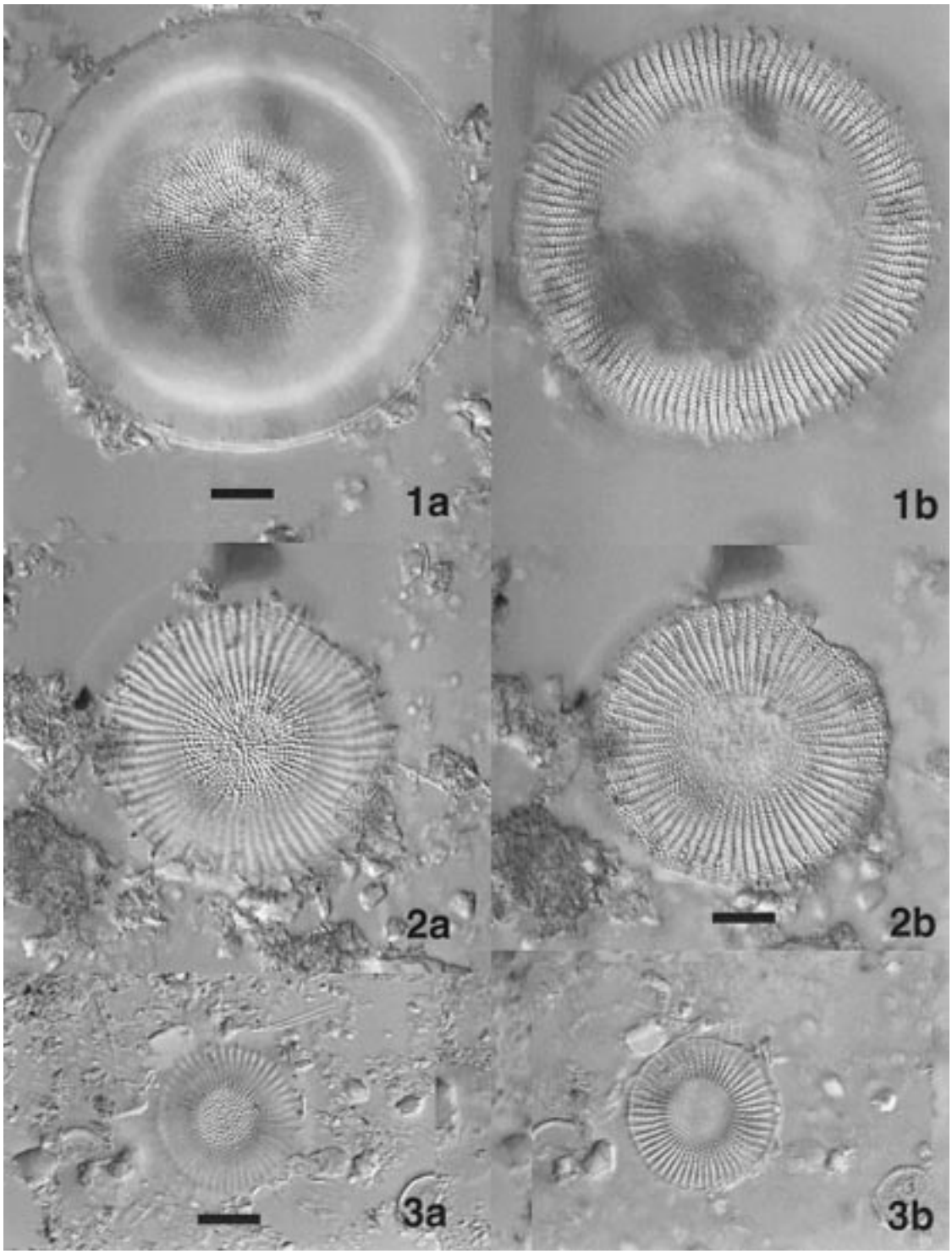
Other studies investigated mechanisms influencing morphological expression in *S. niagarae* valves. Theriot and Stoermer (1984) found genetic components responsible for some morphological variation in the species and identified other species with similar morphologies closely related to, but incorrectly identified as, *S. niagarae.* In a related study, Theriot (1987) found environmental factors responsible for other variations in valve morphology in *S. niagarae* populations. Stoermer et al. (1989) investigated morphological variation in a *S. niagarae* population through time using a Lake Ontario sediment core. The study identified variations in radial puncta number and a decrease in mean valve diameter in material deposited after 1964 and through 1980 (Fig. 2). The trend in puncta number was associated with the lake's increased eutrophication. The *S. niagarae* life cycle (Edlund and Stoermer 1991), like most diatoms (Edlund and Stoermer 1997), requires sexual reproduction to regain the maximum cell size that is diminished through asexual reproduction. Decreased mean valve diameter was associated with silica depletion, inhibiting sexual reproduction in *S. niagarae.* This study reports the absence of *S. niagarae* in Lake Ontario's recent limnological record. Sexual reproduction in *S. niagarae* populations appears to have been inhibited beyond the species' ability to sustain numbers through asexual reproduction, resulting in a local extirpation of the taxon.

Material used in the study was surface sediment derived from cores taken across Lake Ontario's basin (Fig. 4) in August 1994, using a modified Soutar Box corer at stations listed in Table 1. Surface sediments were undisturbed, and there were no apparent physical disturbances of lithology in section. The original box core was subsampled by inserting 7.5-cm-diameter clear plastic tubes into sediments. Sediment distortion was minimized by applying vacuum sufficient to maintain water level inside the tubes equal to that in the box. Material in tubes was sectioned immediately after retrieval, using a hydraulic extruder.

The upper 2 cm of the cores was examined at 0.5-

[1] Received 23 September 1997. Accepted 26 May 1998.

[2] Author for reprint requests; e-mail mjulius@umich.edu.



FIGS. 1–3. Light micrographs of *Stephanodiscus niagarae* and *Stephanodiscus alpinus* from Lake Ontario. Scale bars = 10μm. Material from E. F. Stoermer collection, core LO-E30. FIG. 1. *Stephanodiscus niagarae* from pre-1850 lake sediment. (A) High focus. (B) Low focus. FIG. 2. *Stephanodiscus niagarae* from post-1850 lake sediment. (A) High focus. (B) Low focus. FIG. 3. *Stephanodiscus alpinus*. (A) High focus. (B) Low focus.

cm intervals. With regard to chronology, this 2-cm depth is not temporally uniform across the nine stations sampled. Sediment from station E-30 has been ^{210}Pb dated in other studies (Schelske et al. 1988), and this is the same location for the material studied in Stoermer et al. (1989). Although all the stations sampled are areas of high sediment deposition, station E-30 is typically used for early historical com-

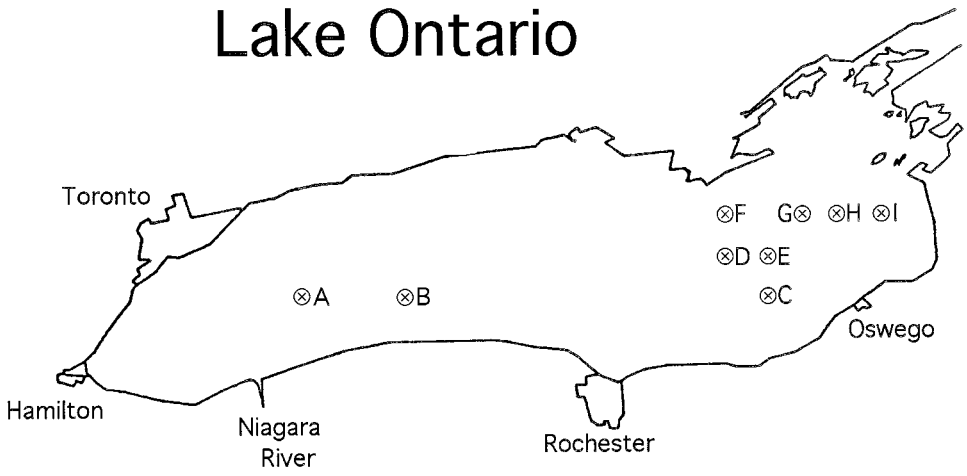


FIG. 4. Map of Lake Ontario showing station locations for coring. A: LO-1, B: E-16, C: E-30, D: G-29, E: G-30, F: H-29, G: H-31, H: H-32, I: H-35.

parisons because the sedimentation rate is slower relative to the other stations sampled (Schelske et al. 1988). Original ^{210}Pb dates were performed at station H-32, because this location is thought to have the highest sedimentation rate and represents the best sampling site for temporal resolution. Deeper sediment was also examined in this core to allow discovery of *S. niagarae* valves (maximum depth interval 6.5–7.0 cm).

^{210}Pb dates for station H-32 were obtained through nondestructive, direct gamma counting of ^{210}Pb using an intrinsic germanium well detector and a 4096 channel multichannel analyzer calibrated at 0.5 keV/channel (Schelske et al. 1994). Freeze-dried samples were weighed and pressed in 14-mm-diameter plastic vials to a nominal depth of 30 mm and then sealed with epoxy resin. Activities of the 46.52- and 609.1-KeV gamma energies of ^{210}Pb and ^{214}Bi, respectively, were measured. The activity measured as ^{210}Pb represented total ^{210}Pb in the sample. Excess ^{210}Pb was obtained by subtracting the activity of ^{214}Bi from that total ^{210}Pb. A factor to correct for changes in efficiency with height was used to calculate activities for each sample. Ages were calculated with a CRS (constant rate of supply) model (Table 2). Using the sedimentation rate calculated in Schelske et al. (1988) for station E-30 and based on the ^{210}Pb dates in this study for station H-32, the 2-cm depth at stations sampled in this study should be no older than 1987 and no younger than 1990.

TABLE 1. *Lake Ontario stations.*

Station	Latitude/Longitude
LO-1	43°30.0′ N; 79°00.0′ W
E-16	43°30.0′ N; 78°18.0′ W
E-30	43°30.0′ N; 76°54.0′ W
G-29	43°38.6′ N; 77°00.0′ W
G-30	43°38.6′ N; 76°54.0′ W
H-29	43°42.9′ N; 77°00.0′ W
H-31	43°42.9′ N; 76°48.0′ W
H-32	43°42.9′ N; 76°42.0′ W
H-35	43°42.9′ N; 76°24.0′ W

For siliceous microfossil analysis, a portion of each section was freeze dried to reduce microfossil breakage associated with other drying methods. A dry, weighed subsample of each section was boiled for 30 min in 30% H_2O_2 at 110° C. Twenty-five milliliters of concentrated HNO_3 were added to the peroxide-sediment suspension, resulting in a rapid exothermic reaction within 5 min. The solution was then heated at 120° C for 1 h. Samples were then rinsed six times with distilled water to remove oxidation byproducts. A portion of each sample was settled upon cover slips and mounted in Hyrax™ for light microscope (LM) observation.

All LM observations were made with either a Leitz Ortholux capable of a 1.32 numerical aperture or a Leica DMRX microscope at 1200× using full immersion optics providing a numerical aperture of 1.40. All diatom valves were examined on two cover slips from each sediment interval (approximately 200,000 valves per cover slip). All specimens were analyzed using the computer imaging system described in Stoermer (1996). Images were captured using a Sony 3 CCD color video camera using NIH

TABLE 2. *Sample depths and median dates of material from station H-32 based on ^{210}Pb analysis (see text).*

Depth (cm)	Date	Error
0.0–0.5	August 1994	
0.5–1.0	1994.1	±0.3
1.0–1.5	1993.5	±0.3
1.5–2.0	1992.7	±0.3
2.0–2.5	1991.9	±0.3
2.5–3.0	1991.2	±0.3
3.0–3.5	1990.4	±0.3
3.5–4.0	1989.4	±0.3
4.0–4.5	1988.2	±0.3
4.5–5.0	1987.2	±0.3
5.0–5.5	1986.0	±0.3
5.5–6.0	1985.2	±0.3
6.0–6.5	1984.0	±0.3
6.5–7.0	1983.3	±0.3
7.0–7.5	1982.3	±0.3
7.5–8.0	1981.5	±0.3

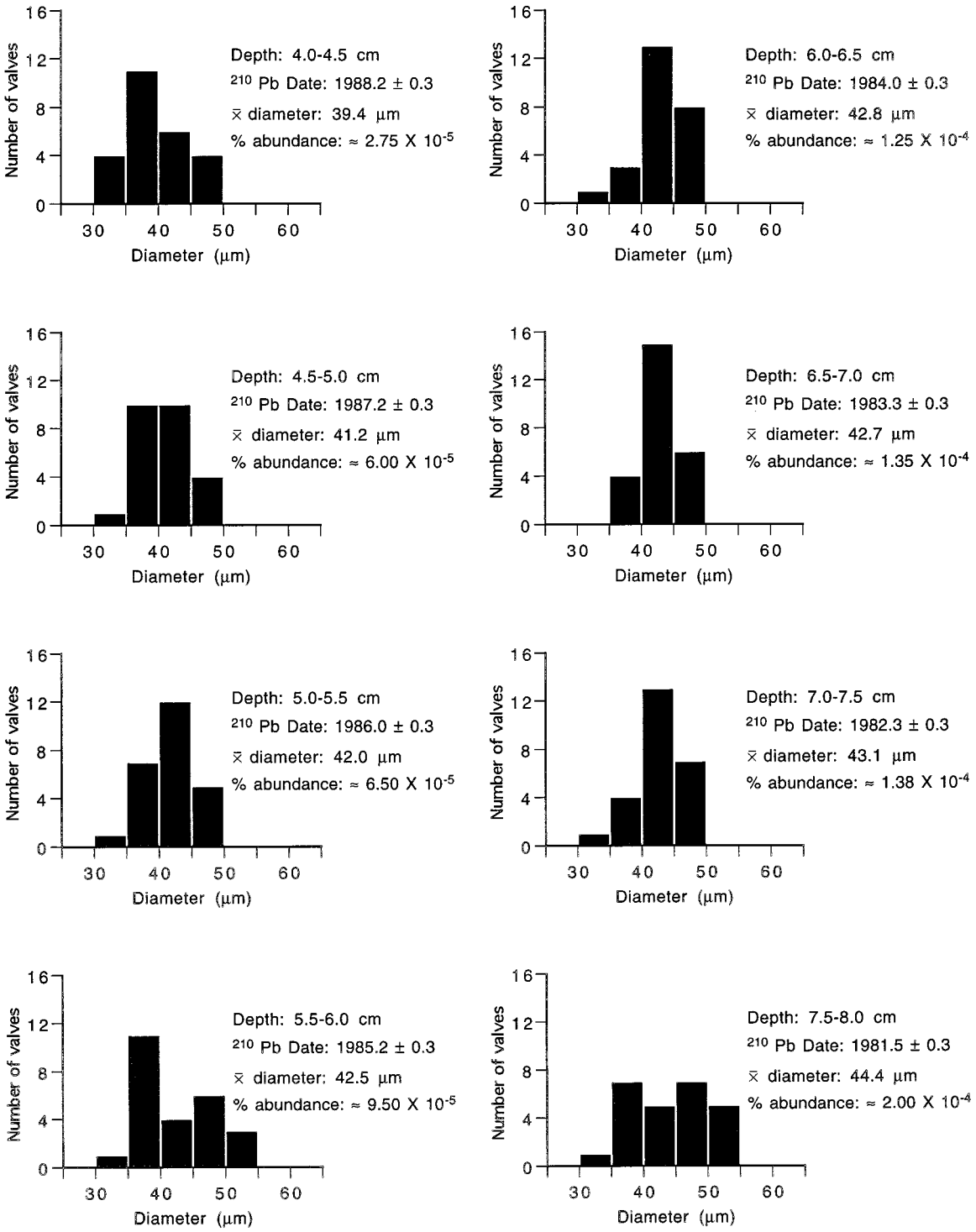


FIG. 5. Histograms for valve diameter of *Stephanodiscus niagarae* in sediment intervals 4.0–8.0 cm in depth from station H-32. Sample size = 25 for all sediment intervals. Accompanying each histogram is information on sample depth, sample age, mean diameter, and percent microfossil abundance of *S. niagarae* (based on a ≈400,000 total microfossil sample size for each sediment interval).

Image 1.59 (written by Wayne Rasband at the U.S. National Institutes of Health and available on their Internet homepage http://rsb.info.nih.gov/nih-image/default.html, or on floppy disk from NTIS, 5285 Port Royal Road, Springfield, Virginia 22161, part PB93-504868) run on an Apple Power Macintosh 8100/110 computer.

All microfossil collections examined in this study were devoid of *S. niagarae* for the first 2 cm. *Stephanodiscus alpinus* (Fig. 3) was the most abundant

Stephanodiscus species identified in the recent sediments. *Stephanodiscus alpinus,* like *S. niagarae,* reaches its maximum abundance at low temperatures (<2° C), achieving its largest population size during winter and spring (Stoermer and Ladewski 1976). However, *S. alpinus* is regarded as a taxon tolerant of highly disturbed environments (Stoermer and Yang 1970; Theriot and Stoermer 1982). Stoermer et al. (1989) found *S. niagarae* in Lake Ontario sediments deposited as late as 1980. Wolin et al. (1991), however, did not include *S. niagarae* among the list of dominant taxa for a 1981–1987 sediment interval, indicating the *S. niagarae* population never exceeded 1% of the microfossil assemblage in samples analyzed for their study. *Stephanodiscus alpinus* was present in all intervals sampled in their study, with relative abundances ranging from <5% to >25% of the microfossil population. Longer paleolimnological records (Stoermer et al. 1985a) identify *S. alpinus* as the dominant *Stephanodiscus* species since 1850, with *S. niagarae* relative abundance ranging from 0.5% to 2.0% during this period.

Using the rough chronology established in the paleolimnological studies described above, we can infer the extirpation of *S. niagarae* in Lake Ontario occurred around 1981–1987. Investigation of overlapping samples in this study from station H-32 helps narrow the date estimation for this extirpation event. Figure 5 illustrates a general decline in the abundance and mean valve diameter for sediment intervals dated from 1981.5 to 1988.2. The 1988.2 sediment sample represents the final sediment interval where *S. niagarae* is identified, narrowing our estimation of the extirpation to 1988.2 ± 0.3, given the error associated with ^{210}Pb dating.

Continued environmental disturbance, creating a completely unfavorable habitat, could explain the disappearance of *S. niagarae.* However, another possible biological explanation exists. *Stephanodiscus niagarae* mean diameter began decreasing in the late 1940s and early 1950s, reaching 42.5 μm by 1980 (Stoermer et al. 1989). This decrease in valve diameter occurs during a period of severe silica limitation generated through increased phosphorus inputs (Schelske et al. 1986) and is probably responsible for inhibited sexual reproduction in the species (Stoermer et al. 1989). Edlund and Stoermer (1991) found a 35-μm average oogonial valve diameter in a cultured *S. niagarae* population. This value also indicates the lower limit for cell size. Two trends consistent with inhibited sexual reproduction can be seen in Figure 5. The mean valve diameter continues to decrease from 1981.5 to 1988.2, reaching 39.4 μm by 1988.2, and a majority of the valves identified in this sediment interval have a diameter below 40 μm. This indicates most of the *S. niagarae* population was reaching the lower size limit for the species. Continued asexual reproduction in the post-1980 population could have decreased mean valve diameter below that needed for viable cells to develop, ultimately resulting in the extirpation of the taxon from the lake.

Further research on *S. niagarae* and Lake Ontario regarding our observation should be performed and should address two sets of questions. The first should involve simple culturing techniques, examining what chemical factors inhibit sexual reproduction. This investigation should focus specifically on those chemical parameters present in post-1940 Lake Ontario. The second study should deal with the population dynamics of a diatom population during an extirpation event. A modeling exercise simulating the reduction in valve diameter and population size could provide useful information. This simulation would provide an estimation of how long it takes a population to disappear and what the mean valve diameter and variance would look like at any given time for this period. If discovered, the factor or factors causing the taxon's disappearance could provide valuable information on long-term ecosystem effects of environmental perturbations and provide a possible mechanism for estimating how long native phytoplankton populations can persist in disturbed environments.

Contribution 597 from the Center for Great Lakes and Aquatic Sciences was supported in part by NSF grant DEB 9521882, NSF grant OCE 9202794, and funds from the Florida Research Foundation, Inc.

Edlund, M. B. & Stoermer, E. F. 1991. Sexual reproduction in *Stephanodiscus niagarae* (Bacillariophyta). *J. Phycol.* 27:780–93.

——— 1997. Ecological, evolutionary, and systematic significance of diatom life histories. *J. Phycol.* 33:897–918.

Ehrenberg, C. G. 1845. Neue Untersuchungen über das kleinste Leben als geologisches Moment. Mit kurzer Charakeristik von 10 neuen Genera und 66 neuen Arten. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der königl. pruess. Akademie der Wissenschaften zu Berlin,* pp. 53–88.

Schelske, C. L., Peplow, A., Brenner, M. & Spencer, C. N. 1994. Low-background gamma counting: applications for ^{210}Pb dating of sediments. *J. Paleolimnol.* 10:115–28.

Schelske, C. L., Robbins, J. A., Gardner, W. S., Conley, D. J. & Bourbonniere, R. A. 1988. Sediment record of biogeochemical responses to anthropogenic perturbations of nutrient cycles in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 45:1291–303.

Schelske, C. L., Stoermer, E. F., Fahnenstiel, G. L. & Haibach, M. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 43:407–15.

Stoermer, E. F. 1996. A simple, but useful, application of image analysis. *J. Paleolimnol.* 15:111–3.

Stoermer, E. F., Emmert, G., Julius, M. L. & Schelske, C. L. 1996. Paleolimnological evidence of rapid recent change in Lake Erie's trophic status. *Can. J. Fish. Aquat. Sci.* 53:1451–8.

Stoermer, E. F., Emmert, G. & Schelske, C. E. 1989. Morphological variation of *Stephanodiscus niagarae* (Bacillariophyta) in a Lake Ontario sediment core. *J. Paleolimnol.* 2:227–36.

Stoermer, E. F., Kociolek, J. P., Schelske, C. L. & Conley, D. J. 1985a. Siliceous microfossil succession in the recent history of Lake Superior. *Proc. Acad. Nat. Sci. Phila.* 137:206–28.

Stoermer, E. F. & Ladewski, T. B. 1976. *Apparent Optimal Temperatures for the Occurrence of Some Common Phytoplankton Species in Southern Lake Michigan.* Publication of the Great Lakes Research Division 18, 49 pp.

Stoermer, E. F., Wolin, J. A., Schelske, C. L. & Conley, D. J. 1985b. An assessment of ecological changes during the recent his-

tory of Lake Ontario based on siliceous microfossils preserved in the sediments. *J. Phycol.* 21:257–76.

——— 1990. Siliceous microfossil succession in Lake Michigan. *Limnol. Oceanogr.* 35:959–67.

Stoermer, E. F. & Yang, J. J. 1970. *Distribution and Relative Abundance of Dominant Plankton Diatoms in Lake Michigan.* Publication of the Great Lakes Research Division 16, 64 pp.

Theriot, E. C. 1987. Principal component analysis and taxonomic interpretation of environmentally related variation in silicification in *Stephanodiscus* (Bacillariophyceae). *Br. Phycol. J.* 22: 359–73.

Theriot, E. C. & Stoermer, E. F. 1982. Observations on North American populations of *Stephanodiscus* (Bacillariophyceae) species attributed to Friedrich Hustedt. *Trans. Am. Microsc. Soc.* 101:368–74.

——— 1984. Principal component analysis of *Stephanodiscus*: observations on two new species form the *Stephanodiscus niagarae* complex. *Bacillaria* 7:37–58.

Wolin, J. A., Stoermer, E. F. & Schelske, C. L. 1991. Recent changes in Lake Ontario 1981–1987: microfossil evidence of phosphorus reduction. *J. Great Lakes Res.* 17:229–40.

Wolin, J. A., Stoermer, E. F., Schelske, C. L. & Conely, D. J. 1988. Siliceous microfossil succession in recent Lake Huron sediments. *Arch. Hydrobiol.* 114:175–98.