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Aquatic Angiosperms at Unusual Depths in Shoal Lake, Manitoba–Ontario

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Shoal Lake (elevation 323 m) was found to contain extensive macrophyte communities growing at depths of 12-14 m and consisting of the angiosperms *Elodea canadensis, Najas flexilis, Potamogeton foliosus, P. zosteriformis, Myriophyllum exalbescens, Ceratophyllum demersum, Megalodonta beckii, Zosterella dubia, Lemna trisulca* and the aquatic moss *Drepanocladus* sp. Aside from one previous record for *E. canadensis* at higher altitude, the above angiosperm species have not been reported at such depths before. These communities were observed throughout two consecutive growing seasons. Plants at these depths received an estimated 0.5-1% of surface light. Besides light, other factors which may have allowed for the existence of these communities were warm summer temperatures in deep water and the presence of oxygen in the sediments during most of the ice-free season.

Key Words: Macrophytes, aquatic angiosperms, depth record, Shoal Lake, Manitoba, Ontario.

Submerged aquatic vascular macrophytes are normally confined to shallower regions of lakes, where light penetration and temperature, in conjunction with other, less well understood factors are conducive to macrophyte growth and reproduction. Normally angiosperms do not occur at depths greater than 10 m in freshwater (Ruttner 1953; Sculthorpe 1967; Hutchinson 1975). Recently Sheldon and Boylen (1977) and Singer et al. (1983) have recorded angiosperms at greater depths but these records apply to acidified lakes of exceptional clarity (ultraoligotrophic), where very little phytoplankton is present to reduce light penetration to deeper strata.

The present paper reports the existence of a diverse established macrophyte community at the unusual depths of 12-14 m in Shoal Lake, a large, nonacidified Precambrian Shield lake on the Manitoba–Ontario boundary. Shoal Lake has a mean elevation of 323 m above sea level and is the source of the water supply for the City of Winnipeg.

Materials and Methods

Sampling was conducted on a semi-monthly or monthly basis during the 1984-5 growing seasons. A set of samples was also collected under ice cover in late February 1985. Water samples were immediately placed on ice in a dark container and frozen within 7 hours. Deep water samples were obtained with a van Dorn sampler. Thawed samples were analyzed according to methods recommended by the American Public Health Association (1975, 1985). Nitrate was determined using an Orion Ionalyzer model 407A with nitrate electrode. The pH was measured directly in the field with a portable pH meter.

Photosynthetically active radiation (PAR) [400-700 nm] was measured using a Li-Cor Integrating Quantum Photometer equipped with an underwater quantum sensor. Temperature and dissolved oxygen were measured with a Yellow Springs Instruments Tele-thermometer and Oxygen Meter, respectively.

Chlorophyll content of water was estimated by filtering 0.2 to 1 L of water in the field through Whatman No. 1 filter paper under suction from a hand vacuum pump. The filter was placed in a plastic bag on ice in darkness, and stored in the laboratory at -20°C in the dark. The filter was ground in a mortar with neutralized acid-washed silica sand and 15 mL 80% acetone containing 10 mM $CaCO_3$ (lime). The homogenate was centrifuged at low speed in a clinical centrifuge. Chlorophyll content of the supernatant was determined using the spectrophotometric method of Arnon (1949).

Standing crop of the deep communities was estimated with the aid of SCUBA; all above-ground plant material was collected by hand within a randomly chosen circle of 20 m radius, and washed and dried at 70°C to constant weight.

Results

The unusually deep macrophyte communities were distributed over a large area, centered at approximately 49°36′N, 95°04′W, near the entrance to Indian Bay of Shoal Lake. This location is henceforth referred to as the DW site. The ranges of chemical and physical parameters obtained at this site during the 1985 growing season are given in Table 1. Most water chemistry parameters showed a wide range of variation during the season, particularly for phosphorus and nitrate concentrations. Amounts of chlorophyll a in the water, indicative of phytoplank-

TABLE 1. Chemical and physical parameters for the DW site at the surface and at depths of 11-12.5 m during 2 May-29 August 1985.

Parameter	Surface	11–12.5 m	Sediments at 12–14 m
pH	6.9–8.0	6.9–7.8	
Total dissolved solids, mg L^{-1}	45–108	52–85	
Total alkalinity, mg L^{-1} $CaCO_3$	62–83	64–88	
Phosphorus (molybdenum reactive), mg L^{-1}	0.07–0.85	0.10–0.91	
Nitrate-N, mg L^{-1}	0.09–> 1.0	0.05–0.7	
Nitrite-N, mg L^{-1}	0–0.001	0–0.002	
Ammonia-N, mg L^{-1}	0–0.05	0–0.05	
Sulphate, mg L^{-1}	1.4–3.1	1.4–3.8	
Chloride, mg L^{-1}	0	0	
Dissolved oxygen, mg L^{-1}	8.9–11.8	5.0–10.4	0–10.6
Chlorophyll a, μg L^{-1}	1.6–> 6	2.6–5.6	
Temperature, °C	8–20.5	5–19	4–16.5
Light, as % of surface	–	0.7–2.5*	
Light, as μE $s^{-1}m^{-2}$	175–2370	2–42*	

*at 10 m; range from full sun to heavy overcast.

ton biomass, attained the highest values in August, when inorganic nutrient levels and temperatures were also high. The phytoplankton communities at the DW site were dominated by diatoms, although bluegreen, green, chrysophycean and dinoflagellate algae were also well represented.

Thermal stratification was generally not very pronounced because of the large surface area relative to volume of the lake, although localized thermoclines of limited duration could occur. Temperature attenuation at the DW site was slight during the ice-free season, even during periods of calm in midsummer, with a maximum observed difference of 5° C between the surface and the bottom of the water column. Water temperatures at 12-14 m varied from 4° C in winter to a recorded late summer maximum of 19°C in 1984 and 17-19°C in 1985.

Dissolved oxygen levels in the sediments approached 0 mg L^{-1} under February cover of 0.75 m ice and 0.5-0.75 m snow, but a week after the ice disappeared in late April, sediments at the DW site contained approximately 90% of surface dissolved oxygen levels. Sediment oxygen concentrations then declined steadily; in mid- July they were still 7.5% of those at the surface. A minimum of close to 0 was observed at the beginning of August, but values had increased again to > 25% by the end of August.

Midday surface incident PAR intensities showed a wide range, depending on degree of cloud cover. A large part of incident PAR (up to 70%) was lost in the first meter of water. Light intensities at 13-14 m were estimated at 0.5-1% of surface incident levels. Attenuation depended largely on phytoplankton density, while the amount of light penetrating below the surface was subject to variations in surface reflection resulting from differences in smoothness of the water surface and the angle of incidence at different times of the season.

A total of 32 aquatic macrophyte species was recorded in Shoal Lake. The macrophyte communities in shallower waters of this lake have been described by Pip and Sutherland-Guy (*in press*). The communities at 12-14 m at the DW site still contained a surprising array of vascular species: *Elodea canadensis* (Common Elodea), *Najas flexilis* (Common Naiad), *Potamogeton foliosus* (Leafy Pondweed), *P. zosteriformis* (Flatstem Pondweed), *Myriophyllum exalbescens* (Northern Watermilfoil), *Ceratophyllum demersum* (Coontail), *Megalodonta beckii* (Water Marigold), *Zosterella dubia* (Water Stargrass) and *Lemna trisulca* (Star Duckweed). A nonvascular aquatic moss, *Drepanocladus* sp., was present as well. Except for *C. demersum* and *L. trisulca*, which are species that have no roots, all other angiosperms were firmly rooted in the sediments and were observed by the diver to be present throughout the entire growing season. The sediments in the area were light and flocculent, with a high organic matter content (25% or more by dry weight). They were easily suspended by even slight water disturbance, yet the diver never observed any turbulence at the site other than that caused by his own movements. Although these communities were established over a wide area during both 1984 and 1985 (at least a hundred thousand square meters), they were very sparse, appearing as individual shoots anchored in shallow depressions in the bottom sediments. Standing crop in mid-July 1985 was estimated at 0.001 g m^{-2} dry weight (compared to values as high as 916 g m^{-2} in water 1 m deep in the same lake (Pip and Sutherland-Guy, *in press*)). The most widespread species at these depths appeared to be *E. canadensis*; other species showed irregular, patchy distributions. Chlorophyll composition of these plants has been examined elsewhere (Pip and Sutherland-Guy, *in press*)). Representative voucher specimens have been deposited in the University of Winnipeg herbarium.

Discussion

The depth limits at which different macrophytes occur in a given lake depend in large part on the amount of light penetration (e.g. Crum and Bachmann 1973; Riemer 1984), since the light compensation point (i.e. the light intensity at which photosynthetic carbon gain equals respiratory loss) for a given species will occur at a greater depth where water is more transparent. Thus depth limits must be qualified by measuring the percentage of surface illumination that actually reaches the plants.

In general it is known that some macrophytes may extend to depths which receive only 1-4% of surface light (Sculthorpe 1967), although many macrophytes appear to require much higher minimum intensities. Several of the macrophyte species recorded in the deep communities in Shoal Lake seemed to tolerate much lower light intensities than the minimum values reported for the same species by other workers. For example Wilson (1941) found that *Megalodonta beckii* required at least 10% of surface light in Trout Lake, Wisconsin, while Blackburn et al. (1961) suggested that *Zosterella dubia* under laboratory conditions required at least 18% of full summer sun for good growth. Wilson (1941) also reported minimum values of 4.5% for *Elodea canadensis* and 3.1% for *Najas flexilis*. However, the bottom light intensities of 0.5-1% at the DW site were still apparently adequate for the growth of nine vascular species, which may have adapted over time to the low light intensities. Some plants are indeed known to be capable of growth at light levels of less than 1%. For example, Blackburn et al. (1961) found experimentally that *Elodea densa* (South American Elodea) can still grow well at approximately 0.3% of full summer sun. Variability in the amounts of light required by a given species in different situations has been noted in other comparisons as well and it has been suggested (e.g. Hutchinson 1975) that other factors may be operating in addition to light to determine lower depth limits for macrophytes in individual lakes.

The maximum depth of occurrence for vascular macrophytes (i.e. angiosperms) in nearly all lakes, even in very clear waters with excellent light penetration, is generally not more than 10 m (Sculthorpe 1967; Hutchinson 1975). On the other hand nonvascular plants, such as *Chara*, *Nitella* and aquatic mosses, which were all represented in Shoal Lake as well, may achieve considerably greater depths (Hutchinson 1975). Among the factors that have been proposed to account for this difference is the effect of hydrostatic pressure on growth and development of plants which contain an internal system of lacunar spaces filled with gas (e.g. Ruttner 1953; Hutchinson 1975). Such spaces are lacking in nonvascular macrophytes. Ferling (1957) found that excess pressure may cause abnormal development in some macrophytes, although of the species he examined, *Elodea canadensis* appeared to withstand high pressures better than *Groenlandia densa* or *Ranunculus circinatus*. Bodkin et al. (1980) reported that some macrophytes, such as *Hippuris vulgaris* (Marestail), may grow normally at pressures corresponding to depths of 13 m, provided that high light intensities (100 μE s^{-1}m^{-2}) are maintained.

The 12-14 m depth records for Shoal Lake are of great interest since they represent the first records of rooted angiosperms at such depths in both a nonacidified lake and at fairly low altitude. Reduced atmospheric pressure in lakes at higher altitudes compensates to some extent for increased hydrostatic pressure at greater depths (Hutchinson 1975). Dangeard (1925) reported *E. canadensis* and *Najas marina* at 12-15 m in Lac d'Annecy in the French Alps. Despite the elevation of this lake, this record has previously been considered doubtful (e.g. Hutchinson 1975). Other records for angiosperms at comparable depths are those of Sheldon and Boylen (1977), who reported *E. canadensis* at 12 m in Lake George, New York, and Singer et al. (1983), who found *Potamogeton robbinsii* (Fern Pondweed) at 14 m in Lake George, and *Utricularia geminiscapa* (Hidden-flower Bladderwort), a rootless species, growing at 18 m in Silver Lake, New York. These latter two lakes are acidified and phosphorus-poor, with high sulphate and nitrate levels and low pH. Singer et al. (1983) suggested that in Silver Lake (elevation 641 m), extreme water clarity was an important factor which contributed towards the unusually deep growth of macrophytes.

Water clarity in Shoal Lake was not exceptional. Values for pH, total alkalinity and phosphorus were much higher during most of the season than the values given by Singer et al. (1983) for Silver Lake. Chlorophyll a values at the study site were also substantially greater than the August value of 0.11-0.14 μg L^{-1} reported for Silver Lake. In Lake George as much as 10% of surface light was still available at 12 m (Sheldon and Boylen 1977). These differences are all the more remarkable in that all previous records of deep water angiosperm communities each involved at most only two species of macrophytes.

Sheldon and Boylen (1977) pointed out that in many lakes the lower boundary for angiosperm growth corresponds to the maximum penetration of the summer thermocline. Differences in temperature at different depths may be significant enough to limit the length of the growing season in deeper waters (Moeller 1980). At low temperatures the ability of macrophytes to use available light for photosynthesis is reduced (Barko et al. 1982). Pokorny et al. (1984) reported that the optimum temperature for photosynthesis in *E. canadensis* at low irradiance levels is 20°C, which is near the maximum late summer temperatures of 17-19°C observed at 12-14 m at the DW site. Singer et al. (1983) also suggested that in Silver Lake, warm deep water with no thermal stratification (18.7°C in late August) was a key factor allowing for deep macrophyte growth.

The generally high content of sediment organic matter in Shoal Lake is interesting in that Barko and Smart (1983) have reported that organic material can inhibit growth of submergerd species, particularly in anaerobic sediments, where many toxic compounds may be generated. According to Armstrong (1978), ability of macrophytes to tolerate such compounds may be associated with efficient transport of oxygen from shoots to roots to assist in detoxification. It is here that the internal lacunar system may be important (Williams and Barber 1961). The sediments of Shoal Lake at 14 m contained some oxygen during much of the growing season. Thus sediment toxicity was reduced. This may have been an additional factor which permitted macrophytes to penetrate into deeper waters. The 12 m record for *E. canadensis* reported for Lake George by Sheldon and Boylen (1977) was also associated with aerobic sediments.

In conclusion, a combination of factors probably operates in Shoal Lake to allow macrophytes to colonize depths beyond those normally utilized in most water bodies. These factors may have been sufficient light intensities, warm deep water, and presence of oxygen in the sediments. Hydrostatic pressure did not appear to be important, since Shoal

most water bodies. These factors may have been sufficient light intensities, warm deep water, and presence of oxygen in the sediments. Hydrostatic pressure did not appear to be important, since Shoal

Lake is at a lower elevation than any other previously reported lake containing deep water comunities. These observations support the contention of Singer et al. (1983) that it is inaccurate to view depth limitation in a given water body as the product of only a single variable.

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Literature Cited

American Public Health Association. 1975 *and* 1985. Standard methods for the examination of water and wastewater. American Public Health Association, New York.

Armstrong, W. 1978. Root aeration in wetland conditions. Pp. 269-297 *in* Plant life in anaerobic environments. *Edited by* D. D. Hook and R. M. M. Crawford. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Arnon, D. I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidases in *Beta vulgaris*. Plant Physiology 24: 1–15.

Barko, J. W., D. G. Hardin, and **M. S. Matthews.** 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. Canadian Journal of Botany 60: 877–887.

Barko, J. W., and **R. M. Smart.** 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. Journal of Ecology 71: 161–175.

Blackburn, R. D., J. M. Lawrence, and **D. E. Davis.** 1961. Effects of light intensity and quality on the growth of *Elodea densa* and *Heteranthera dubia*. Weeds 9: 251-257.

Bodkin, P. C., U. Posluszny, and **H. M. Dale.** 1980. Light and pressure in two freshwater lakes and their influence on the growth, morphology and depth limits of *Hippuris vulgaris*. Freshwater Biology 10: 545-552.

Crum, G. H., and **R. W. Bachmann.** 1973. Submersed aquatic macrophytes of the Iowa Great Lakes region. Iowa State Journal of Research 48: 147–173.

Dangeard, P. 1925. Limite de la végétation en profondeur de quelques plantes submergées du Lac d'Annecy. Comptes Rendus à l'Académie des Sciences, Paris 180: 304-306.

Ferling, E. 1957. Die Wirkungen des Erhöhten hydrostatischen Druckes auf Wachstum und Differenzierung submerser Blütenpflanzen. Planta 49: 235–270.

Hutchinson, G. E. 1975. A Treatise on Limnology. Volume III. Limnological Botany. John Wiley & Sons, New York.

Moeller, R. E. 1980. The temperature-determined growing season of a submerged hydrophyte: tissue chemistry and biomass turnover of *Utricularia purpurea*. Freshwater Biology 10: 391-400.

Pip, E., and **C. Sutherland-Guy.** *In press*. Diversity, biomass distribution and metabolic status of aquatic macrophytes in relation to water depth in Shoal Lake (Manitoba-Ontario). Archives für Hydrobiologie.

Pokorny, J., J. Kvet, J. P. Ondok, Z. Toul, and **I. Ostry.** 1984. Production-ecological analysis of a plant community dominated by *Elodea canadensis* Michx. Aquatic Botany 19: 263-292.

Riemer, D. N. 1984. Introduction to Freshwater Vegetation. Avi Publishing Company, Westport, Connecticut.

Ruttner, F. 1953. Fundamentals of Limnology. University of Toronto Press, Toronto.

Sculthorpe, C. D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold Limited, London.

Sheldon, R. B., and **C. W. Boylen.** 1977. Maximum depth inhabited by aquatic vascular plants. American Midland Naturalist 97: 248-254.

Singer, R., D. A. Roberts, and **C. W. Boylen.** 1983. The macrophytic community of an acidic lake in Adirondack (New York, U.S.A.): a new depth record for aquatic angiosperms. Aquatic Botany 16: 49-57.

Williams, W. T., and **D. A. Barber.** 1961. The functional significance of aerenchyma in plants. Symposium of the Society for Experimental Biology 15: 132-144.

Wilson, L. R. 1941. The larger aquatic vegetation of Trout Lake, Vilas County, Wisconsin. Transactions of the Wisconsin Academy of Arts, Science and Letters 33: 135-146.

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