MAXIMUM DEPTH INHABITED BY AQUATIC VASCULAR PLANTS

BY

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Maximum Depth Inhabited by Aquatic Vascular Plants[1, 2]

ABSTRACT: *In situ* observations of submerged, rooted aquatic plants by a diver equipped with SCUBA have shown that the maximum depth distribution of a number of submerged species in a clear freshwater lake (Lake George, New York) is greater than previously reported. Maximum depth for any species was 12 m for *Elodea canadensis*. Water clarity is sufficient to allow 10% of the light intensity hitting the surface during midsummer to penetrate to this depth. The number of submergent species drops linearly from 38 at 1 m to one at 12 m. Data are presented for the maximum depth of occurrence for 28 vascular macrophyte species, and population densities of these species at their preferred and maximum growth depths compared. The effect of several environmental parameters on depth inhabited by rooted aquatics is discussed.

INTRODUCTION

In most freshwater ecosystems, vascular plants are reported to be limited to regions less than 5 m in depth, and in many lakes poor in water clarity, they are limited to less than 2 m (Sculthorpe, 1967). Literature reports of hydrophytes growing at depths exceeding several meters are infrequent. Notable exceptions include *Ceratophyllum* sp. at 9 m (Arber, 1920), *Potamogeton pusillus* at 7 m (Wilson, 1935) and *P. spirillus* and *Isoetes* sp. at depths of 5 m (Muenscher, 1944). Limits of 10 m have been reported for certain Scottish lochs (Spence, 1972), lakes in Northern England (Pearsall, 1920) and Green Lake, Wisconsin (plants not identified; Rickett, 1924). Classical taxonomic keys (Muenscher, 1944; Fassett, 1957) include little information on the specific depth range of a given species, although unqualified and vague designations such as "shallow" and "deep" are attached to many descriptive notations.

To document maximum depth limits for a number of aquatic species, a study was undertaken to determine the distribution, abundance and limiting depth for 28 species of rooted macrophytes found in Lake George, New York. This lake offered a good ecological situation for study because of its oligotrophic status, exceptionally high water clarity, and species diversity of submergent plants.

Lake George is situated on the eastern side of the Adirondack Mountains, with an overall length of 51 km and a mean width of 2.3 km. Maximum depth is approximately 60 m. Transparency is exceptionally high (Fig. 1) with secchi disc readings commonly 6-7 m and values recorded as high as 13.5 m (Ferris and Clesceri, 1974). A well-developed thermocline exists during the summer months as deep as 12-13 m. The maximum surface water temperature typically reaches 25 C in the peripheral littoral areas. The lake is somewhat divided near the middle by a narrow channel dotted with islands separating the lake into an oligotrophic northern basin and an increasingly productive southern basin resulting partially from the urbanization of the villages around the southern end of the lake. An approximately fivefold difference in rooted macrophyte productivity exists between the two basins.

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METHODS

Observations were made from June 1973 to August 1975 while diving with self-contained underwater breathing apparatus (R.B.S.) at 50 randomly chosen sites around the periphery of the lake at a distance of 2-4 km from each other. At each site an underwater transect approximately 5 m wide was made perpendicular to the shore from the shoreline to about 17 m deep. Depth and abundance measurements for each species were recorded underwater by the diver on an opaque plastic sheet (roughened lucite) with a no. 2 graphite pencil. Depth was measured by a capillary-type depth gauge. Plant densities were determined *in situ* by the diver using a scale previously devised. The scale was validated by use of conventional sampling devices to remove plants from the water and determining the number of plants/m² for each point on the scale. The exponential scale so constructed encompassed six orders of magnitude and allowed densities from 0.001 plant/m² to 2500 plants/² to be scored. The scale has proven invaluable for quick assessment of relative densities allowing an extensive study to be made of macrophyte growth patterns throughout the lake. Unidentified plants were removed from the water for identification using standard taxonomic keys (Muenscher, 1944; Fassett, 1957).

Relative light intensity measurements were made with a GM underwater photometer (Kahl Scientific Co., El Cajon, California). Temperature was measured *in situ* by a diver using a mercury thermometer or from the surface using a temperature compensated DO meter (Yellow Springs Instruments, Yellow Springs, Ohio) to measure dissolved oxygen concurrently.

RESULTS

Although 38 species of submerged rooted macrophytes were found at some depth among the 50 stations, 10 were observed only rarely and their presence

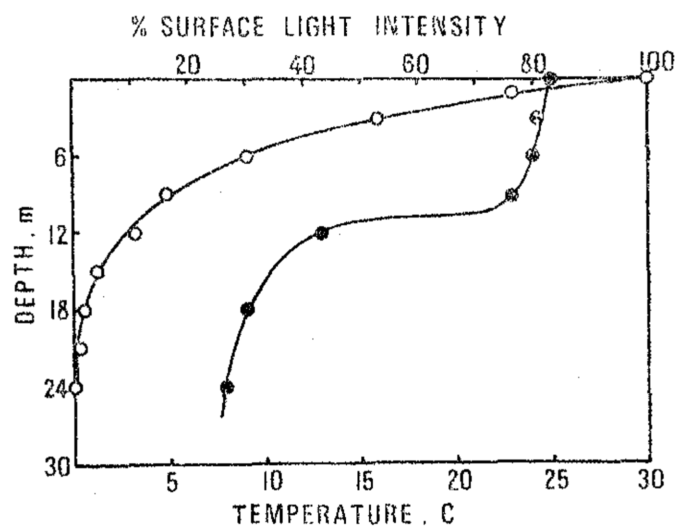

Fig. 1.—Typical light penetration on a clear midsummer day and average midsummer temperature profile in Lake George. Closed symbols represent water temperature and open symbols represent the percent surface light intensity

is not recorded in the data presented here. Depth, plant density and number of stations at which each species was found for both prevalent and maximum depths are summarized in Table 1. Prevalent depth is equated to the number of times a species is found in the 50 stations. For most species maximum depth was 1-3 m greater than the prevalent depth for that species and equals or extends the range reported in the literature for each species by 1-5 m. In each instance species abundance was considerably less at maximum depth than at the prevalent depth. Table 1 includes only those species with depth maxima of more than 2 m; thus, all emergent plants normally inhabiting shore areas of less than 1-2-m depth are not represented. Population densities at depths of 10 m or greater were 0.01 to 10 plants/m² for *Elodea canadensis* and 0.02 to two plants/m² for *Potamogeton robbinsii*. *Potamogeton robbinsii* and *Isoetes macrospora* were the most abundant species at depths greater than 6 m, with population densities as high as 100-1000 plants/m².

Ten percent of the surface light intensity reaches 12 m, the maximum depth observed for any rooted vascular plant, and the thermocline also appears at 12 m (Fig. 1). Figure 2 summarizes the presence or absence of 38 species in the 50 stations studied. There are presently 224 aquatic plant species known to occur in or on the periphery of Lake George in less than 1 m of water (E. C. Ogden *et al.*, 1976). At 1-m depth, the number of emergent and submergent species is reduced to 51. The emergent species (plants that have much of their vegetative structure above the water surface) have been omitted from the 1-m

TABLE 1.—Depth extension of rooted macrophytes in Lake George[a]

Species	Prevalent depth		
	Depth m	Abundance[b] plants/m²	Number of stations present
Bidens beckii	2-7	16-400	18
Elatine minima	1	500-2,500	13
Elodea canadensis	1-7	16-400	22
Eriocaulon septangulare	1	500-2,500	31
Heteranthera dubia	1-3	16-400	18
Isoetes echinospora	1-5	16-400	18
I. macrospora	5-7	100-1,000	32
Juncus pelocarpus	1-3	16-400	8
Lobelia dortmanna	1-2	3-300	6
Myriophyllum alterniflorum	1-3	3-300	12
M. tenellum	1-2	500-2,500	18
Najas flexilis	1-5	500-2,500	41
Potamogeton amplifolius	2-5	16-400	28
P. crispus	1-3	1-16	3
P. gramineus	1-5	3-300	46
P. illinoensis	3	0.02-2	2
P. pectinatus	1	3-300	3
P. perfoliatus	1-5	3-300	31
P. praelongus	2-5	3-300	19
P. pusillus	1-5	16-400	39
P. robbinsii	2-7	100-1,000	40
P. spirillus	1	0.1-10	3
P. zosteriformis	2-5	3-300	7
Ranunculus longirostris	1-3	1-16	9
Sagittaria graminea	1-2	16-400	14
Subularia aquatica	1-2	16-400	8
Utricularia resupinata	1-2	500-2,500	16
Vallisneria americana	1-5	100-1,000	41

value in Figure 2. No emergents are found in the 2-m depth or greater.

DISCUSSION

Maximum depth varied considerably among the 28 species studied; however, all species were observed to grow at depths ranging from 1 m to their maximum, although all depths were not necessarily represented at any one station. While each species had definite maximum and minimum depths for growth, each had a preferred depth or depth range as evidenced by greater densities and the number of stations at which they were observed (Table 1). Species were found at their preferred depths more commonly among the 50 stations than at their maximum depths, where they were found at only one or a few stations. Selective pressures which may have limited maximum growth at all stations are not presently known. Water chemistry, light penetration and temperature are fairly constant environment parameters at any given depth throughout the littoral zone of Lake George. It has been noted from *in situ* observations that sediment character, although variable throughout the lake, was relatively consistent at any single station.

Water depth has a pronounced effect on the diversity of species present, which drops linearly with increased depth (Fig. 2). With less competition by

TABLE 1.—(continued)

Species	Maximum depth		
	Depth m	Abundance[c] plants/m^2	Number of stations present
Bidens beckii	7	1-16	1
Elatine minima	2	0.05-5	5
Elodea canadensis	12	0.01-1	1
Eriocaulon septangulare	3	0.02-2	1
Heteranthera dubia	5	3-300	2
Isoetes echinospora	7	0.01-1	1
I. macrospora	9	100-1,000	5
Juncus pelocarpus	3	0.1-10	4
Lobelia dortmanna	2	3-300	4
Myriophyllum alterniflorum	5	3-300	4
M. tenellum	3	500-2,500	7
Najas flexilis	9	0.1-10	6
Potamogeton amplifolius	7	0.02-2	2
P. crispus	3	1-16	1
P. gramineus	7	0.1-10	4
P. illinoensis	7	0.05-5	1
P. pectinatus	3	0.02-2	1
P. perfoliatus	7	3-300	1
P. praelongus	7	0.1-10	3
P. pusillus	9	0.1-10	2
P. robbinsii	10	0.02-2	1
P. spirillus	5	0.01-1	1
P. zosteriformis	5	0.1-10	4
Ranunculus longirostris	5	0.001-0.1	1
Sagittaria graminea	3	16-400	4
Subularia aquatica	2	0.05-5	4
Utricularia resupinata	3	16-400	4
Vallisneria americana	7	16-400	6

[a] Does not include those species with depth maxima of less than 2 m

[b, c] Abundance is based on *in situ* density measurements made by the diver using an exponential scale designed to approximate submergent plant densities

other species, several species have successfully filled these deeper niches. Notable are *Potamogeton robbinsii* and *Isoetes macrospora* with extensive plant beds of 100-1000 plants/m^2 at 6-9 m. Many of the species that have floating or emergent fruiting structures (namely, *Potamogeton* and *Vallisneria*) are restricted to vegetative propagation when they grow in deeper water. A curve similar to that represented by Figure 2 can be generated if species number is plotted against light attenuation in the water column. Therefore, it is difficult to distinguish between the effects upon plant growth due to increasing depth or light availability. The maximum depth of 12 m for *Elodea canadensis* indicates that vascular plants are not strictly confined to the upper 10 m as suggested by Ruttner (1963) and Sculthorpe (1967).

Light is usually considered the factor limiting depth reached by vascular plants. Generally, maximum depth for growth depends upon the depth at which the light intensity falls below the light-compensation point for photosynthesis as well as the quality of light penetrating to any given depth. Sculthorpe (1967) states that hydrophytes may colonize suitable substrates to a depth receiving only 1 to 4% of the light intensity hitting the surface of the water. In Lake George the greatest depth reached by rooted macrophytes is 12 m, a depth which, in midsummer, receives 10% of the light intensity hitting the surface (Fig. 1). Depths receiving more than 1% of the light exceed 18 m, which is lower than the limit for growth of 15 m by the macroalga, *Nitella flexilis* (Stross, 1972). *Nitella* has been found as deep as 27 m in a volcanic lake in Japan (Jimbo *et al.*, 1955). The colonial blue-green alga, *Nostoc*, was also found to depths of 7 m in spheres as large as several centimeters diameter

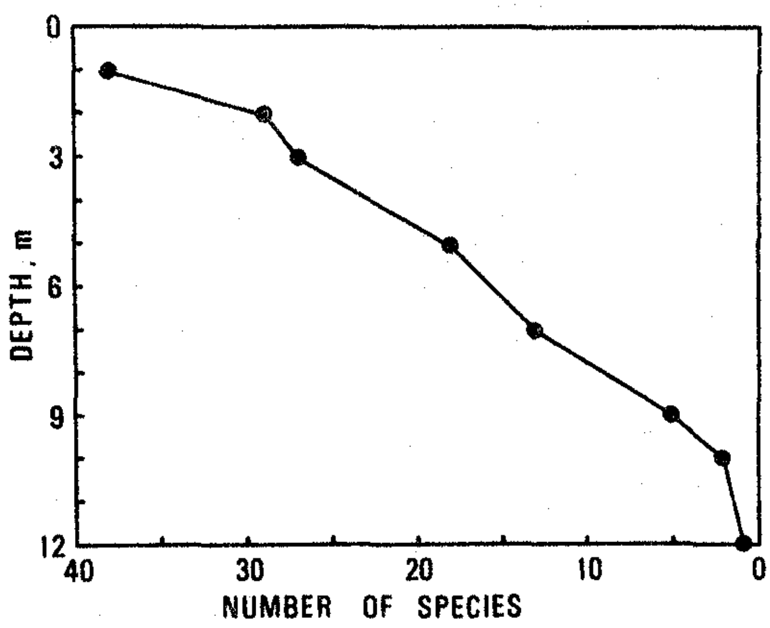

Fig. 2.—Relationship between the number of submerged rooted aquatic plants and water depth

in Lake George. Studies by Juday (1934), limited to bryophytes and periphytic algae, noted growth at depths of 18-20 m in Crystal Lake, Wisconsin. Several species of aquatic mosses have been found as deep as 120 m in Crater Lake, Oregon (Hasler, 1938) and 175 m in Lake Tahoe, California and Nevada (Frantz and Cordone, 1967).

Because of the productivity of many bodies of water, light intensity varies according to the concentration of seston, water color and the seasonal fluctuations in these parameters. Spence (1964) found the greatest depths for growth in clear, calcareous waters, shallower limits in brownish-colored waters and the least colonized depths in highly eutrophic waters. In many eutrophic freshwater lakes there can be considerable competition between the macrophytes and the phytoplankton in the water column for light. In Lake George such competition has not been noted even in the more productive southern basin. Epiphytic associations with macrophytes, which would deplete the light intensity reaching the macrophyte leaf surface even further, are not great at the present time (Sheldon and Boylen, 1975).

In stratified lakes the photic zone and epilimnion roughly coincide. Many submergent macrophytes do not display extensive ranges of temperature tolerance (Sculthorpe, 1967). Summer water temperatures in the epilimnion of Lake George fluctuate within a small range between 22 and 25 C (Fig. 1). Temperature would not be expected to exert a selective force within this temperature range. Throughout the summer the water column to 12 m (our extent of measurement) and the underlying sediment remain aerobic. Therefore, dissolved oxygen content especially in the area of root growth would not be a limiting factor for rooted aquatics. Arber (1920) suggests that the maximum depth of occurrence coincides with the maximum depth of the thermocline, which in Lake George occurs between 12-13 m. It is probable that the lower limits of the photic zone are determined by an interaction between light penetration and suitable temperatures for growth above the thermocline. The growth of rooted macrophytes at such extreme depths in lakes of greater clarity than Lake George may be limited by a shallower thermocline or other factors such as hydrostatic pressure (Ferling, 1957; Ruttner, 1963) or available nutrient levels which would explain their absence from these lakes. An excess of 1-atm pressure has been shown to curtail metabolic functions in aquatic plants containing gas-filled lacunae (Ferling, 1957). This pressure differential corresponds to 10-m depth in freshwater lakes. Sparse macrophyte populations have been reported for Crater Lake, a geologically young lake with high water clarity (Secchi disc readings of greater than 40 m) and low nutrient levels (Hutchinson, 1957). A similar situation has been noted for Lake Tahoe (Frantz and Cordone, 1967). Both of these lakes are considered ultraoligotrophic. Lake George has sufficient nutrients to support a somewhat abundant growth of vascular plants without providing such extensive phytoplankton productivity as to reduce the availability of light at 10 to 12 m to prevent macrophyte growth at these depths.

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