Aquatic Botany, 22 (1985) 21—32
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

EFFECTS OF FISH NESTS ON PATTERN AND ZONATION OF SUBMERSED MACROPHYTES IN A SOFTWATER LAKE

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(Accepted 8 February 1985)

ABSTRACT

Carpenter, S.R. and McCreary, N.J., 1985. Effects of fish nests on pattern and zonation of submersed macrophytes in a softwater lake. *Aquat. Bot.*, 22: 21—32.

Nests of centrarchid fishes maintain patches of diaspore-propagated submersed aquatic plants (principally *Elatine minima* (Nutt.) and *Isoetes braunii* Dur.) between 0.9 and 2.4 m depth in a softwater oligotrophic lake. Nests are cleared of vegetation in May—June, and abandoned by fish in June. By August, many nests are colonized by diaspore-propagated species that do not spread vegetatively on horizontal stems. About 75% of the nests are reoccupied by fish the following May, and some new nests are formed. Nests not reoccupied by fish are colonized by rhizomatous plants of 4 species that have not been observed to flower or set seed in the lake. Rhizomatous plants reach frequencies near 100% by 14 months after abandonment. Pattern analyses show that patch sizes of diaspore-propagated species correspond to the size of fish nests. Conventional explanations of macrophyte zonation based on depth, exposure, and competition are insufficient in this lake; effects of disturbance must be considered as well.

INTRODUCTION

Depth zonation of submersed aquatic plants is one of the most evident phenomena in limnology (see Hutchinson, 1975, and Spence, 1982, for thorough documentation). Understandably, a lot of research has attempted to explain the arrangements of plant species on depth gradients. For example, Spence and Chrystal (1970a, b) and Sand-Jensen (1978) have shown correlations between species' photosynthetic responses to light and depth of occurrence. However, depth ranges of submersed plants are often more restricted than physiological tolerances of light and temperature would predict (Spence, 1982). Most explanations of depth zonation invoke interspecific competition, either implicitly or explicitly. Hutchinson (1975, p. 118) expresses the concensus in a clear way:

> On passing from the margin to the deep water of a lake, the higher plants encountered are adapted to an environment that changes gradually: the arrangement of plants, no doubt owing to competitive phenomena, often appears rather more discontinuous than the environmental gradient on which it depends ...

0304-3770/85/$03.30

The potential importance of competition is supported by several experimental studies of co-occurring macrophyte species (Titus and Adams, 1979; McCreary et al., 1982; Titus and Stephens, 1983; Yeo and Thurston, 1984).

An alternative hypothesis, which has received less attention, is that depth-dependent disturbances influence macrophyte zonation. Raup (1975) described the effect of wave-pushed ice on vegetation in shallow water. Spence (1982) attached great importance to wave-mixed depth as a factor in macrophyte distribution. Above the wave-mixed depth, wave action is effective in moving particles and thereby influences turbidity, light extinction, turbulence (which affects solute exchange by submersed leaves), and particle deposition (which affects sediment texture and settling of seeds and spores).

Nests of centrarchid fishes, common in littoral zones of northern temperate lakes, are a source of depth-dependent disturbance that has not been investigated. When in use, these nests are barren of aquatic plants. The colonization sequence after the fish abandon the nests could be a major factor in depth zonation and patterns of co-occurrence among macrophytes. This paper analyzes the effects of fish nests on the submersed vegetation of a softwater lake.

MATERIALS AND METHODS

Study site

Roach lake (Fig. 1) lies on the border of Vilas County, WI (Sec. 7, T43N R8E) and Gogebic County, MI (Sec. 10, T44N R42W) in the University of Notre Dame Environmental Research Center. The 48-ha watershed, on deep glacial till with soils of acid stony-sand loams, is forested with northern mesic conifer-hardwoods. Roach lake is a seepage lake with clear water (Secchi-disk transparency = 4—6 m). The water is acidic (pH = 4.5—6.0) and poorly buffered (alkalinity < 0.2 meq l^{-1}). The thermocline lies at ca. 6 m and only the southern basin (Fig. 1) has a distinct hypolimnion. The lake's surface area is 36.4 ha, mean depth is 5.3 m, and maximum depth is 11.6 m.

The fish fauna includes 3 centrarchid species that form elliptical nests. The most important nest-forming species is the pumpkinseed sunfish (*Lepomis gibbosus* (L.)). Pumpkinseeds favor thin silt over gravel in relatively shallow water for nesting (Ingram and Odum, 1941; Colgan and Ealey, 1973). Largemouth bass (*Micropterus salmoides* Lacépède) nest on any substrate coarser than silt (Carlander, 1977). Smallmouth bass (*M. dolomieui* Lacépède) nest on sand and gravel (Carlander, 1977). All 3 species nest in spring or early summer in Wisconsin (Johnson, 1971; Schneberger, 1972).

Sampling

Vegetation was sampled by SCUBA divers using the line-intercept method (Lind and Cottam, 1969) in June—August of 1981—1983. Two types of

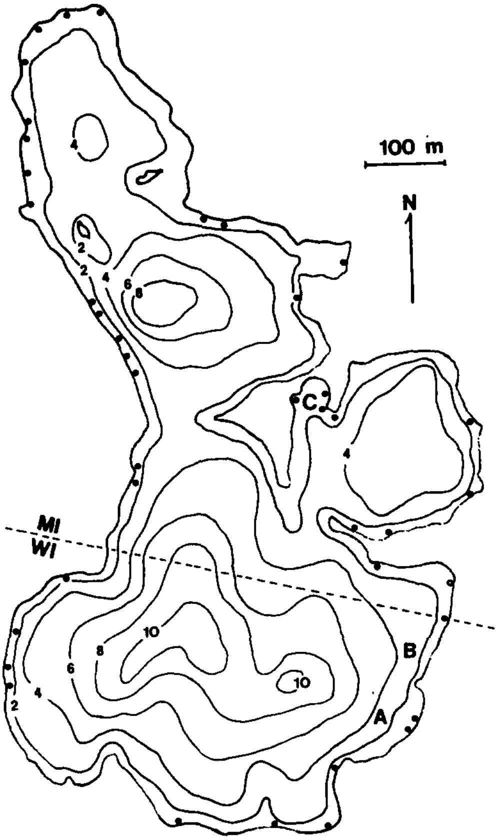


Fig. 1. Bathymetry of Roach lake. Letters denote sampling sites. Dots show locations of transects used in determining fish nest abundance. Contour interval 2 m.

sample were collected. First, to determine frequency and composition of the vegetation at Site A (Fig. 1), six 10-m transects were placed parallel to depth contours in order to eliminate heterogeneity due to depth zonation. The first end-point of each transect was placed by a blind throw in order to reduce bias. Species presence was recorded in contiguous 5-cm segments of the transects. Equitability was calculated for each transect as $J' = (-\Sigma p_i \log p_i)/\log S$ where p_i is the relative frequency of species i and s is the total number of species (Pielou, 1975). Secondly, in order to analyze the pattern of the vegetation, 9 transects 25—30 m long were placed deliberately through plant beds parallel to depth contours at Sites A, B and C (Fig. 1). Species presence was recorded in contiguous 5-cm segments.

Fish nests were sampled using 40 belt transects (1-m wide) placed randomly around the lake's perimeter (Fig. 1). Transect locations were selected by computer using a pseudo-random number generator and placed on a digitized map of the lake's perimeter. In the field, transect locations were determined by sightings to islands and shoreline features. Transects were oriented from the shore to the 3-m depth contour. Depth at the center of each nest was recorded. We recorded the lengths of the major and minor axes of each nest, and assumed that nests were elliptical to calculate areas.

Colonization of nests by plants was determined by constructing artificial nests between 1.5 and 2.0 m depth at Site A (Fig. 1) in June 1982. SCUBA divers removed macrophytes and the upper 5—10 cm of unconsolidated sediment, exposing firm sandy sediment. In general appearance, shape, and size, artificial nests were not distinguishable from real nests. The yellow plastic pegs that marked each nest, and our frequent visits, appeared to discourage fish that attempted to occupy the artificial nests. Artificial nests were established in two areas, one dominated by *Myriophyllum tenellum* Bigel. and the other dominated by *Eleocharis acicularis* R. and S. and *Juncus pelocarpus* Meyer f. *submersus* Fassett. In each area, 3 control (undisturbed) plots, 3 rimmed artificial nests, and 3 non-rimmed nests were established. Rimmed nests were enclosed by 15-cm-tall polyethylene edging placed 5—10 cm into the sediment to prevent invasion by rhizomatous plants. All 18 plots were sampled on 27 and 28 July 1983 by recording species' presence in grids of 5 X 5 cm contiguous quadrats. The entire area of each artificial nest was sampled (74—122 quadrats). In control areas, a 50 X 50 cm grid (100 quadrats) was sampled.

Dynamics of fish nests were followed from 1981—1983 in a 10 X 10-m permanent quadrat at Site B. Nests were marked on their perimeters using numbered flags. Depth to center, major axis length, and minor axis length were recorded for each nest. Each year new nests were marked and added to the sample. Annual records were kept of nest usage by fish, and plant species present on the perimeter and floor of each nest.

Data analysis

Pattern analysis of transect data used variance-spacing diagrams constructed by a random-pairing method (Goodall, 1974). Patch size was taken to be the average spacing (based on 8 independent analyses) of the first variance peak larger than the variance of a random independent pattern (Carpenter and Chaney, 1983).

To compare data on fish-nest area with measurements of patch length obtained from pattern analyses, it was necessary to determine the mean length of randomly-placed straight lines through the nests. This was accomplished for 75 fish nests by constructing an ellipse with the same axes as each nest, randomly choosing 2 points on the perimeter of the ellipse, and calculating the distance between the points. Distances obtained for 100 independent point pairs were averaged for each nest analyzed.

To test the comparability of linear and areal data, simulated vegetation maps were constructed by randomly placing elliptical patches in a contrasting background. Patches had normally distributed axis lengths based on the estimated mean and standard deviation of actual fish nest axes. Line intercept samples of the maps were analyzed by the random pairing method. Eight independent random pairing analyses were computed for samples of 3 independent maps.

RESULTS

Submersed vegetation

The submersed vegetation of Roach lake included 9 vascular plant species and 2 moss species (Table I). This list excludes 2 floating-leaved species that occur in sheltered bays, *Nuphar advena* (Ait) Ait f. and *Sparganium fluctuans* (Morong) Robinson.

Vascular plants fall into 2 distinct categories, based on the mode of propagation. Diaspore-propagated species lack horizontal stems. New individuals are produced from seeds or spores. The 5 diaspore-propagated species included an annual angiosperm (*Elatine minima* (Nutt.) Fisch. & Meyer), a perennial fern ally (*Isoestes braunii* Dur.), and 3 perennial angiosperms (Table I). Rhizomatous species spread principally via horizontal stems. In 6 summers of sampling Roach lake (1979—1984), no flowers or seeds have been found on any submersed rhizomatous plants. A few emergent, fertile *Juncus pelocarpus* have been found growing on the lake's shores.

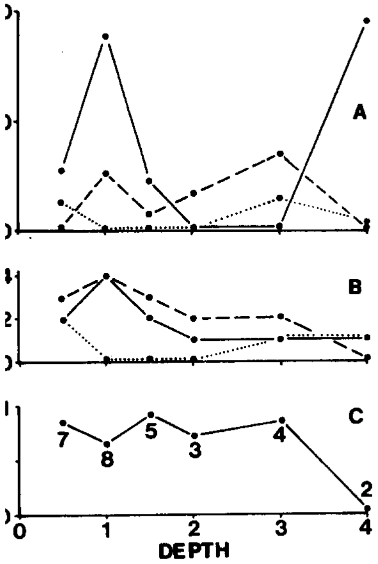
Diaspore-propagated species were most numerous between 1 and 3 m depth (Fig. 2A). Greatest richness of diaspore-propagated species occurred

TABLE I

Submersed flora of Roach lake, with mean frequency (%) in a sample of six 200-intercept lines at Site A (0.5-, 1.0-, 1.5-, 2.0-, 3.0- and 4.0-m depth)

Species	Frequency
Diaspore-propagated vascular plants	
Elatine minima (Nut.) Fish. & Meyer	9.0
Eriocaulon septangulare With.	1.1
Isöetes braunii Dur.	6.3
Lobelia dortmanna L.	2.8
Pontederia cordata L. f. *taenia* Fassett	0.7
Rhizomatous vascular plants	
Eleocharis acicularis (L.) R. and S.	1.4
Gratiola lutea Rafin. f. *pusilla* (Fassett) Pennell	0.7
Juncus pelocarpus Mye f. *submersus* Fassett	1.9
Myriophyllum tenellum Bigel.	30.3
Bryophytes	
Drepanocladus exannulatus (BSG) Warnst.	4.8
Sphagnum platyphyllum (Lindb.) Warnst.	0.3

n (Fig. 2B). Rhizomatous species had distinct frequency peaks at 1 and Fig. 2A). All 4 rhizomatous species occurred at 1 m, but only *Myrio-ım tenellum* occurred at 4 m (Fig. 2B). The maximum depth reached . *tenellum* was ca. 4.5 m, and mosses predominated at greater depth. num depth reached by mosses was 7 m. Equitability (J') of all species ɔughly constant between 0.5 and 3.0 m depth, but dropped sharply in ›arly monospecific vegetation at 4 m (Fig. 2C).



Depth distribution of vegetation at Site A, based on 200 5-cm intercepts at each (A) Frequency of rhizomatous species (solid line), diaspore-propagated species line), and bryophytes (dotted line) vs. depth. (B) Number of species vs. depth. in Panel A. (C) Equitability (J'; Pielou, 1975) vs. depth. Numbers indicate species ; at each depth.

ests

ı nests occurred between 0.9 and 2.4 m depth (Fig. 3A). Mean depth 62 m (n = 75, s = 0.40). Nest area ranged from 0.07 to 0.55 m^2 (Fig. [ean nest area was 0.246 m^2 (n = 75, s = 0.103). Nest depth and area weak positive correlation ($r = 0.252, p = 0.030$) because bass tended to arger nests in deeper water than the pumpkinseed sunfish. Mean nest ɣ was 1.88 nests m^{-1} shoreline ($n = 40, s = 1.76$). The high variance:mean 1.65) reflected the aggregations of nests around submerged objects ; fallen trees. On an areal basis, mean nest density was 0.0652 nests/m^2 the 3-m depth contour (n = 40, s.e. = 0.0116). Within the depth range ch nests actually occurred (0.9—2.4 m), mean nest density was 0.140 n^2.

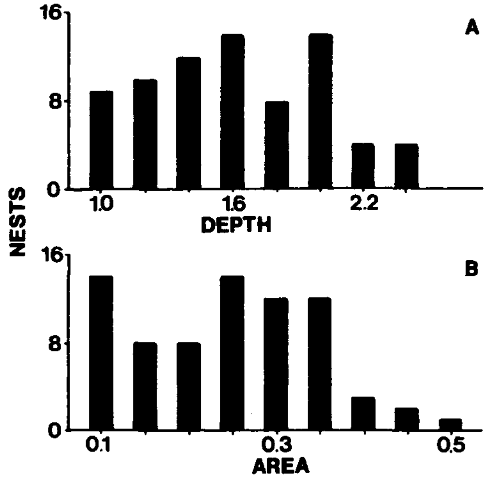


Fig. 3. (A) Numbers of nests in 0.2-m depth classes (n = 75). (B) Numbers of nests in 0.05-m^2 classes of nest area (n = 75).

Colonization of nests

Fish abandoned nests during June. Within 4—8 weeks, the level floors of the nests were colonized commonly by diaspore-propagated species (Table II). Rhizomatous species encroached down the sloping sides of the nests, but only rarely reached the floors of the nests during the first season of abandonment.

TABLE II

Mean frequency (%) per nest at Site B. Data are presented for nests used by fish in June, then sampled in July or August, at Site B

	Frequency	
	18 August 1982	25 July 1983
Diaspore-propagated species		
Elatine minima	38.2	82.1
Eriocaulon septangulare	0	3.6
Isoetes braunii	26.5	28.6
Lobelia dortmanna	8.8	7.2
Pontederia cordata f. *taenia*	8.8	14.3
Rhizomatous species		
Eleocharis acicularis	11.8	0
All species	44.1	85.7
Number of nests sampled	34	28

If a nest was not used by a fish the following June, it was occupied by both diaspore-propagated and rhizomatous species within 14 months after abandonment. Artificial nests protected with rims had frequencies of diaspore-producing species similar to control plots after 14 months (Fig. 4). However, very few rhizomatous plants grew over or under the rims into these artificial nests. In contrast, artificial nests without rims were very similar to control plots with respect to both diaspore-propagated and rhizomatous plant frequencies after 14 months.

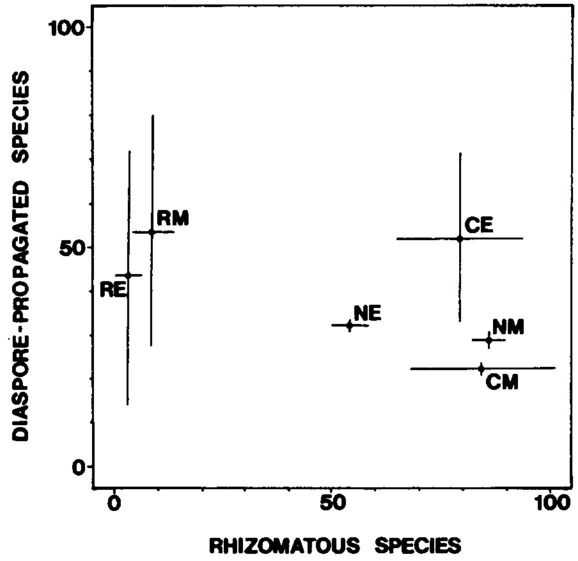


Fig. 4. Mean frequency of diaspore-propagated species vs. mean frequency of rhizomatous species in the artificial fish nests after 14 months. Each point is the mean of frequencies for 3 plots. Each plot's frequencies are based on 74—122 quadrats. Vertical and horizontal bars show ± s.e. First letters denote treatment type (C = control, N = non-rimmed, R = rimmed) and second letters denote area (E = *Eleocharis—Juncus*, M = *Myriophyllum*).

Vegetation pattern

Random pairing pattern analyses of diaspore-propagated species showed mean patch sizes ranging from 0.25 to 1.10 m (Fig. 5A). Seven of the 8 transects analyzed had mean patch sizes between 0.25 and 0.55 m.

The mean lengths of randomly-placed lines across 75 fish nests were strikingly similar to the patch sizes detected for diaspore-producing species (Fig. 5B). Random pairing analyses of transects through simulated vegetation maps confirm the accuracy of this procedure for detecting patches associated with fish nests (Fig. 5A). Mean patch lengths detected by random pairing clustered closely around the grand mean length of randomly placed lines across all fish nests (0.33 m).

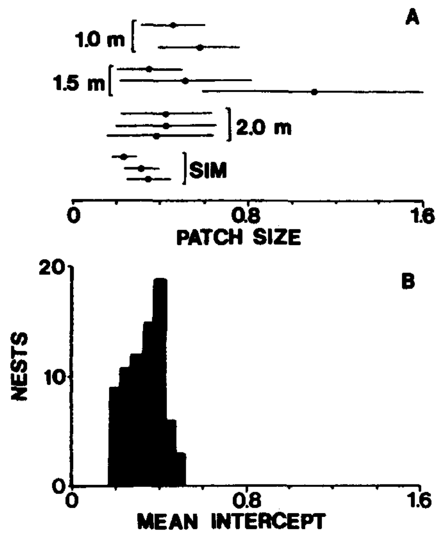


Fig. 5. (A) Mean patch size (m) ± s.e. ($n = 8$) of diaspore-propagated species at 3 depths and of simulated vegetation as determined by random-pairing analysis. (B) Histogram of number of nests versus mean length (m) of 100 randomly-placed straight lines through each nest. Based on 75 nests.

Fish nest dynamics

The number of active fish nests in the 100-m^2 permanent quadrat ranged from 33 to 40 (Table III). Each spring, 75% of the previous year's nests were re-occupied by fish. Each year, 8 abandoned nests were occupied by plants. One or 2 nests were filled by silt or terrestrial leaf litter each year. New nest formation was the most variable aspect of fish nest dynamics, with 13 new nests formed in June 1982 and 3 new nests formed in June 1983.

TABLE III

Dynamics of marked fish nests in 100-m^2 permanent quadrat at Site B, 1981—1983

Year	Annual gain or loss of nests				Nest number
	New nests	Lost nests		Persistent nests	
		Occupied by plants	Silt- or detritus-filled		
1981	13	8	1	27	36
1982	3	8	2	30	40
1983					33

DISCUSSION

Elatine minima and *Isoetes braunii* are the most important colonizers of fish nests in Roach lake. *E. minima*, a prolific self-pollinated annual (Fassett, 1939), is common on sandy sediments in water less than 3-m deep (Wilson, 1935; Swindale and Curtis, 1957), but further details of its ecology are not known. *Isoetes* species have been characterized as colonizers restricted to open habitats with few neighboring plants (Pearsall, 1920; Seddon, 1965; Sand-Jensen, 1978). Sand-Jensen (1978) showed that *Isoetes lacustris* L. had lower photosynthetic capability than its stoloniferous competitor *Littorella uniflora* (L.) Aschers. and pointed out that the ability of *L. uniflora* to occupy space totally, preempted colonization by *I. lacustris*.

Our results show that fish denude nest areas of vegetation in May or June. Nests are abandoned by fish in June and colonized during July and August by a mixture of *Elatine minima*, *Isoetes braunii*, and other plants. The following May or June, about 75% of the previous year's nests are reoccupied by fish and again denuded of vegetation. Some new nests are formed. By July to August of the year following abandonment, nests not reoccupied by fish are further colonized by rhizomatous plants that grow in from the nest edges. Patches of diaspore-propagated species intermingled with rhizomatous species could potentially persist many years in these abandoned nests, since most of these species are perennials.

Spatial heterogeneity in submersed vegetation is commonly attributed to variations in depth and exposure (Spence, 1982). We have demonstrated heterogeneity independent of depth and exposure, by sampling transects at constant depth with uniform exposure.

Both ice-push (Raup, 1975) and wave action (Spence, 1982) are sources of disturbance which can produce patchiness at scales shorter than a few meters in aquatic plant communities. Ice-push may cause the decreasing frequency of macrophytes from 1.0 to 0.5 m (Fig. 2), but cannot be a factor in water deeper than the maximum thickness of 0.8—1.0 m in Roach lake.

In small lakes such as Roach lake, significant wave action is limited to shallow depths. Under the prevailing west-to-northwest winds, Site A is exposed to heavier wave action than the other shores of the lake. We estimated wave-mixed depths for Site A using the forecasting equations recommended by Spence (1982) and described in detail by Smith (1979). The maximum wave-mixed depth of 1.9 m occurred when wind speed exceeded 50 km h^{-1}. At typical wind velocities of 10—20 km h^{-1}, the wave-mixed depth is only 0.4—0.7 m. The low frequency of macrophytes at 0.5 m (Fig. 2) may be due to waves. However, the gradient of decreasing diversity from 1—4 m is too deep to be affected significantly by waves.

The pattern of vegetation in Roach lake between 1- and 2-m depth is strongly influenced by fish nests. Patch sizes of diaspore-propagated species are similar to sizes of fish nests (Fig. 5). Analogous correspondence between patch sizes of colonizing tree species and sizes of canopy gaps have been reported in temperate and tropical forests (Richards and Williamson, 1975; Williamson, 1975).

Disturbance caused by nesting fish maintains high frequencies of diaspore-propagated macrophytes in the 0.9—2.4-m depth zone in Roach lake. This effect of fish nests on pattern and diversity is analogous to the long-recognized effects of canopy gaps in forests (Cooper, 1913; Watt, 1925). More recently, the list of disturbances that enhance spatial heterogeneity and diversity has expanded to include aquatic examples such as tubes of polychaete worms in soft marine sediments (Woodin, 1978), wave damage in the rocky intertidal zone (Paine and Levin, 1981), and flood damage in riparian moss communities (Kimmerer and Allen, 1982).

We have demonstrated a dynamic patch structure in submersed vegetation that occurs on relatively short scales in space (0.2—0.8 m) and time (1 to 2 growing seasons). In contrast, most studies of macrophyte zonation assume that community composition is homogeneous over very broad spatial scales (tens to hundreds of meters horizontally, and one metre or more in depth), and constant for many growing seasons (Spence, 1982). One can easily think of disturbances that create openings in macrophyte vegetation on even smaller scales than fish nests (e.g., excavation by benthic invertebrates or foraging ducks). Further experimentation is needed to determine conditions for establishment of diaspore-propagated species, rates of competitive exclusion in the absence of disturbance, and the relative importance of physiological limitation and competition in determining the lower depth limits of macrophytes. A comprehensive explanation of submersed macrophyte zonation must consider effects of disturbance on a variety of scales, in addition to the commonly-studied factors such as light, temperature, and substrate.

ACKNOWLEDGEMENTS

We are grateful to Dr. R.P. McIntosh and Dr. J.S. Denslow for their comments on a draft of this paper. Field work was aided by A. Bergquist, F. Brown, J. Chaney, M. Jaynes, and Mr. and Mrs. O.J. Stewart. Dr. R.E. Andrus kindly identified the bryophytes. The work was supported by the Faculty Research Fund of the University of Notre Dame.

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