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IMPLICATIONS FOR FAUNAL HABITAT RELATED TO ALTERED MACROPHYTE STRUCTURE IN REGULATED LAKES IN NORTHERN MINNESOTA

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Abstract: Water-level regulation has altered the plant species composition and thus the structure of nearshore aquatic macrophyte communities in two regulated lakes in northern Minnesota as compared with a nearby unregulated lake. Results of previous faunal studies in the regulated lakes were used as a basis for assessing the effects of vegetation changes on faunal communities. The unregulated lake with mean annual water-level fluctuations of 1.6 m supported structurally diverse plant communities and varied faunal habitat at all depths studied. Mean annual fluctuations on one regulated lake were reduced to 1.1 m, and dense beds of four erect aquatic macrophytes dominated the 1.75-m depth that was never dewatered. We suggest that this lack of plant diversity and structural complexity resulted in diminished habitat for invertebrates, reduced availability of invertebrates as food for waterbirds and fish, reduced winter food supplies for muskrats, and reduced feeding efficiency for adult northern pike, yellow perch, and muskellunge. Mean annual fluctuations in the other regulated lake were increased to 2.7 m, and rosette and mat-forming species dominated the 1.25-m depth that was affected by winter drawdowns. We suggest that the lack of larger canopy plants resulted in poor habitat for invertebrates, reduced availability of invertebrates as food for waterbirds and fish, and poor nursery and adult feeding habitat for many species of fish. In addition, the timing and extent of winter drawdowns reduced access to macrophytes as food for muskrats and as spawning habitat for northern pike and yellow perch. In regulated lakes throughout the world, indirect effects on aquatic fauna resulting from alteration of wetland and aquatic macrophyte communities should be considered when water-level management plans are developed.

Key Words: Aquatic macrophytes, structural diversity, faunal habitat, water-level regulation, reservoirs.

INTRODUCTION

Wetland and aquatic macrophytes provide structural habitat for aquatic fauna in freshwater lakes, and they also affect other aspects of the environment in which the fauna live. Macrophytes are colonized by epiphytes, which provide food for invertebrate grazers. Invertebrates also find refuge from predation and sites for oviposition in macrophyte areas. Dead macrophytes and their associated bacteria are a food source for detritivores. Living macrophytes are a direct food source for aquatic herbivores, including invertebrates, fish, waterfowl, and muskrat, and they also provide shelter for many of these organisms (Carpenter and Lodge 1986). Different macrophyte communities provide habitats with different structure, cover, and food for aquatic fauna, with much of the difference in quality dependent on species diversity, density, and structural aspects of the plants (Engel 1985). The relations between macrophyte community structure and the various individual components of the faunal community are well documented (e.g., Bellrose 1950, Weller and Spatcher 1965, Crowder and Cooper 1982, Brown et al. 1988). However, the relations among altered hydrology, altered plant communities, resultant altered faunal habitat, and the differences in observed fauna have generally not been explored.

Wilcox and Meeker (1991) investigated the effects of two water-level regulation schemes on littoral mac-

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rophyte communities in two large lakes (Rainy and Namakan) in Voyageurs National Park, Minnesota by making comparisons with an unregulated lake (Lac La Croix). Changes in both species composition and structure of the macrophyte communities resulted from alteration of water-level regimes in the regulated lakes. The effects of water-level regulation on faunal communities in the regulated lakes were studied independently by others; however, these studies of invertebrates (Kraft 1988), aquatic birds (Reiser 1988), muskrats (Thurber et al. 1991), and fish (Kallemeyn 1987a, 1987b) did not interpret differences in faunal communities between lakes on the basis of differences in habitat provided by macrophytes.

In this paper, we assess the data from the macrophyte study to explore differences in the physical structure of the plant communities at different depths in the lakes and interpret how the structural changes might influence the faunal habitat provided. We review the literature on use of macrophyte habitat by different faunal groups to reinterpret the results of the faunal studies with respect to our findings on habitat differences.

STUDY AREA

Voyageurs National Park is situated on the United States-Canada border in the State of Minnesota (Figure 1). Water levels in a chain of large lakes on the Rainy River are regulated by several dams. The largest of the lakes is Rainy Lake, which has a total surface area of 89,357 ha, of which about 14,600 ha are in the park. Namakan Reservoir is upriver from Rainy Lake and consists of Namakan, Kabetogama, Sand Point, Crane, and Little Vermilion lakes. Namakan, Kabetogama, and Sand Point lakes are at least partially within the park and have a within-park surface area of 18,410 ha.

Lac La Croix, in Boundary Waters Canoe Area, is a natural lake upriver from Rainy Lake and the lakes of Namakan Reservoir and is similar to those lakes in most aspects except that its water levels are not regulated. The mean annual fluctuation of water levels in Lac La Croix is about 1.6 m (Figure 2). Lake levels peak in late May or early June and then decline gradually until spring runoff begins during the following April.

Water levels in Rainy Lake and Namakan Reservoir have been regulated by the International Joint Commission since 1970 in accordance with a water management program that sets acceptable high and low limits (termed "rule curves") for water levels throughout the year (Figure 2). Modeling has shown that the mean annual fluctuations of water levels under natural conditions would be 1.9 m for Rainy Lake and 1.8 m for Namakan Lake, but regulation results in mean annual fluctuations of 1.1 m and 2.7 m, respectively (Flug 1986). The rule curves can allow annual fluctuations as low as 0.6 m on Rainy Lake and as high as 3.0 m on Namakan Reservoir. Under the management plan, the lakes are regulated to reach peak levels in late June or early July, rather than immediately following spring runoff as much as a month earlier. Levels are then held stable throughout the summer and allowed to decline gradually through autumn and winter, as opposed to a gradual decline that would begin naturally immediately after the peak.

The annual water-level regime is more variable in Lac La Croix than in the regulated lakes because regulation reduces variability in Rainy Lake and Namakan Reservoir. Although Rainy and Namakan lakes deviate from the guidelines as much as 19% of the time, the annual variation is more extreme at Lac La Croix, ranging from 0.3 m to 3.0 m. Water quality and clarity are similar in the three study lakes (Kepner and Stottlemyer 1988, Minnesota Department of Natural Resources, unpublished data).

For the macrophyte study, two sites each were selected at Rainy Lake, Namakan Lake, and Lac La Croix. Details on site selections are given in Wilcox and Meeker (1991). At Rainy Lake, the sites selected were just east of Dove Bay (R1) and at Alder Creek (R2); at Namakan Lake, they were at Sheen Point (N1) and Deep Slu (N2); at Lac La Croix, they were at the east (L1) and west (L2) sides of Lady Boot Bay (Figure 1). Some of these sites were among those used for the faunal studies: Kraft (1988) studied invertebrates at Sheen Point in Namakan Lake; Reiser (1988) studied aquatic birds at Deep Slu in Namakan Lake; Thurber et al. (1991) studied muskrats at Alder Creek in Rainy Lake; and Kallemeyn (1987a, 1987b) studied fish at stations near Dove Bay in Rainy Lake and near Sheen Point and Deep Slu in Namakan Lake.

ANALYSIS OF MACROPHYTE COMMUNITIES

Vegetation was sampled along four transects at each study site in 1987 (see Figure 2), as described in Wilcox and Meeker (1991). The transects were established nearly parallel to the shoreline at altitudes (described as depth from mean high water) that represented specific habitat types in the non-regulated control lake, Lac La Croix. By also sampling at these altitudes on the regulated lakes, the effects of altered hydrologic regimes on plant communities could be assessed. The four transects at each site were at depths of 0.0, 0.5, 1.25, and 1.75 m. Twenty 1 × 1 m sampling quadrats were randomly located on each of the four transects at each of the six sites. At each quadrat, species identifications and percent cover estimations were made. Importance Values were calculated for each taxon as the sum of relative frequency and relative mean cover

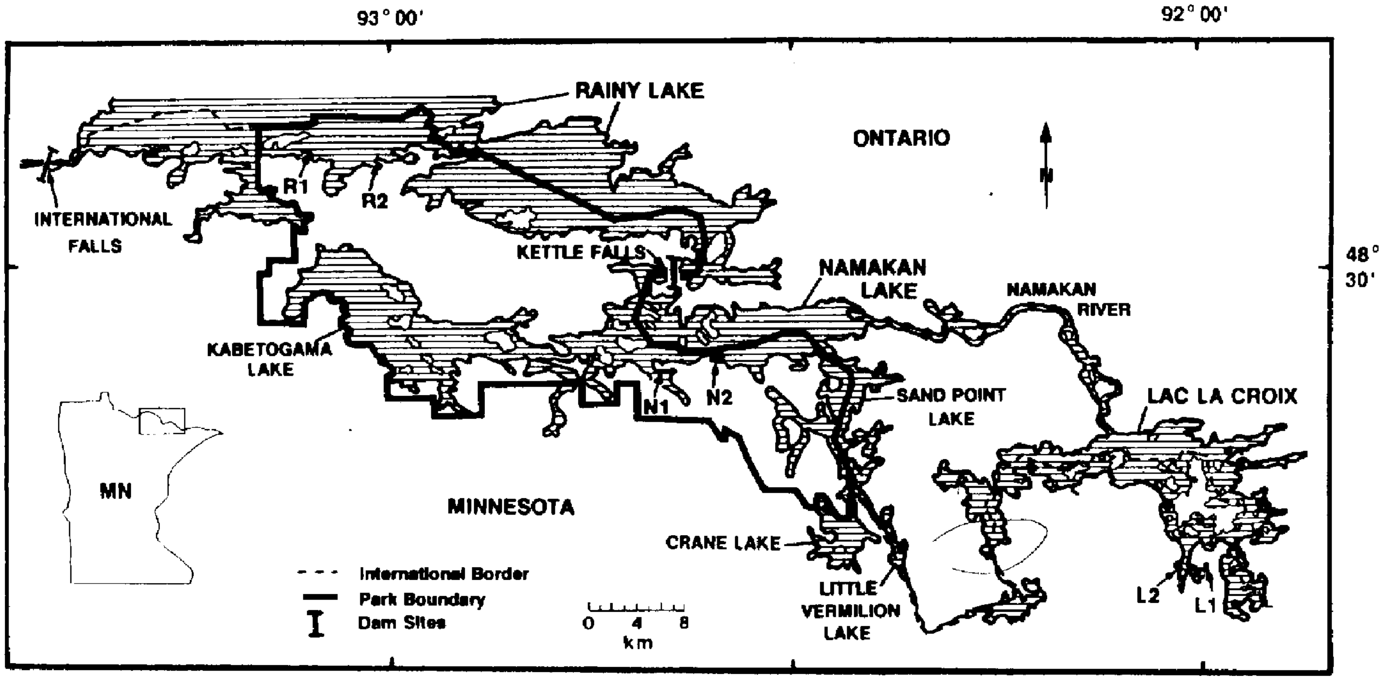

Figure 1. Map of study area in northern Minnesota, showing boundary of Voyageurs National Park, the major lakes, dam sites, and study sites (Wilcox and Meeker 1991).

on each transect. Plant names conform to the nomenclature of Voss (1972, 1985) whenever possible; taxa not included in those references are named according to Gleason and Cronquist (1963).

To assess the faunal habitat characteristics provided by the vegetation at each depth sampled in each lake, we separated the 30 most important taxa (total Importance Value) found in the study into six groups according to general plant structural characteristics (as might be viewed by aquatic fauna). These groups were erect terrestrials, thin-stem emergents, mat formers, low rosettes, low growth aquatics, and erect aquatics. The Importance Values of the selected species were totalled by transect for each lake. The erect terrestrial species were subsequently excluded from further discussion because they were similar among lakes and do not generally provide aquatic habitat. For similar reasons, the shoreline transects were also excluded. A schematic model of the habitat provided by macrophytes was generated using different plant shapes to represent the taxa in each structural group. One shape each was used for mat formers, low rosettes, and low growth aquatics. For thin-stem emergents, one shape represented 2 species of *Carex*, another shape represented 2 species of *Eleocharis*, and one each was used for *Glyceria borealis* and *Polygonum lapathifolium*. For erect aquatics, one shape represented *Bidens beckii* and *Myriophyllum*, another shape represented 3 species of *Potamogeton*, another shape represented *Sparganium fluctuans* and *Vallisneria americana*, and another represented *Nymphaea odorata*. The various shapes were plotted for each depth in each lake in proportion to the totals of mean Importance Value.

INFLUENCE OF MACROPHYTE STRUCTURE AND COMPOSITION ON FAUNA

Structure of Aquatic Vegetation

The shallow waters (0.5 m) of Lac La Croix supported a structurally diverse plant community. Plant cover at the lake bottom was provided by mat formers and low rosettes (Table 1, Figure 3). Cover was extended higher into the water column by low-growth aquatics. Thin-stem emergents and erect aquatics provided cover through all or nearly all of the water column; the erect aquatics had more underwater surface area and cover than the thin-stem emergents (which also provided cover for wildlife above the water surface). In deeper waters in Lac La Croix, only low-growth and erect aquatics were present; however, a diverse assemblage of these species created a patchy environment with leaf surfaces for colonization and cover at all depths, plus areas of open water.

Plant structure in the shallow waters of Rainy Lake differed from that in Lac La Croix in 1987 (Table 1, Figure 3). No low-growth or erect aquatics were present because the transect was dewatered during that unusually dry season (Wilcox and Meeker 1991). Thin-stem emergents, primarily *Polygonum lapathifolium*, replaced the aquatic species. At depths of 1.25 m, erect aquatics were present in numbers similar to Lac La

Croix, but the lake bottom contained fewer low-growth aquatics. Instead, there were numerous low rosettes and some mat formers. These structure types offer less surface area and cover than do low-growth aquatics. At depths of 1.75 m, only erect aquatics were found in Rainy Lake. The patchiness, interspersed open-water areas, and dense cover at the lake bottom found in Lac La Croix were missing.

Plant structure in the shallow waters (0.5 m) of Namakan Lake also differed from that in Lac La Croix in 1987 (Table 1, Figure 3). Very few low-growth or erect aquatics were present, and thin-stem emergents were dominant in this low-water year. At depths of 1.25 m, low-growth and erect aquatics were also scarce, and virtually no cover was present in the upper portion of the water column. Mat formers and low rosettes were dominant, and these structure types presented less surface area for colonization than the low-growth aquatics of Lac La Croix. At depths of 1.75 m, Namakan Lake more closely resembled Lac La Croix; however, it was less structurally complex, and the mat formers and low rosettes favored by drawdowns were also present.

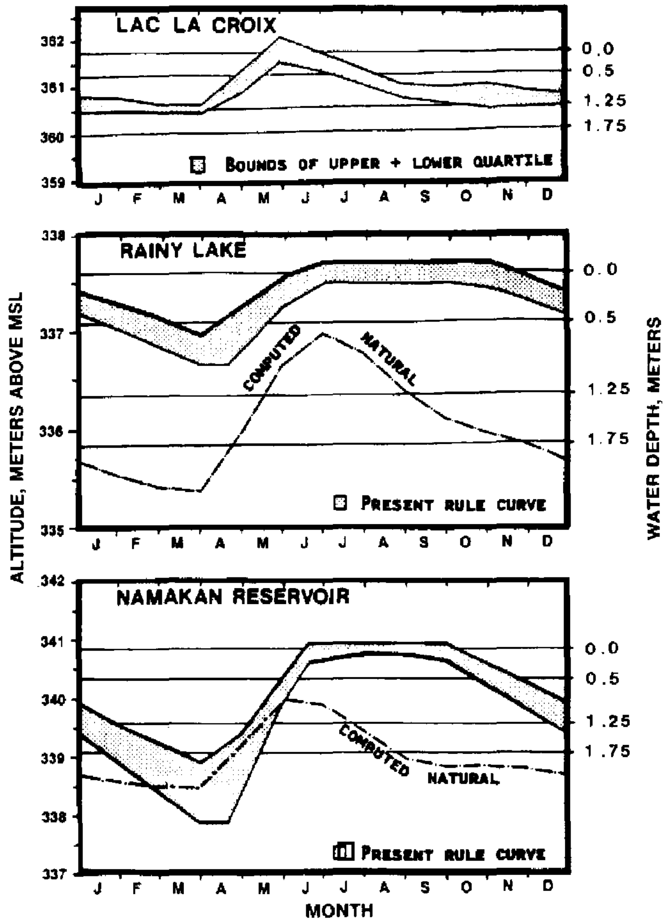

Figure 2. Water-level regimes for Lac La Croix, Rainy Lake, and Namakan Reservoir, showing bounds of variation, computed natural water levels, and water depths of 0.0, 0.5, 1.25, and 1.75 m for the study transects (adapted from Flug 1986 and Wilcox and Meeker 1991).

Influence of Vegetation on Aquatic Fauna

Invertebrates. Kraft (1988) compared the macroinvertebrates of Rainy Lake and three lakes in Namakan Reservoir at 1-, 2-, 3-, 4-, and 5-m depths to assess the effects of winter drawdown. In general, he observed that invertebrate species richness at the 1- and 2-m depths was greatest in Rainy Lake. At the 3-, 4-, and 5-m depths not affected by drawdown, species richness was greater in Namakan Reservoir. In Rainy Lake, diversity was greatest at 1 m and decreased with depth; in Namakan Reservoir, the greatest diversity occurred at 3 m or deeper. Kraft attributed these differences to excessive winter drawdowns in Namakan Reservoir that caused stranding of organisms. The differences in habitat provided by macrophytes at various depths were not considered, but we believe that they may also be a factor.

Associations between invertebrate taxa and the structure of aquatic macrophytes have been studied extensively. Some invertebrates show definite preferences for certain macrophyte taxa (Rosine 1955, Krull 1970, Gerrish and Bristow 1979, Dvorak and Best 1982, Cyr and Downing 1988a, 1988b), and invertebrate use of macrophytes varies with the seasons (Rosine 1955, Rooke 1986, Brown et al. 1988). Plants with dissected leaves may support more invertebrates than those with broad leaves (Krecker 1939, Andrews and Hasler 1943, Gerking 1957, Gerrish and Bristow 1979), although this observation is disputed (Brown et al. 1988, Cyr and Downing 1988a). Invertebrate numbers may be maximized when beds of submersed plants are interspersed with emergent vegetation (Voigts 1976). Alternatively, vegetated areas with little shading from macrophyte litter and resultant increased substrate temperatures may have more invertebrates (Murkin et al. 1982).

Perhaps the best explanation for the relation between invertebrates and macrophytes in our study comes from the work by Brown et al. (1988). In their study of Lake St. Clair, both species richness and density of invertebrates increased as the taxonomic diversity of the macrophyte community increased. They concluded that invertebrate abundance and diversity were not related to surface area *per se* but to vertically structured heterogeneity of surface area within the water column resulting from understory and overstory macrophytes. The occurrence of both low-growth and upright (erect) growth forms produced the best habitat.

Based on the criteria of Brown et al. (1988), invertebrate habitat in our study would be maximized along

Table 1. Mean Importance Values (IV)[1] of the most prominent plant taxa at depths of 0.5, 1.25, and 1.75 m sampled in Lac La Croix, Rainy Lake, and Namakan Lake. Taxa are separated into morphologically similar groups.

Lake:	La Croix			Rainy			Namakan		
Water depth (m):	0.5	1.25	1.75	0.5	1.25	1.75	0.5	1.25	1.75
Thin-stem emergents									
Carex lacustris Willd.	—	—	—	0.2	—	—	3.3	—	—
Carex rostrata Stokes	—	—	—	0.4	—	—	13.5	—	—
Eleocharis obtusa (Willd.) Schultes	—	—	—	8.6	—	—	—	—	—
Eleocharis smallii Britton	7.8	—	—	0.7	2.9	—	1.4	—	—
Glyceria borealis (Nash) Batch.	13.3	—	—	1.5	—	—	9.3	7.9	—
Polygonum lapathifolium L.	—	—	—	24.6	—	—	15.9	5.4	—
Total	21.1	0.0	0.0	36.0	2.9	0.0	43.4	13.3	0.0
Mat-formers									
Elatine minima (Nutt.) Fischer & C. Meyer	4.2	—	—	—	—	—	6.9	3.5	4.4
Eleocharis acicularis (L.) R. & S.	21.2	—	—	5.5	7.2	—	6.5	21.6	7.1
Ranunculus reptans L.	—	—	—	3.4	—	—	20.2	21.3	0.9
Total	25.4	0.0	0.0	8.9	7.2	0.0	33.6	46.4	12.4
Low rosettes									
Isoetes echinospora Durieu	1.2	—	—	—	18.8	—	4.2	5.1	7.2
Sagittaria spp.	5.6	—	—	0.2	9.5	—	0.3	5.6	0.5
Tillaea aquatica L.	—	—	—	0.8	—	—	9.0	12.1	5.9
Total	6.8	0.0	0.0	1.0	28.3	0.0	13.5	22.8	13.6
Low-growth aquatics									
Chara spp.	—	6.0	8.1	—	—	—	—	2.3	28.5
Najas flexilis (Willd.) Rostk. & Schmidt	5.5	21.6	14.9	—	4.0	—	0.8	2.1	5.0
Nitella spp.	—	2.2	7.8	—	—	—	—	—	—
Potamogeton robbinsii Oakes	—	0.5	9.7	—	4.3	—	—	—	—
Potamogeton spirilis Tuckerman	4.4	3.5	2.5	—	—	—	—	1.0	1.4
Total	9.9	33.8	43.0	0.0	8.3	0.0	0.8	5.4	34.9
Erect aquatics									
Bidens beckii Torr.	3.1	11.9	0.6	—	0.4	—	—	—	—
Myriophyllum spp.	1.3	16.6	14.0	—	0.7	—	—	—	1.7
Nymphaea odorata Aiton	5.7	14.5	6.6	—	—	—	—	2.7	2.9
Potamogeton amplifolius Tuckerman	—	—	13.0	—	—	—	—	—	—
Potamogeton foliosus Raf.	—	0.5	3.9	—	4.6	2.3	—	—	4.5
Potamogeton richardsonii (Benn.) Rydb.	0.3	3.9	2.9	—	4.0	15.9	0.5	0.5	10.6
Sparganium fluctuans (Morong) Robinson	5.7	—	—	—	14.0	—	—	0.3	—
Vallisneria americana Michaux	—	5.1	11.1	—	25.4	78.6	—	5.2	9.5
Total	16.1	52.5	52.1	0.0	49.1	96.8	0.5	8.7	29.2
Grand total	79.3	86.3	95.1	45.9	95.8	96.8	91.8	96.6	90.1

[1] Derived from sum of relative frequency and relative mean cover.

all transects of Lac La Croix. In Rainy Lake, invertebrate habitat at depths of 1.75 m would be considered poor because only erect macrophytes are present. In Namakan Lake, invertebrate habitat at the 1.25-m depth would be poor because there are few erect macrophytes extending through the water column. The remaining transects in Rainy and Namakan lakes have more vertical structural diversity, but they are less diverse floristically than their counterparts in Lac La Croix and would not offer equivalent habitat if the relation found between faunal diversity and density and plant taxonomic diversity (Brown et al. 1988) is true.

Assessments of individual taxa help to illustrate the potential effects of altered macrophyte structure on invertebrates. Kraft (1988) identified a number of invertebrate taxa as being affected by water-level regulation and stranding in Voyageurs National Park. Three of these taxa (*Caenis*, *Asellus*, gastropods) have affinities for aquatic vegetation; we believe that they may

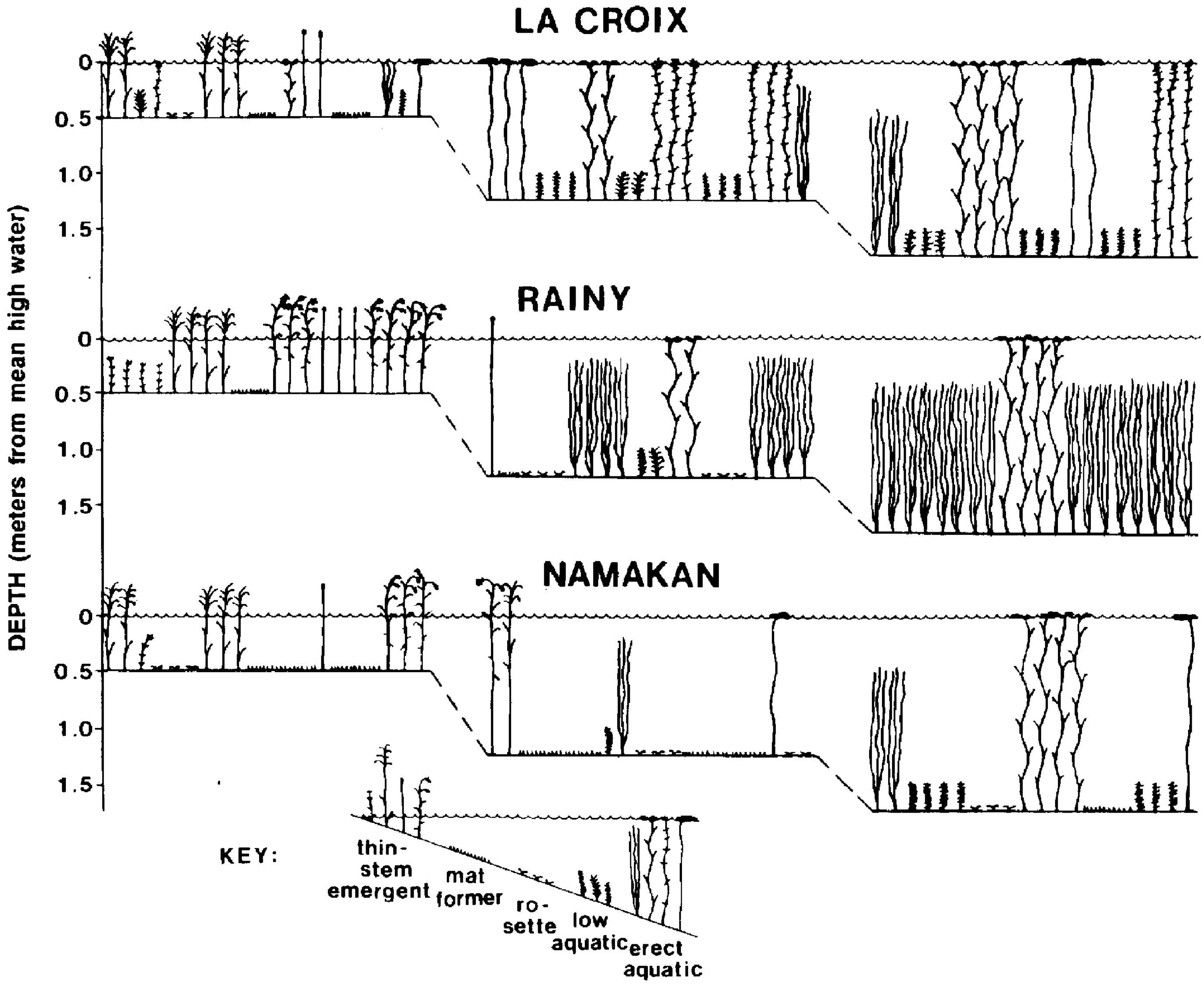

Figure 3. Schematic model showing cross-sections of the littoral zone of study sites in Lac La Croix, Rainy Lake, and Namakan Lake. The general structural groups of the 30 most important taxa are depicted at the water depths sampled along contours of 0.5, 1.25, and 1.75 m.

be responding to vegetation changes as well as to winter exposure.

The nymph of the mayfly *Caenis* often is found among aquatic vegetation (McCafferty 1981); typical habitat is quiet water at the edge of lakes overgrown with vegetation (Edmunds et al. 1976). Most nymphs (80%) collected by Kraft (1988) in Rainy Lake were from the 1-m depth. In Namakan Reservoir, only 53% of the nymphs were from this depth, where plant cover is sparse (see 1.25-m depth in Figure 3); the remaining 47% were found in deeper waters, where more erect and low-growth aquatic plants occur.

The isopod *Asellus* seldom comes into open water but remains hidden under rocks, vegetation, and debris; it is rarely found in water more than a meter deep (Pennak 1978). Voigts (1976) found *Asellus* to be most common in the emergent zone of Iowa marshes where there was floating dead vegetation. In Rainy Lake, 99% of the *Asellus* collected were from the 1-m depth (Kraft 1988). No *Asellus* were collected in Namakan Reservoir, in which winter drawdown extends far below the 1-m depth and the vegetation at 1 m is sparse (Figure 3). Again, vegetation changes may have affected the ability of this invertebrate to survive.

Gastropods are grazers, and most occur in shallow water (less than 3-m deep), where food is usually available. Some taxa, such as *Physa, Gyraulus,* and the Hydrobiidae, are found in greatest abundance in areas with moderate amounts of aquatic vegetation (Voigts 1976, Pennak 1978). In Rainy Lake, Kraft (1988) found that 82% of the gastropods collected were from the 1-m depth. Only 26% of the gastropods collected in

Namakan Reservoir were from this depth where vegetation was sparse (see Figure 3); 63% were collected at the 2-m depth, which had more dense vegetation. Since the winter drawdown zone includes the 2-m depth contour, drawdown and stranding may not be the cause of redistributed gastropod populations. Instead, alterations in the structure of the plant community and the habitat that it provides may have caused the changes described.

Aquatic Birds. Reiser (1988) encountered 14 species of birds that used the portions of Rainy Lake and Namakan Reservoir affected by water-level fluctuations. Most of these species have affinities for wetland and aquatic vegetation. Reiser attributed decreased reproductive rates of red-necked grebe (*Podiceps grisegena* Boddaert) and common loon (*Gavia immer* Brunnich) to flooding of nests when water levels were increased in June of each year. However, she also recognized that other species may be affected by depauperate nesting sites resulting from alterations in plant communities caused by water-level regulation.

Many species of birds are associated with wetland and aquatic macrophyte communities, and some display definite associations with particular vegetational stages. Johnsgard (1956) attributed these associations to the presence of suitable nest substrate, protective cover, food availability, territorial requirements, or combinations of these factors. He found that environmental changes caused by fluctuating water levels resulted in a redistribution of bird populations throughout a system of wetlands in east-central Washington that was affected by dam construction. Bird species remained a part of the biotic community only as long as the successional stage of the vegetation was within the tolerance limits of the species (Johnsgard 1956). The physical structure of the vegetation, rather than its taxonomic composition, is of greatest importance to nesting birds (Weller 1978). The vegetation stage commonly recognized as ideal for many bird species is the hemi-marsh, a 1:1 ratio of emergent vegetation and open water (Weller and Spatcher 1965). However, Prince (1985) found fewer species nesting in areas with poorly developed submersed vegetation and concluded that the value of the submersed community is underrated. Only the nearshore areas of Lac La Croix, Rainy Lake, and Namakan Lake would provide the combination of emergent and submersed vegetation deemed ideal for nesting and cover (Figure 3). However, many of the emergents depicted in Figure 3, especially for Rainy Lake, were annuals that emerged as a result of unusually low water levels in 1987. Thus, if natural water-level fluctuations were restored, a gradual drawdown of water levels in Rainy and Namakan lakes during the summer might encourage the growth of emergent vegetation over a wider area in normal years.

Aquatic vegetation (as foliage, shoots, tubers, and seeds) constitutes a portion of the diet of many birds (Weller 1981). However, invertebrates often represent a greater part of the diet, especially during the breeding period. For instance, Murkin et al. (1982) concluded that although blue-winged teal (*Anas discors* L.) and mallards (*Anas platyrhynchos* L.) preferred hemi-marsh habitat, their densities were dependent on invertebrate abundance. Thus, a loss of invertebrate numbers and diversity at depths of 1.75 m on Rainy Lake and 1.25 m on Namakan Lake because of the lack of structurally diverse vegetation could result in decreased food availability for some bird species.

Muskrats. Thurber et al. (1991) found the effects of water-level regulation on muskrats (*Ondatra zibethicus* L.) in Voyageurs National Park to be greatest under the increased fluctuations of the Namakan Reservoir management program; population density was about half that in Rainy Lake. Muskrat lodges were built during stable water periods in late summer or early autumn and then stranded by winter dewatering, likely resulting in increased vulnerability to predation (Bellrose and Low 1943, Thurber et al. 1991). Macrophytes that are used as food also would become inaccessible following these winter drawdowns.

When ice forms on Lac La Croix, water levels have already receded about 1 m from the springtime high; they remain fairly stable during the winter. Despite the thickness of the ice, muskrats would have access to the plants occurring at depths of 1.25 and 1.75 m during most of the winter. Potential foods include *Potamogeton, Myriophyllum, Nymphaea odorata,* and *Vallisneria americana.* These are not preferred muskrat foods but are acceptable to the opportunistic muskrat (Errington 1941, Stearns and Goodwin 1941, Takos 1947, Bellrose 1950).

In Rainy Lake, muskrat lodges would probably be built in water deep enough to provide access to food such as *Carex, Eleocharis, Glyceria borealis,* and *Polygonum lapathifolium* at depths of 0.5 m for part of the winter, but access would be lost by February. Plants at 1.25 and 1.75 m, such as *Potamogeton, Sagittaria, Myriophyllum, Sparganium fluctuans,* and *Vallisneria americana,* should be accessible all winter; however, some foods available at Lac La Croix (e.g., *Nymphaea odorata*) do not grow at these depths in Rainy Lake.

In the Namakan reservoir lakes, where the problem of lodge dewatering is the greatest and overwinter survival of muskrats is low (Thurber et al. 1991), even the vegetation at depths of 1.25 and 1.75 m is not available for much of the winter. If natural water-level fluctuations were restored, access to foods such as *Potamogeton, Sagittaria, Myriophyllum, Nymphaea odorata,* and *Vallisneria americana* would be increased during the winter. In addition, more emergent vegetation used as food by muskrats would likely grow in the littoral zone if a water regime that included summertime drawdowns was restored. A greater interspersion of emergent and open aquatic habitat also may reduce the intensity of mink (*Mustela vison* Schreber) predation on muskrats (Proulx et al. 1987).

Fish. Kallemeyn (1987a, 1987b) studied year-class strength of northern pike (*Esox lucius* L.) and yellow perch (*Perca flavescens* Mitchill) in Rainy Lake and Namakan Reservoir. These species have well-documented associations with aquatic macrophyte communities (Scott and Crossman 1973, Lee et al. 1980, Becker 1983). Kallemeyn found that the reproductive success of both species was greater in years with higher lake levels in the spring and concluded that the higher lake levels provided access to increased areas of flooded vegetation that could serve as spawning substrate. While this spawning activity is perhaps the most important interaction between fish, water levels, and vegetation at Voyageurs National Park, there are other fish species and other values, such as feeding and nursery habitat, that are worthy of further consideration.

Forty-eight species of fish have been found in the lakes of Voyageurs National Park (L. Kallemeyn, pers. comm.). At least 12 of the species found in the regulated lakes are known to use wetland or aquatic macrophyte communities during one or more life history stages (Scott and Crossman 1973, Lee et al. 1980, Becker 1983, Dawson and Hellenthal 1986, Janacek 1988). These species include muskellunge (*Esox masquinongy* Mitchill), northern pike, golden shiner (*Notemigonus crysoleucas* Mitchill), blacknose shiner (*Notropis heterolepsis* Eigenmann and Eigenmann), black bullhead (*Ictalurus melas* Raf.), tadpole madtom (*Noturus gyrinus* Mitchill), rock bass (*Ambloplites rupestris* Raf.), pumpkinseed (*Lepomis gibbosus* L.), bluegill (*Lepomis macrochirus* Raf.), largemouth bass (*Micropterus salmoides* Lacepede), black crappie (*Pomoxis nigromaculatus* Lesueur), and yellow perch. The taxonomic diversity and structural complexity of the vegetation play major roles in determining the habitat values of the plant communities to these fish.

Habitat Uses. Species richness and abundance of aquatic macrophytes have been shown to influence fish community structure (Poe et al. 1986). Intermediate levels of structural complexity may be the best habitat both in terms of foraging and growth of the predator and stability of the fish-invertebrate prey interaction (Crowder and Cooper 1979, 1982). As indicated in the section on invertebrates, prey diversity and the availability of specific preferred food organisms for foraging by fish also may be affected by differences in the structural complexity of the macrophyte community. An important aspect of the piscivore fish-prey interaction is visibility. Vegetation in the water column can produce visual barriers and alter the behavior of both predator and prey (Savino and Stein 1982, 1989a, 1989b, Savino 1985). Floating plants (as in leaves of water lilies) produce shade that can also affect visibility (Helfman 1979). The structure and density of vegetation may produce physical barriers that restrict movements of large fish and thus provide juvenile fish with refuge from predators (Engel 1987, 1988).

Macrophyte communities in coastal wetlands serve as spawning and nursery areas and support high densities and diversities of young fish (Holland and Huston 1984, Chubb and Liston 1986). The suitability of vegetated areas for spawning is determined by timing in relation to water depth and temperature and by the physical nature of the vegetation. Northern pike prefer to spawn on mats of grasses and sedges that remain from the previous growing season (Franklin and Smith 1963, McCarraher and Thomas 1972); yellow perch prefer to use areas of submersed vegetation for spawning (Krieger et al. 1983). However, if water levels are too low when spawning temperatures are reached, the preferred substrate may be out of the water and unavailable. These adverse conditions were characterized for Namakan Reservoir by Kallemeyn (1987a, 1987b). Others have also shown the relation between successful spawning and water levels for northern pike (Johnson 1957, Franklin and Smith 1963, Hassler 1970) and yellow perch (Nelson and Walburg 1977, Martin et al. 1981). Similar arguments might be made for other species present in Lac La Croix (Crossman 1976, D. Friedl, pers. comm.) and Rainy and Namakan lakes.

Habitat Loss. To assess the losses in fish habitat related to altered macrophyte communities, we developed a table showing predicted fish use of macrophytes at each depth in each lake (Table 2), based on reviews of the literature described in the previous section. The plant communities along all transects in Lac La Croix are structurally diverse and of intermediate density. Plant materials suitable as spawning substrate are available to the applicable fish species at the proper depth when the water reaches critical temperatures. Similarly, suitable nursery and adult feeding habitats are available for all species. The habitat provided at 0.5 m differs somewhat from that in deeper water, while habitats at 1.25- and 1.75-m depths are similar (Figure 3).

The predicted fish use at depths of 0.5 and 1.25 m in Rainy Lake does not differ from that in Lac La Croix, except that three additional species (muskellunge, black bullhead, largemouth bass) are present (Table 2). The 1.75-m depth does not differ from Lac La Croix in spawning or nursery habitat, but macrophyte cover extending throughout the water column could limit

Table 2. Predicted fish use of macrophytes as spawning, nursery, and adult feeding habitat at depths of 0.5, 1.25, and 1.75 m in Lac La Croix, Rainy Lake, and Namakan Reservoir (refer to Figure 3).

Lake	Activity	0.5-m Depth	1.25-m Depth	1.75-m Depth
Lac La Croix	Spawning	northern pike black crappie yellow perch	golden shiner yellow perch	golden shiner yellow perch
	Nursery	northern pike rock bass pumpkinseed black crappie yellow perch	northern pike golden shiner rock bass pumpkinseed black crappie yellow perch	northern pike golden shiner rock bass pumpkinseed black crappie yellow perch
	Adult feeding	golden shiner blacknose shiner rock bass	northern pike golden shiner blacknose shiner tadpole madtom rock bass pumpkinseed black crappie yellow perch	northern pike golden shiner blacknose shiner tadpole madtom rock bass pumpkinseed black crappie yellow perch
Rainy Lake	Spawning	muskellunge[1,2] northern pike black bullhead[1] largemouth bass[1] black crappie yellow perch	golden shiner black bullhead[1] largemouth bass[1] yellow perch	golden shiner yellow perch
	Nursery	northern pike black bullhead[1] rock bass pumpkinseed largemouth bass[1] black crappie yellow perch	muskellunge[1,2] northern pike golden shiner black bullhead[1] rock bass pumpkinseed largemouth bass[1] black crappie yellow perch	muskellunge[1,2] northern pike golden shiner rock bass pumpkinseed largemouth bass[1] black crappie yellow perch
	Adult feeding	golden shiner blacknose shiner black bullhead[1] rock bass	muskellunge[1,2] northern pike golden shiner blacknose shiner black bullhead[1] tadpole madtom rock bass pumpkinseed largemouth bass[1] black crappie yellow perch	golden shiner blacknose shiner tadpole madtom rock bass pumpkinseed black crappie
Namakan Reservoir	Spawning	black bullhead[1,3] black crappie	golden shiner largemouth bass[1,4] black crappie	golden shiner largemouth bass[1,4] yellow perch
	Nursery	northern pike black bullhead[1,3] rock bass pumpkinseed bluegill[1,4,5] largemouth bass[1,4]		northern pike golden shiner black bullhead[1,3] rock bass pumpkinseed bluegill[1,4,5]

Table 2. Continued.

Lake	Activity	0.5-m Depth	1.25-m Depth	1.75-m Depth
		black crappie		largemouth bass[1,4]
		yellow perch		black crappie
				yellow perch
	Adult feeding	golden shiner	golden shiner	northern pike
		blacknose shiner	blacknose shiner	golden shiner
		black bullhead[1,3]	rock bass	blacknose shiner
		rock bass	pumpkinseed	black bullhead[1,3]
			bluegill[1,4,5]	tadpole madtom
			largemouth bass[1,4]	rock bass
			black crappie	pumpkinseed
			yellow perch	bluegill[1,4,5]
				largemouth bass[1,4]
				black crappie
				yellow perch

[1] Does not occur in Lac La Croix.
[2] Does not occur in Namakan Reservoir.
[3] Occurs only in Kabetogama Lake of Namakan Reservoir.
[4] Occurs only in Sand Point Lake of Namakan Reservoir.
[5] Does not occur in Rainy Lake.

efficient use of this area for feeding by adult northern pike, yellow perch, and muskellunge.

The predicted fish use of the 0.5-m depth in Namakan Reservoir for nursery and adult feeding habitat and of the 1.75-m depth for all habitat purposes is the same as that in Lac La Croix, except that three additional species (black bullhead, bluegill, largemouth bass) are present. Unlike Lac La Croix, northern pike and yellow perch cannot use vegetation at depths of 0.5 m in Namakan Reservoir for spawning because it has not yet been flooded when spawning occurs. Shoreline vegetation has thus far been omitted from this discussion because the vegetation does not differ much among lakes (Wilcox and Meeker 1991). Although shoreline vegetation is often out of the water, it can flood during high water years and provide spawning habitat for northern pike and yellow perch in Lac La Croix. In Namakan Reservoir, the shoreline vegetation would be accessible for spawning only in extremely high water years because water levels are regulated to peak later in the summer.

Muskellunge were once stocked in Kabetogama Lake of Namakan Reservoir, but they failed to become established (D. Friedl, pers. comm.). There are many possible explanations for the failure of this stocking effort, but lack of access to nearshore vegetation for spawning because of low springtime water levels is one probable reason. Low water levels in the spring also prevent yellow perch from spawning on vegetation at the 1.25-m depth in Namakan Reservoir. The sparse nature of this vegetation also precludes its use as nursery habitat by any species because protective cover is lacking. Adult tadpole madtoms would avoid this area for feeding because cover is lacking, and adult northern pike would not be successful in ambushing prey there because they would be highly visible.

Regulation of water levels on Rainy Lake and Namakan Reservoir does affect fish habitat. However, the adverse effects in Rainy Lake are in deeper waters and can be compensated for by habitat available in shallower water. Those species that require the use of wetland or aquatic macrophyte communities during one or more life history stages can find suitable habitat. In Namakan Reservoir, conditions are more limiting. The deeper waters do provide some structurally diverse habitat to compensate for the poor habitat present at intermediate depths. However, those fish species that spawn in nearshore vegetated areas in the spring are severely limited by the current regulation scheme that delays water-level peaks and does not allow access to the nearshore or shoreline vegetation during the spawning season.

CONCLUSIONS

Wilcox and Meeker (1991) showed that water-level regulation in Rainy and Namakan lakes altered the composition and structure of aquatic macrophyte communities in those lakes. In this analysis, we have synthesized those findings with the results of other studies and suggested that alterations of aquatic plant communities resulted in altered habitat values for various fauna. Habitat was altered both through changes in the structural complexity of the plant beds and through lost availability of preferred plant species. Invertebrates may be affected adversely by the loss of structural complexity at certain depths in Rainy and Namakan lakes. In particular, gastropods, the mayfly *Caenis,* and the isopod *Asellus* all seem to be severely affected in Namakan Lake. Birds have less hemi-marsh habitat available in the regulated lakes, and decreased invertebrate populations may translate to a decreased food supply for many of them. Muskrats may lack adequate food supplies under the ice following winter drawdown in Namakan Lake and suffer excess mortality due to starvation and predation by mink. Macrophytes extend vertically throughout the water column along the deepest contour studied in Rainy Lake and could limit feeding by adult northern pike, yellow perch, and muskellunge. In Namakan Lake, northern pike and yellow perch may not have access to plant beds for spawning because of low water levels in the spring. Fish use of the 1.25-m depth in Namakan Lake for nursery and adult feeding habitat also may be limited because almost no protective cover is available.

If the National Park Service is to manage for natural faunal communities in Rainy and Namakan lakes, our findings suggest that natural macrophyte communities must be restored to provide the required habitat. Such restoration requires that water levels be regulated to approximate the amplitude and timing of natural systems such as Lac La Croix.

These findings are of importance for ecologically sound management of regulated lakes throughout the world. Water-level management plans for existing regulated lakes and environmental assessments associated with construction of new reservoirs generally consider the effects of fluctuations on riparian, hydropower, recreation, and other interests, including direct effects on aquatic fauna. However, indirect effects on aquatic fauna may also result from alteration of wetland and aquatic plant communities. These effects should be considered when water-level management plans are developed.

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