

RAPID ESTABLISHMENT OF FISH IN ISOLATED PEATLAND BEAVER PONDS

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Abstract: Previous research has demonstrated that beavers (*Castor canadensis*) dramatically alter fish habitat in streams by their dam-building activities. Although less well-known, beavers also flood closed peatlands by damming seepage rather than streamflow. Our study focuses on the establishment of fish communities in isolated beaver ponds created in small, ombrogenous peatlands lacking any open water prior to beaver occupation. We selected 16 ponds that ranged in age from 4 to 42 years and three unaltered peatlands to determine whether beaver promote the use of peatlands by fish and if the patterns of individual species were related to macrophyte density. Fish were present in ponds as young as four years old, and five of the six species of fish were present in ponds ≤ 16 years old. Submersed macrophyte abundance explained 40% of the variation in fish diversity. Rapid colonization of fish in beaver-altered peatlands provides further evidence of how beavers increase the complexity of biological food webs in boreal regions. Moreover, this work provides an even greater understanding of the historical role of beavers as ecosystem engineers in peatland dominated landscapes.

Key Words: beaver ponds, colonization, fish dispersal, fish diversity, macrophytes, Minnesota, peatlands, succession

INTRODUCTION

Beaver (*Castor Canadensis*, Kuhl) ponds are associated with streams (Snodgrass 1997, Schlosser and Kallemeyn 2000) or peatlands (Rebertus 1986, Ray et al. 2001) that are embedded in terrestrial landscapes. Ponds rapidly undergo colonization by aquatic organisms, including macroinvertebrates (McDowell and Naiman 1986), macrophytes (Snodgrass 1997, Ray et al. 2001), and fish (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). The persistence of beaver ponds over several decades facilitates the establishment of biological communities by providing a mosaic of habitats differing in age, size, isolation, and years since abandonment (Schlosser and Kallemeyn 2000, Ray et al. 2001, Wright et al. 2002).

Schlosser (1995) demonstrated that beaver ponds functioned as production or source habitats for fish and as reproductive sinks for the associated stream when examined at the watershed scale. Given the magnitude of beaver activities in many streams, additional studies

have been conducted that emphasized the keystone role of beaver ponds in structuring fish assemblages (see Schlosser 1995, Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). Snodgrass and Meffe (1998) reported that the greater the duration of dam maintenance and pond existence, the greater the likelihood that a lentic-type trophic structure will develop. High plant and macroinvertebrate production in beaver ponds also will directly influence the consumer community. However, little, if anything, has been reported that demonstrates whether beaver activity in peatlands creates patches that are colonized by fish communities. Beaver modifications in peatlands may be locally or regionally extensive (Rebertus 1986, Torretti 2002), potentially representing a significant source of fish habitat. For example, Rebertus (1986) found that 21% of nearly 500 peatlands he studied in north central Minnesota, USA had been impounded by beavers. Similarly, Torretti (2002) reported that beavers impounded $> 2\%$ of the surface area of the largest peatlands in northern Michigan. In both cases, beavers cre-

ated open water patches in parts of the peatland unassociated with stream habitat.

Beavers alter closed peatlands by dredging canals and damming seepage outlets (Rebertus 1986, Mitchell and Niering 1993). When beavers dam the seepage outlets, the water level is raised and anchored mat vegetation is reduced entirely or floating islands emerge and become surrounded by open water. Over time, open water habitats are colonized by aquatic vegetation, and this community undergoes changes that are punctuated by changes in the dominant life form (e.g., submersed to floating-leaved macrophytes; Ray et al. 2001).

Impounded peatlands are isolated patches, similar to kettle lakes, and thus, colonization by immigrating biota and assembly rules for communities should be very different than in streams. Current spatial theory on fish community assembly suggests that regional geomorphology, as it relates to habitat connectivity, strongly influences fish dispersal and can be used to predict the likelihood of fish establishment in north temperate lakes (Tonn et al. 1990, Schlosser and Kallemeyn 2000), isolated wetlands in the prairie pothole region (Peterka 1989), and Atlantic Coastal Plain (Snodgrass et al. 1996), but this theory has not been tested for isolated beaver ponds.

This study complements macrophyte studies (Ray et al. 2001) conducted on the same ponds, providing a unique opportunity for studying the potential interrelationships between the development of the two distinct biological communities (fish and aquatic plants) and the processes that are unique or linked to community assembly. Specifically, our objectives were to determine if beavers create fish habitat in peatlands and whether fish assemblage patterns are associated with characteristics of the macrophyte community. To describe fish assemblages, we documented composition, richness, and diversity of fish species in beaver ponds ranging in age from 4 to 42 years. These ponds represented different stages of vegetation development (Ray et al. 2001) and potentially various stages of fish community assembly.

METHODS

Study Site

We sampled 16 beaver ponds in a 100-km² area centered in a terminal moraine near Backus in Cass County, Minnesota, USA (46° 50' N, 94° 34' W). Over 700 small lakes and peatlands, most less than a few hectares in size, are scattered in depressions and kettle holes in the moraine. The upland forest is a mixed deciduous-conifer type, dominated by aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera*

Marsh.), balsam fir (*Abies balsamea* L.), and pines (*Pinus resinosa* Soland., *P. strobes* L., and *P. banksiana* Lamb.). The beaver ponds we sampled ranged from 4 to 42 years in age and 0.36 to 8.75 ha in area, but 11 were less than 2 ha. Prior to beaver colonization, none of these peatlands had measurable expanses of open water or were associated with streams. The average depth of beaver ponds ranged from 101.7 to 195.0 cm, and the average pH and specific conductance ranged from 5.96 to 7.28 and 40 to 82.5 μ S/cm, respectively. Most lakes in the study area are 3–5 m deep (maximum 16 m) and support permanent fish communities (Minnesota County Biological Survey 1998).

In addition to the 16 beaver impoundments, we sampled the lagg zones (a moat-like band of water along the periphery of a peatland) of three "reference peatlands" to determine whether these zones potentially support fish prior to beaver-pond formation. These peatlands were sampled in June after spring thaw, so the lags were at or near their maximum width and depth. Two of the peatlands had lags that ranged from 1 to 3.6 m in width and 12 to 32 cm in depth and were unaltered by beaver. The third peatland had recently been enlarged by beaver but was included as a "reference peatland" because additional unaltered peatlands were unavailable. The third peatland had lagg widths of 4.5–15 m and an average depth of 54 cm.

Pond Dating

The ages of beaver ponds were determined from interviews with local trappers, previous research in the study area by one of us (AJR), aerial photographs, and tree-ring analysis. Rebertus (1982, 1986) censused all or parts of the study area from 1976 to 81, in 1984, and in 1987. Aerial photographs (mostly 1:20,000) provided intermittent coverage of all or part of the study area during the following years: 1939, 1949, 1960, 1966, 1969, 1977, 1979, 1980, 1984, 1986, 1990, 1992, 1994, and 1996. The gaps between years of coverage were used to date some ponds within one or two years, or to provide approximate dates that were later refined using tree-ring analysis. The approach for dating ponds using tree-ring analysis was described in detail in Ray et al. (2001). In brief, increment cores from live and dead standing trees located in or near a pond's margin were examined for an abrupt change in tree ring width that could be used as evidence of a response to elevated water levels, drowning of nearby competitors, or death. Multiple cores were used to find consistent dates, and increment cores were later cross-dated with live unaffected trees of the same species. Ponds dated by this technique were usually accurate within one or two years.

Fish Sampling

Sampling was conducted over a 5-week period beginning June 20, 1998. Fish were collected using 40 × 20-cm Gee's minnow traps with 2.5-cm opening on both circular ends; traps were baited with salted crackers. Three traps were randomly placed in habitats containing submersed and floating-leaved vegetation, but free of a floating mat, for a period of 24 hours. Therefore, 24 hours of sampling represented a total trap time of 72 hours per pond. After 24 hours, traps were checked for fish, and trapped fish were counted, identified, and then returned to the water. We are aware of the inherent biases caused by baiting (Layman and Smith 2001); however, this method has been used successfully in similar studies (He and Lodge 1990, Hanson and Riggs 1995, Snodgrass *et al.* 1996, Langston and Kent 1997, Schlosser and Kallemeyn 2000) aimed at documenting the composition of fish communities in wetlands. Because certain fish species are less likely to enter traps already occupied by another species (He and Lodge 1990), baited traps may increase the likelihood of capturing more species per sampling period that may not otherwise enter unbaited traps. Although other methods may have been more effective, minnow traps were chosen because of the abundance of submersed woody debris and floating peatland mats in the beaver ponds. So, while our species lists may not be comprehensive, they are sufficient for demonstrating fish colonization, documentation of fish species, and an estimate of community richness in these beaver ponds. Voucher specimens were preserved, and taxonomic identification was verified at the Michigan Department of Natural Resources Marquette Fish Hatchery, Marquette, Michigan, USA.

Vegetative Sampling and Physical Measurements

We sampled submersed vegetation using a rake method described by Deppe and Lathrop (1993). Abundance of submersed aquatics was recorded using a 0 to 5 scale (0=0%, + = <1%, 1=1 to 20%, 2=21 to 40%, 3=41 to 60%, 4=61 to 80%, and 5=81 to 100%) based on the coverage of vegetation recovered compared to size of rake head (Deppe and Lathrop 1993, Ray *et al.* 2001). Cover of floating-leaved vegetation was visually estimated in floating quadrats (size ranging from 1.0 × 0.35 m for Lemnaceae to 2.0 × 2.0 m for *Nymphaea* and *Nuphar*) and recorded using the same scale as described for submersed macrophytes. Ponds were sampled systematically in a grid-like pattern, with 20–25 points/ha in smaller ponds (<2 ha) and 10–15 points/ha for larger ponds. We also compiled a more comprehensive species list through a

timed survey of the whole basin (see Ray *et al.* 2001 for details).

Water depths, specific conductance, pH, and secchi depth were taken at multiple locations in each pond and averaged for each impoundment. The "degree of isolation" was defined as the number of lakes or neighboring beaver ponds >0.2 ha that occurred within a designated buffer around our target pond. We calculated this index for buffers of 0.25, 0.50, and 0.75 km.

Data Analyses

Fish richness represents the total number of species identified in each pond from individuals caught in traps, whereas macrophyte richness represents the total number of species identified during a timed comprehensive search of each pond. Simpson's Index (SI) was calculated for each fish assemblage using raw trap data—specifically, the number of each species captured per pond. A Fishers' exact test was used to determine if the presence of beaver in peatlands was positively associated with the presence of fish. To complete the test, we examined a 2 × 2 contingency table including the data for all ponds with cells based on fish presence or absence on one margin and beaver presence or absence on the other margin. We were particularly interested in how fish diversity and richness varied with biological and physical variables, so Pearson correlations were used to examine these relationships. Since multiple comparisons were explored, probabilities were corrected using the Bonferroni correction method (Sokal and Rohlf 1995). Linear and non-linear regression relationships (e.g., fish diversity and macrophyte abundance) were examined using Sigma Plot (version 6.00, SPSS 2000).

RESULTS

No fish were captured in the lagg zones of the three reference peatlands. These reference sites were either unaltered by beaver or within the early stages of alteration (i.e., current years activity). Beyond these three reference ponds, 16 ponds that had undergone extensive alteration were used to characterize fish communities. Ponds sampled ranged in age from 4 to 42 years, with 9 of the 16 ponds surveyed falling between 14 and 27 years of age; the median pond age was 26 years. None of the three control peatlands had fish, while 15 of the 16 (94%) beaver-colonized ponds had fish, and the Fishers' exact test indicated that the presence of beaver in peatlands was positively associated with the presence of fish ($p=0.004$).

Six species of fish were captured in the 16 beaver ponds sampled from June to August 1998 (Table 1).

Table 1. List of fish species identified in study impoundments with their abbreviations in parentheses. The age of the pond where each fish species first appeared is also listed.

Scientific Name, Common Name (Acronym)	Pond Age at First Appear- ance
<i>Lepomis gibbosus</i> (Linnaeus), pumpkinseed (PS)	31
<i>Culaea inconstans</i> (Kirtland), brook stickleback (BS)	16
<i>Phoxinus eos</i> (Cope), northern redbelly dace (NRD)	16
<i>Phoxinus neogaeus</i> (Cope), finescale dace (FD)	14
<i>Pimephales promelas</i> (Rafinesque), fathead minnow (FM)	16
<i>Umbra limi</i> (Kirtland), central mudminnow (CM)	4

The central mudminnow was the most common species, occurring in 13 of 16 ponds. Finescale dace was present in 63% of ponds, and brook stickleback occurred in 50% of the ponds sampled (Table 2). The central mudminnow was the only fish species captured in the youngest pond (age 4; Tables 1 and 2). With the exception of pumpkinseeds, all other fish species were present in ponds of intermediate age (14–16 years old). Pumpkinseed were found only in one of the oldest ponds; traps collected in this pond contained only pumpkinseed. This pond was the largest (8.75 ha) and deepest (mean 1.90 m) in the study and also had a greater coverage of floating-leaved macrophytes than any other pond in the study (Table 2).

Submersed macrophyte abundance ranged from just under 9% rake coverage in a 5-year-old pond to approximately 65% coverage in a 26-year-old pond ($40.4 \pm 3.9\%$; mean ± 1 S.E.). The average coverage of floating-leaved macrophytes was $23.1 \pm 5.2\%$ (mean ± 1 S.E.) and varied from $< 1\%$ coverage to 73% (Table 2).

No relationships were found between fish community metrics and physical characteristics of ponds. However, using linear regression, submersed macrophyte abundance explained much of the variation in fish diversity, estimated by Simpson's Index, ($r^2=0.48$, 0.004, Figure 1) and following the equation:

$$\text{Fish diversity (SI)} = 0.0115 \times + -0.0973$$

Although a preliminary linear regression model failed a Kolmogorov-Smirnov normality test and one point was predicted to be an outlier, a plot of the residuals also revealed a linear relationship and further amplified the presence of the outlier. Therefore, the outlier was removed for the final analysis (SPSS 2000). This equation implies that fish diversity is a function of submersed macrophyte abundance.

DISCUSSION

Our work clearly demonstrates that beaver excavation and flooding activities assisted in making peatlands inhabitable by fish. This occurs directly, by deepening the free water column and creating open water, and/or indirectly, by facilitating the establishment of aquatic macrophytes, invertebrates, and algal communities. The species of fish collected from the isolated beaver ponds in this investigation are all described as common to quiescent bog lakes or beaver ponds and streams (Scott and Crossman 1973, Phillips et al. 1991) and have been reported in lotic ponds in other regions of Minnesota (Schlosser 1995, Schlosser and Kallemeyn 2000). What is not known is whether these fish species are directly linked to patches created by beavers as has been supported for other aquatic organisms occupying beaver-modified habitats (Wright et al. 2002). If so, these patches may represent refuges for smaller fish species that also occur in peatland lakes but, in contrast to lakes, lack larger predatory fish.

Magnuson et al. (1998) suggested that the processes responsible for colonization and establishment of fish in isolated north temperate lakes are operating on time scales of centuries to millennia. In our study area, however, some fish species readily colonized isolated beaver ponds. Beaver ponds as young as four years of age contained fish and two of the richest ponds examined were < 20 years old. Our data suggest that the abundance of submersed macrophytes was the most important biological predictor for the diversity of fish assemblages in beaver ponds. Even though the relationship was significant, only a limited number of ponds were sampled, and consequently, additional sampling will be necessary to verify this conclusion. The first fish species to colonize beaver ponds, the central mudminnow, appeared in a 4-year-old pond contemporaneous with the first macrophytes (Lemnaceae, *Utricularia* spp.; Ray et al. 2001), and five species of fish and more than a dozen species of macrophytes were present in ponds < 20 years old. Extensive submersed macrophyte beds may also assist in the maintenance of multi-species fish assemblages by creating structurally complex habitats (Crowder and Cooper 1979). Macrophytes also provide cover for fish and support a rich and abundant prey base (Peterka 1989). Several of the fish species inhabiting these ponds have adhesive eggs (Scott and Crossman 1973, Phillips et al 1991), suggesting the possibility that fish eggs and macrophytes may be co-transported into beaver ponds (Langston and Kent 1997). Likely vectors may include animals that feed on aquatic plants and regularly move between ponds, such as beavers (Northcott 1972),

Table 2. List of ponds detailing the physiochemical and biological attributes of each. The number of neighboring ponds is denoted by (D25, D50, and D75) and refers to the total number of neighboring ponds within 0.25, 0.5, and 0.75-km radii of each pond. The fish species are listed by the following acronyms (BS = brook stickleback, CM = central mudminnow, FD = finescale dace, FM = fathead minnow, NRD = northern redbelly dace, and PS = pumpkinseed).

Pond No.	Pond Age (yrs)	Fish Richness			Fish Diver-sity (SI)		Subm Cover (%)	Flt/ld Cover (%)	D25	D50	D75	Pond Area (ha)	Average Pond Depth (cm)	pH	Sp cond (μ S/cm)	Average Fish Rich/trap	Fish Species
		Pond Richness	Fish Richness	Fish Richness	Fish Richness												
1393102B	26	3	0.43	64.1	12.5	4	9	16	0.92	101.7	6.53	50	2	CM, NRD, BS			
1393103A	27	2	0.36	39.9	47.5	6	11	23	5.55	132.3	6.63	82.5	0.5	CM, BS			
1393112A	41	1	0	52.2	20.4	2	3	7	0.62	102.8	6.38	33.3	1	CM			
1393112C	42	2	0.38	33.4	3.8	1	4	8	0.57	140.7	6.19	43.3	1	CM, NRD			
1393114A	20	1	0	29.2	4.1	1	3	9	0.53	129	7.28	53.3	1	CM			
1393116A	32	5	0.56	36.2	40.6	4	8	12	4.34	108.8	5.96	40	3.5	CM, NRD, BS, FD, FM			
1393116C	25	1	0	19.1	48.2	2	4	10	0.6	103.5	6.24	60	0.3	FD			
1393116F	14	2	0.46	62.3	6.8	2	5	9	2.25	118.4	6.4	50	1.3	CM, FD			
1393123A	31	3	0.14	31	72.9	1	3	10	8.75	195	6.15	50	2.7	PS, NRD, FD			
1393124A	18	5	0.73	53.8	7.1	2	5	10	0.77	109.4	6.97	55	4.3	CM, NRD, BS, FD, FM			
1393125A	16	5	0.69	49.6	0.5	0	2	5	0.36	121.7	6.68	80	3	CM, NRD, BS, FD, FM			
1393126A	26	2	0.5	32.3	25.2	1	4	11	3.49	104.1	7.29	133.3	1.3	CM, BS			
1393126B	17	3	0.51	59.2	22.9	2	4	9	1.63	142.6	6.24	43.3	1.7	CM, BS, FD			
1393129A	31	4	0.61	41.1	27.6	3	6	12	1.41	119	6.64	43.3	2.8	CM, NRD, BS, FD			
1393129C	4	1	0	33.9	1.6	4	7	10	1.18	90.5	6.33	43.3	0.3	CM			
1403135A	5	0	0	8.7	28.1	1	3	7	1.33	88.2	7.62	163.3	0	None			
Lagg 1	N/A	0	0	N/A	N/A	N/A	N/A	N/A	N/A	31.7	N/A	N/A	N/A	N/A	None		
Lagg 2	N/A	0	0	N/A	N/A	N/A	N/A	N/A	N/A	12.3	N/A	N/A	N/A	N/A	None		
Lagg 3	N/A	0	0	N/A	N/A	N/A	N/A	N/A	N/A	54.3	N/A	N/A	N/A	N/A	None		

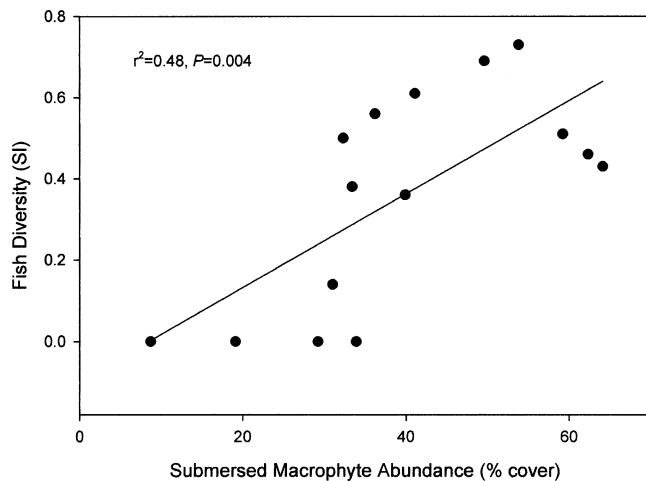


Figure 1. Linear regression of fish diversity estimated by Simpson's Index as a function of submersed macrophyte abundance (% cover) measured using the Deppe and Lathrop (1993) rake technique (see Methods for description of measurement and Results for model parameters).

moose and white-tailed deer (Aho 1978), and waterfowl (Beard 1953).

Contrary to current theory of landscape configuration, spatial connectedness, or proximity (Maguire 1963, Magnuson et al. 1998, Schlosser 1998, Schlosser and Kallemeyn 2000), no apparent spatial patterns emerged that could explain the composition of fish assemblages in this archipelago. Some of the impounded peatlands were isolated by a distance of >0.25 km from their nearest neighboring pond or lake with no discernable hydrologic connection; however, terrestrial barriers of <50 m separated most ponds. In stream/floodplain systems, seasonal flooding provides temporary connections between normally isolated systems, providing a mode of dispersal for colonizing fish (Chapman and Kramer 1991, Scheerer 2002). Also, preliminary results from some studies of isolated wetlands in the United States Upper Coastal Plain show that the presence or absence of fish is determined by a hydrologic connection to a source of colonists (Snodgrass et al. 1996, Langston and Kent 1997). Although small ephemeral rivulets were observed connecting some of the ponds in this study during spring thaw, the hydrologic variation in these systems is apparently less common than those described by Snodgrass et al. (1996) in their investigations of fish in isolated wetlands of the Upper Coastal Plain. The connections observed in our investigation are ephemeral and could potentially provide a temporary hydrologic mode of dispersal for fish colonists; however, there were no fish present in the control peatlands, where hydrologic conditions did not differ from the beaver modified peat-

lands, indicating that this may not have been important.

We conclude that beaver-flooded peatlands, like streams, support multi-species fish assemblages, and the attributes of these assemblages are influenced directly by some biological (macrophyte community structure) and potentially by physical characteristics (e.g., temporary connectedness) of these habitats. Beaver-flooded peatlands were rapidly colonized, reinforcing the idea that habitat isolation did not act as a dispersal barrier for many fish species. Previous research documented that 21% of the peatlands in this area were altered by beaver flooding (Rebertus 1986). Therefore, beaver modifications such as these, when considered at the landscape scale, offer considerable habitat for fish, increase the complexity of biological food webs, and contribute to biological diversity.

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