

A fossil record of colonization and response of lacustrine fish populations to climate change

Michael G. Newbrey and Allan C. Ashworth

Abstract: To study fish species colonization and the response of populations to climate change, we reexamined a well-preserved late Pleistocene to early Holocene fossil fish assemblage from lake deposits on the Missouri Coteau, North Dakota. The fossil fishes in the assemblage include complete specimens of yellow perch (*Perca flavescens*), brassy minnow (*Hybognathus hankinsoni*), blacknose shiner (*Notropis heterolepis*), banded killifish (*Fundulus diaphanus*), and brook stickleback (*Culaea inconstans*). The sequence of colonization is explained by individual thermal and relative water velocity tolerances for each species. There are six peaks in fish abundance during approximately 1000 years, indicating a response to environmental perturbations. Charcoal deposition from fires is inferred to represent episodic droughts during which nutrient levels were reduced and fish abundance declined. The fluctuations follow an overall trend of increased fish abundance during a time when lake-marginal vegetation changed from a spruce to a deciduous forest in response to climatic warming. This study provides insight into the complex effects of a changing climate on fish populations and demonstrates the potential of using fossils to examine the long-term abundance patterns of contemporary fish species.

Résumé : Nous avons examiné à nouveau une collection de poissons fossiles bien conservés datant de la fin du Pléistocène au début de l'Holocène et provenant de dépôts lacustres sur le coteau Missouri au Dakota du Nord afin d'étudier la colonisation des espèces de poissons et la réaction des populations au changement climatique. Les poissons fossiles dans la collection comprennent des spécimens entiers de perchaudes (*Perca flavescens*), de ménés laiton (*Hybognathus hankinsoni*), de museaux noirs (*Notropis heterolepis*), de fondules barrés (*Fundulus diaphanus*) et d'épinoches à cinq épines (*Culaea inconstans*). La séquence de la colonisation s'explique par les tolérances individuelles des espèces à la température et à la vitesse relative du courant. Il y a six maximums d'abondance des poissons sur une période d'environ 1000 ans qui correspondent à des réactions à des perturbations de l'environnement. Les dépôts de charbon de bois provenant de feux représentent, dans notre interprétation, des périodes de sécheresse répétées durant lesquelles les concentrations de nutriments et l'abondance des poissons diminuent. Les fluctuations suivent une tendance générale d'accroissement de l'abondance des poissons au moment où la végétation des rives lacustres a changé d'une forêt d'épinettes à une forêt décidue en réaction au réchauffement du climat. Notre étude fournit une perspective sur les effets complexes d'un climat changeant sur les populations de poissons et démontre le potentiel de l'étude des fossiles pour déterminer les patterns d'abondance de répartition à grande échelle des espèces contemporaines de poissons.

[Traduit par la Rédaction]

Introduction

We reexamined fossils and data from an exceptionally well-preserved late Pleistocene to early Holocene (i.e., 11 000 years ago) fish assemblage located on the Missouri Coteau, North Dakota. The fishes include blacknose shiner (*Notropis heterolepis*) (Cyprinidae), brassy minnow (*Hybognathus hankinsoni*) (Cyprinidae), banded killifish (*Fundulus diaphanus*) (Fundulidae), yellow perch (*Perca flavescens*) (Percidae), and brook stickleback (*Culaea inconstans*) (Gasterosteidae) (Bickley 1970; Cvancara et al. 1971). These species are also extant in North Dakota today (Power and Rychman 1998).

In this study we explore the relationships among species colonization and fish population responses to climate change using fire frequency, gastropod abundance, and plant pollen from a record that is approximately 1000 years in length. Our objectives are to examine the order of colonization of fishes with regard to life-history characteristics; describe the changes in fish abundance associated with charcoal deposition; describe fish abundance with a proxy for lacustrine nutrients that increase during a shift in terrestrial vegetation (i.e., climate change); and show that the proxy for lacustrine nutrients varies with the relative abundance of charcoal.

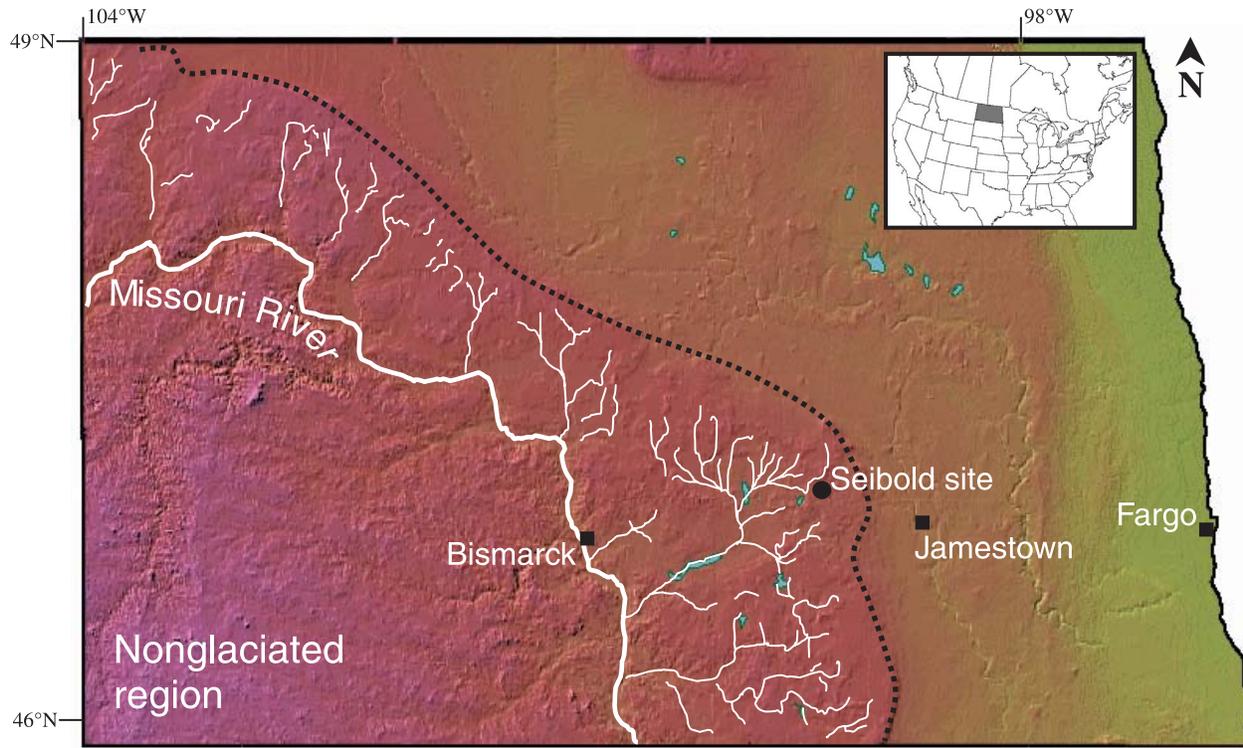
This fossil record permits us to examine freshwater-fishery data and its effects of climate change on fish populations.

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Fig. 1. Ancient tributaries (i.e., fine white lines) of the late Pleistocene to early Holocene Missouri River are based on the distribution of sand and gravel deposits mapped by Clayton et al. (1980). The black dotted line indicates the eastern edge of the Missouri Coteau. All of North Dakota except the southwest was glaciated (the location of North Dakota in the USA is shown in the inset map). The shaded relief map is modified from Sterner (1995).



These data allow us to effectively detect the response of fish to climate change because there are no confounding effects of anthropogenic harvest and other impacts such as are found in contemporary fish populations. Also the data permit us to describe ecological processes occurring on longer time scales than is possible from studies of living fish.

Materials and methods

Study site

The Seibold site (47.02°N, 99.18°W) is an ephemeral wetland on the Missouri Coteau, near Buchanan, North Dakota (Fig. 1). Cvancara et al. (1971) and Ashworth and Brophy (1972) described the geological and paleolimnological setting of the deposit. The site represents a small basin (100 m in diameter) that was probably part of larger lake complex which formed on an ice-cored moraine at the end of the late Wisconsinan glaciation.

The site has excellent preservation of terrestrial and aquatic plants and animals, which permits taxonomic assignments of many fossils to species. Near the base of the deposit is a continuous sequence of lacustrine sediments containing complete fish skeletons. The fossils come from a sedimentary unit composed of brown to green organic mud overlain by calcareous mud. Bickley (1970) referred to the deposit as the fish-bearing unit. A pollen profile from the fish-bearing unit indicated that the lake was initially surrounded by spruce, which was later replaced by a mixed assemblage of deciduous trees, shrubs, herbs, and grasses (Cvancara et al. 1971). The

radiocarbon age of the decline of spruce pollen is 9750 ± 140 [I-4537] radiocarbon years before present. Converted to calendar years, this represents an age of 11 065 calendar years before present (BP) (CALIB 4.4; Stuiver and Reimer 1993; Stuiver et al. 1998a, 1998b). The age of decline of spruce pollen (Cvancara et al. 1971) is consistent with the age of decline of spruce pollen at Moon Lake 130 km south-east of the Seibold site (Laird et al. 1996; Grimm 2001) and at Spiritwood Lake 46 km east of the Seibold site (McAndrews 1970). The span of time represented by the fish-bearing unit is uncertain. However, based on comparison with the Moon Lake pollen record, the fish-bearing unit probably represents about 1000 years of deposition, from approximately 11 500 to 10 500 calendar years BP.

Paleoecological context

To understand the ecological patterns of the Seibold fish assemblage, information about the origin of the lake and its climatic history is briefly discussed. The Missouri Coteau is a broad band of low morainic hills that stretches from Saskatchewan to South Dakota (Clayton et al. 1980). The moraines, representing a complex of active and stagnant ice features, were deposited at the end of the Wisconsinan ice age. Large volumes of ice remained buried in the till and outwash deposits into the late Quaternary (Clayton 1967). The stagnant ice terrain had greater topographic relief than the morainic hills today (Clayton and Cherry 1967). The melting of buried ice formed kettle lake basins and also provided meltwater for the rivers. Soils formed on the adjacent

Table 1. Limiting environmental factors for the species recovered as fossils from the Seibold site.

	Sequence of colonization (observed)	Maximum water velocity		Northerly extent of geographic range		Minimum spawning water temperature	
		Flow rate	Citation	Latitude (°N)	MAT _{air} (°C)	°C	Citation
Yellow perch	1	Moderate	Otto and Rice 1974	62	-5.2	6.7	Weber 1975
Brassy minnow	1	Moderate	Becker 1983; Copes 1975	55	-0.3	10.0	Dobie et al. 1956
Blacknose shiner	2	Slow-moderate	Becker 1983	55	-3.5	?	—
Brook stickleback	3	Slow	Becker 1983	68	-9.5	4.5	Carlander 1969
Banded killifish	3	Slow	Becker 1983	49	2.0	21.0	Richardson 1939

Note: Fishes are arranged in chronological order of colonization, with yellow perch and brassy minnow found in the oldest sediments. Northern latitude represents the northerly extent of the range of each species. The mean annual air temperature (MAT_{air}) is from the northerly range of the species. The minimum spawning water temperature is the lowest spawning temperature noted in the literature.

ice-cored moraines and were colonized by vegetation, similar to those of the Klutlan Glacier in the Yukon Territory, Canada, today (Birks 1980).

The vegetation of the Missouri Coteau, based on pollen studies, changed around 11 000 calendar years BP from open spruce forest to a mosaic of deciduous woodland and prairie uplands (Grimm 2001). The short- to medium-grass prairie surrounding the Seibold wetland today is very different from forested habitats, which colonized the area following the retreat of the ice. Fritz et al. (1991) and Laird et al. (1996) reported increasing lake salinity in North Dakota between 11 000 and 9000 calendar years BP, a change that is consistent with the climate becoming warmer and drier. We interpret the greater frequency of deposits of charcoal in the upper part of the Seibold fish-bearing unit to be due to fires associated with the trend to warmer and drier climatic conditions.

The ecological ramifications for the fish populations are complex, owing to the landscape and climatic changes we have outlined. Climate change directly affects water temperature, evaporation rates, flow regimes, and water levels in lakes and rivers. As stagnant and buried ice melted, the gradient and flow regimes of rivers connecting the Seibold Paleolake to the Missouri River drainage changed dramatically. The faster flowing, colder water rivers of the late glacial system were replaced, after melt-out of stagnant ice, by sluggish warm-water streams and finally by a nonintegrated drainage during the early Holocene.

Data and sampling

Data for fish species richness and fish and gastropod abundance within the fish-bearing unit are taken from Bickley (1970, his Fig. 6). Bickley examined the fish-bearing unit (i.e., a 15 cm × 20 cm × 37 cm thick stratigraphic section) at 1-cm intervals and counted and reported fish and gastropods for every 2 cm of thickness (i.e., 1–2.9 cm). The species of fossil gastropods include *Gyraulus parvus* Say, *Helisoma anceps* Menke, *Helisoma campanulatum* Say, *Promenetus exacuus* Say, *Physa gyrina* Say, *Lymnaea stagnalis* L., *Annicola limosa* Say, and *Valvata tricarinata* Say. Bickley (1970, his Figs. 7–9) also counted charcoal fragments derived from a 7.62-cm² area continuously throughout the fish-bearing unit. Although Bickley did not indicate the charcoal-sampling interval, we assume that he used a 1-cm sampling interval based on his sampling for fishes, inverte-

brates, and spruce needles. He filtered his samples through 63-µm mesh, but did not indicate the size of charcoal particles sampled. Pollen was sampled at depths of 50, 45, 40, 30, and 0 cm. Fish, charcoal, and pollen data were described from the same unit, but from different locations relative to the lake margin. Consequently, the thicknesses of all fish-bearing-unit samples for charcoal and pollen were standardized to Bickley's sediment-depth values (Bickley 1970, his Fig. 6).

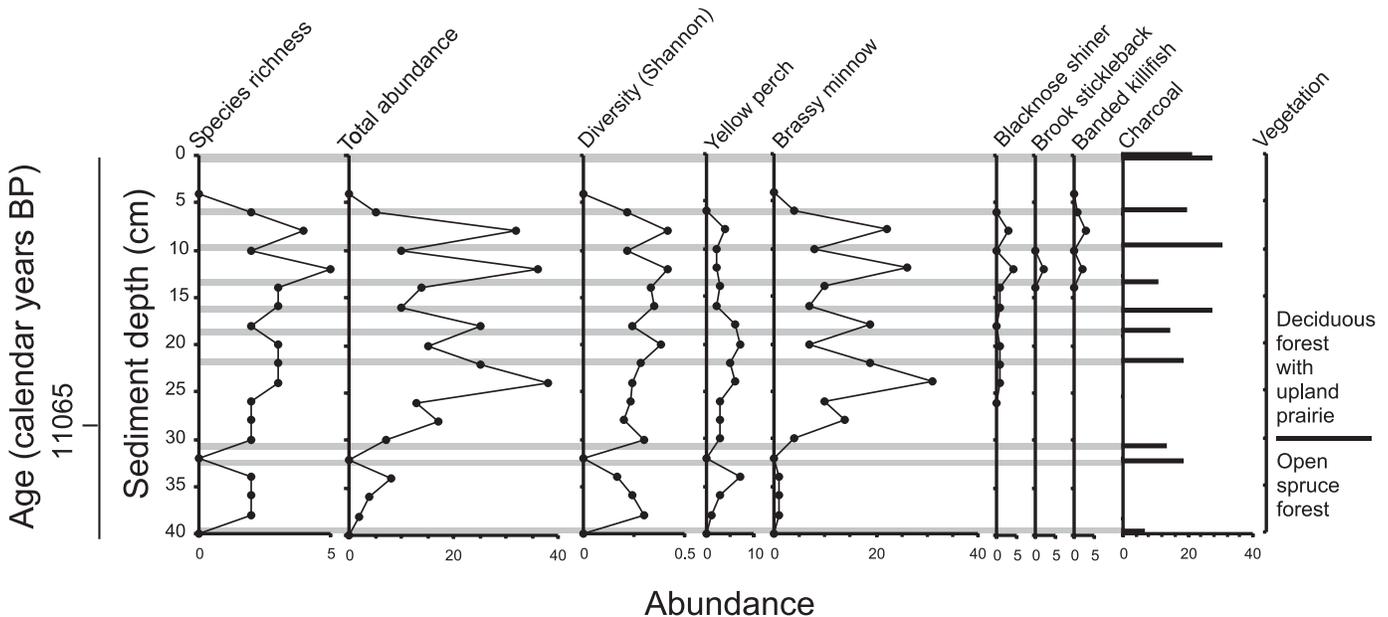
Colonization

To explain colonization of fishes (i.e., the order of appearance of taxa) at the site and to provide paleoecological interpretations, we examined contemporary life-history characteristics to better understand the probable ecological affinities of the fossil fish taxa. We feel that colonization of the site can be best described by ranking each taxon according to its swimming abilities (e.g., tolerance for fast- or slow-moving meltwater) and thermal preferences. Either swimming abilities or thermal preferences could have prevented fish from migrating to the Missouri Coteau from the Missouri River. For example, fish that cannot tolerate relatively fast-moving meltwater should be the last to arrive after the meltwater has dissipated. Fish with higher spawning temperatures and generally warmer thermal life histories should also be the last to arrive. Conversely, fish with preferences for lower temperatures should be the first to arrive if they were able to negotiate faster moving water. We compiled information about water-velocity preferences and minimum water temperatures necessary for spawning for each species from the sources listed in Table 1. We also assumed that the minimum temperature limit for each species is correlated with the mean annual air temperature at the northern limit of its range today. Information about the geographic distributions of the species is from Lee et al. (1980) and mean annual air temperatures from Hoare (2003).

Temporal changes associated with climate

To describe the changes in the aquatic system in relation to climate, we examined the mean differences among the various fish measures, gastropod abundance, and charcoal concentration across the change in vegetation. We used the Mann-Whitney nonparametric *t* test to determine if the mean number of fish, species richness, diversity, and gastropod abundance differed among the 2-cm intervals between

Fig. 2. A profile of the fish-bearing layer from Seibold Lake showing fish species richness, total abundance, diversity (Shannon Index), and abundance of five species in relation to charcoal concentration and vegetation. Shaded lines indicate fire events. Fish abundance and charcoal concentration are derived from Bickley (1970). Vegetation interpretation is from Cvancara et al. (1971).



sediments with high concentrations of boreal forest pollen (38–32 cm in depth) and those with mainly deciduous pollen (30–0 cm in depth). We calculated fish diversity using the Shannon Diversity Index (Zar 1984). Total fish abundance was described using a polynomial regression because fish abundance would decrease to zero as the system converted to a wetland (Cvancara et al. 1971). All tests were performed with SYSTAT® version 10.0 (2002) and α was set at ≤ 0.05 .

Impact of fire

The stratigraphic distribution of fossil fish and gastropod abundance was used to examine the effect of fire marked by charcoal deposition. The change in abundance (Δ) of the organisms for each stratigraphic sample was determined by subtraction, e.g., total of fish_{38-cm level} – total of fish_{36-cm level} = Δ fish_{36-cm level}. The change in abundance was recorded for each group of organisms, one representing change before (i.e., calculated for levels from 36 to 4 cm in depth) and another representing change after (i.e., calculated for levels from 38 to 6 cm in depth) charcoal deposition. An example of how change before deposition was calculated is shown above. Change after deposition was calculated in a similar way, e.g., total of fish_{36-cm level} – total of fish_{34-cm level} = Δ fish_{36-cm level}. Two-sample *t* tests were used to determine if there were significant differences in the mean changes of abundance between charcoal and noncharcoal layers.

Impact of changes in nutrients

To examine the effects of changes in nutrient levels in relation to environmental perturbations, we examined the relationships between charcoal concentration and gastropod and fish abundances. The relationship between gastropod and fish abundances from 4 to 38 cm in sediment depth was analyzed using linear regression. Gastropod abundance is as-

sumed to be dependent on periphyton and thereby on the availability of nutrients, although we recognize that fish and gastropod abundances can also be limited by factors not quantifiable with the available Seibold data (e.g., water levels or salinity). Charcoal abundance in relation to fish or gastropod abundance was analyzed using linear regression to test whether environmental events correlated with charcoal concentration had a significant impact on gastropods and fishes. Data on fish and gastropod abundances and charcoal concentration were natural-log-transformed. Fish abundances and charcoal concentrations were summed with a value of 1 prior to transformation.

Results

Colonization

Fish species first appeared at different times in the stratigraphic column interpreted here as a pattern of colonization (Fig. 2). Yellow perch and brassy minnow were the first to appear, followed by blacknose shiner, and finally by brook stickleback and banded killifish (Fig. 2). When yellow perch and brassy minnow appeared in the fossil record, the vegetation was an open spruce forest, but by the time that blacknose shiner, brook stickleback, and banded killifish appeared, the vegetation had changed to open deciduous woodland.

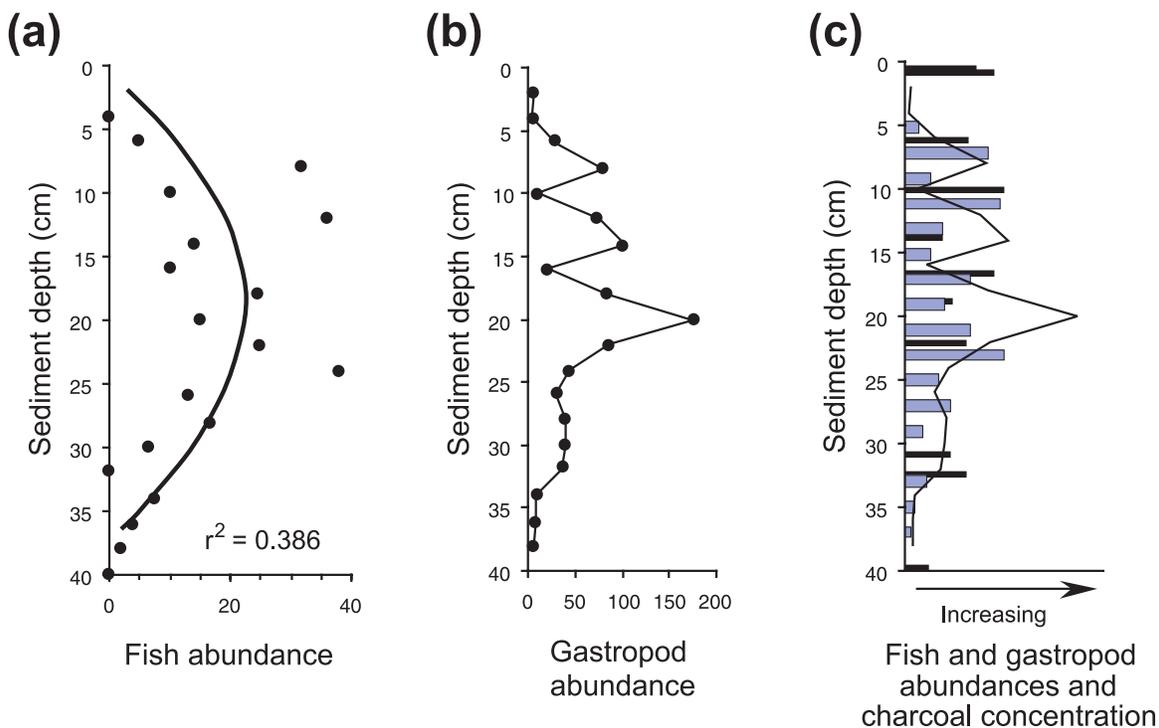
The sequence of colonization corresponds to the descending order of relative water-velocity tolerances for each species (Table 1). Yellow perch and brassy minnow tolerate moderate water velocities and were the first to be recorded at the site. Blacknose shiner appears second and tolerates slow to medium water velocities, followed by brook stickleback and banded killifish, which prefer slow-moving water. The sequence of colonization does not correspond to increases in water temperatures. Brook stickleback have very

Table 2. A comparison of the means and standard errors for fish species richness, fish and gastropod abundances, and fish diversity by dominant vegetation type, spruce or deciduous trees.

Variable	Spruce (mean ± 1 SE)	Deciduous trees (mean ± 1 SE)	<i>U</i>	<i>p</i>
Species richness	1.6±0.40	2.8±0.27	14.5	0.055
Fish abundance	4.2±1.50	20.0±3.16	6.5	0.010
Diversity (Shannon Index)	0.20±0.06	0.30±0.02	24.5	0.430
Gastropod abundance	19.8±7.28	65.3±13.15	13.0	0.054

Note: Mann–Whitney *U* tests were used to determine significant differences (boldface *p* value; α was set at 0.05).

Fig. 3. (a) Relationship between total fish abundance and sediment depth ($y = -0.069x^2 + 2.582x - 2.091$, $r^2 = 0.386$, 95% confidence interval = -0.121 to -0.016, 0.317 to 4.848, -23.027 to 18.845). (b) Relationship between total gastropod abundance and depth of the fish-bearing-layer sediments. (c) Relationship of total gastropod abundance (line), total fish abundance (shaded bars), and charcoal concentration (solid bars) with sediment depth.



cool thermal tolerances but were third in the order of appearance, along with the banded killifish, which has warmer life-history characteristics.

We recognize that predator-sensitive fish such as brassy minnow, blacknose shiner, banded killifish, and brook stickleback may respond to abundance of yellow perch. We examined the fish-abundance data using regression analysis and found no significant relationships between the abundances of yellow perch and the prey species.

Temporal changes associated with climate

Species richness and diversity (Shannon Index) fluctuate as the lake ages, but there are no significant increases in either measure (Table 2). Species richness increased from two to five fish after the shift from boreal to deciduous vegetation. Total fish abundance increased following the shift from spruce to deciduous vegetation (Fig. 2). During the spruce-dominated period (i.e., sediment depths 38–32 cm), relative fish abundance is low (mean = 4.2; Table 2). How-

ever, during the time when the landscape was deciduous-dominated, relative fish abundance significantly increased to a mean of 20.0 from 30 to 0 cm sediment depth (Mann–Whitney *U*-test statistic = 6.5, $p = 0.010$). Total fish abundance increased significantly in a parabolic relation to sediment depth until senescence ($r^2 = 0.386$; 95% confidence interval = -0.121 to -0.016, 0.317 to 4.848, and -23.027 to 18.845; Fig. 3a). During the spruce-dominated period, relative gastropod abundance, our proxy for nutrients, was low (mean = 19.8; Table 2; Figs. 3a, 3b). Relative gastropod abundance increased to a mean of 65.3 during the time when the landscape was deciduous-dominated; however, the relationship was not significant ($p = 0.054$).

Impact of fire

Fish abundance fluctuated between 30% and 70% and was characterized by six peaks in total abundance, most of the variation being produced by changes in abundance of brassy minnow. Five of the six peaks in fish abundance occur be-

Fig. 4. Relationships between fish and gastropod abundances and charcoal concentration. (a) Regression analysis indicates a significant relationship between charcoal concentration and gastropod abundance (Δ); fish abundance (\square) was summed with a value of one prior to transformation but was not found to be significant. (b) Total fish abundance and gastropod abundance (i.e., our proxy for nutrient levels); both variables were natural-log-transformed and a regression analysis indicates a significant relationship.

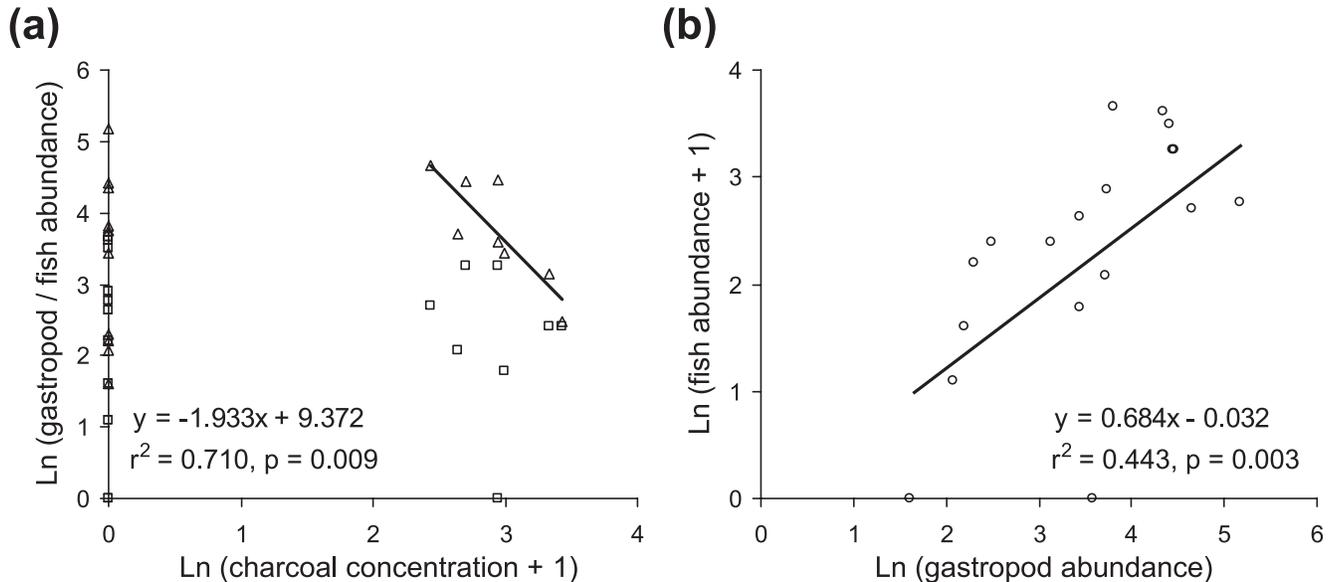


Table 3. Comparisons between the mean changes in fish and gastropod abundances before and after charcoal deposition.

	Charcoal (mean \pm 1 SE)	No charcoal (mean \pm 1 SE)	<i>t</i>	<i>p</i>
Gastropod abundance				
Δ before	-14.1 \pm 21.70	11.2 \pm 12.10	1.019	0.330
Δ after	16.3 \pm 20.08	-13.1 \pm 13.32	-1.218	0.246
Fish abundance				
Δ before	-8.5 \pm 5.09	7.3 \pm 4.36	2.4	0.033
Δ after	4.4 \pm 4.87	-4.1 \pm 5.59	-1.145	0.270

Note: Two-sample *t* tests were used to test for significant differences as indicated by the test statistic (*t*) and probability values (*p*); α was set at 0.05. The boldface *p* value indicates a significant relationship.

tween intervals with high concentrations of charcoal that are assumed to represent fire events (Fig. 2). In several, but not all, locations in the sediment column (i.e., 30–33.9, 13–16.9, 9, and 6 cm in depth), high charcoal concentrations occurred during intervals of relatively lower fish abundance. There was no significant correlation between the amount of charcoal and fish abundance (Fig. 4a). The mean change in fish abundance prior to charcoal deposition is -8.5, which is significantly lower than the mean change in abundance not associated with charcoal deposition (7.3; $p = 0.033$; Table 3). There are no significant changes in gastropod abundance before charcoal deposition and none in gastropod or fish abundance after it (Table 3).

Impact of changes in nutrients

Gastropod abundance fluctuated within the fish-bearing unit and was characterized by four distinct peaks (Figs. 3b, 3c). Gastropod abundance was negatively correlated with charcoal concentration ($r^2 = 0.710$, $p = 0.009$; Fig. 4a). Fish

abundance significantly increased with gastropod abundance, which is our proxy for nutrients ($r^2 = 0.443$, $p = 0.003$; Fig. 4b).

Discussion

The data show three distinct types of patterns that are superimposed on one another. First, fish species colonized the lake in a sequence that may be explained in terms of their life-history characteristics. Second, total abundance of fish increased during a time of climatic transition as indicated by a vegetational shift from an open spruce to an open deciduous forest. Third, fish-abundance fluctuations and population declines are correlated with episodic droughts inferred from charcoal deposition.

Colonization

The change in climate from relatively cold and moist to warm and dry conditions resulted in changes in the landscape and fluvial systems that periodically allowed access for species with different autecologies. Access to the site for some fish was dependent on landscape subsidence resulting from the melting of stagnant ice and the reduction of fluvial gradients and water velocities. Additionally, the climate warmed and became drier as indicated by the vegetation and charcoal records. During the drier periods, discharge from rivers would be relatively decreased, allowing fish with preferences for slow-moving water to access the site.

Fish colonized Seibold Lake in a sequential manner. Yellow perch and brassy minnow have life-history characteristics that enable them to be early colonizers of the deglaciated landscape. They tolerate relatively low spawning and water temperatures (Dobie et al. 1956; Weber 1975) and are able to negotiate faster flowing water (Otto and Rice 1974; Copes 1975; Becker 1983), which is characteristic of cooler and

wetter climates. The third species to colonize the lake was the blacknose shiner. This species has an ecology that allows it to cope with moderately low temperatures, but tolerates only slow to moderate water velocities compared with yellow perch and brassy minnow (Becker 1983). The brook stickleback and banded killifish were the last species to colonize the lake. The brook stickleback today tolerates a wide range of thermal regimes (Reisman and Cade 1967; Carlander 1969), but its ability to be an early colonizer is limited by relatively slow-flowing water (Becker 1983). The brook stickleback may be expected to have colonized the lake relatively early with yellow perch, given its tolerances for colder water. However, higher water velocities in rivers probably hampered brook stickleback colonization. Only as the current slowed could fish with preferences for lower water velocity colonize the lake. The banded killifish requires relatively low water velocities and warm water for spawning (Richardson 1939; Becker 1983).

The Missouri River drainage likely acted as a source (Stewart and Lindsey 1983), and perhaps a refugium, for fishes that colonized the Missouri Coteau, as is thought to be so for the brassy minnow (Burr and Page 1986). There is strong evidence that meltwater from the drainage of the ice-cored moraines was to the southwest, based on a dendritic pattern of sand and gravel fluvial deposits originating in the Missouri Coteau and trending to the southwest (Clayton et al. 1980). We interpret this pattern to represent a series of tributaries of the Missouri River. The presence of fossil bivalves at several locations in the sand and gravel fluvial deposits within the morainic deposits of North Dakota (Clayton 1961, 1967) provides further insight into fish colonization (Sherrod 1963). The reproduction and dispersal of many bivalves depend on fishes transporting glochidia in their gills.

The colonization of previously glaciated terrain has probably occurred numerous times, because major glaciations and interglaciations are known to have occurred about every 100 000 years during the past 1 million years of the Quaternary period (i.e., the last 2 million years) (Shackleton and Hall 1990). In the northern latitudes of North America and Europe, fish populations would have been forced to relocate as habitats were glaciated and deglaciated. Following each glaciation, the warming climate would expand the northern potential range of fish (e.g., Miller 1958; Cavender 1986; Robison 1986 and references therein).

Fluctuating abundance

Fluctuations in fish abundance can be explained in terms of either mass mortality (i.e., death assemblages) or increased abundance (i.e., productivity). We prefer the latter interpretation for the following reasons. The time scale of deposition of the fish-bearing unit is approximately 1000 years and encompasses shifts in vegetation from spruce to deciduous woodland, suggesting that increased fish fossil deposition (i.e., peak abundance) occurred over longer time periods with more individuals existing and dying in the system as opposed to potential annual events (e.g., winter-related fish kills). Population cycles of brassy minnow, blacknose shiner, brook stickleback, and banded killifish, which span, on the average, 160 years, would have ample time to recover from perturbations caused by annual events or fire. With respect

to fire, studies on Minnesota lakes failed to show substantial effects on lake productivity (McColl and Grigal 1975; Wright 1976; Bradbury 1986), and a study of fish growth after the Yellowstone National Park fires also failed to show an effect (Gresswell 2004), suggesting that in Seibold Lake neither mass mortality nor fish abundance would be strongly affected by fire.

Fish abundance at the Seibold site varies in a manner that is independent of colonization of the species. We show that decreases in fish abundance are correlated with charcoal deposition and that fish abundance increased throughout the fish-bearing unit until 8 cm in depth. We suggest that fire events are related to drought cycles associated with warming climatic conditions, which influences fish abundance in three potentially interacting ways, by periodically limiting nutrient inputs, increasing eutrophication, or changing population structure and overall productivity.

First, nutrients may be limited by episodic drought, thereby periodically limiting system productivity. The changes in fish abundance associated directly with charcoal layers are significantly less than those associated interhorizons. This suggests to us that more change in abundance is associated with the onsets of droughts and not directly with fire events. Fire is linked to drought and it has been suggested that it is the drier conditions, rather than fire, that limit input of nitrogen and, ultimately, productivity (Kilham et al. 1996; Theriot et al. 1997; Gresswell 1999). Nutrients derived from the atmosphere tend to dominate annual trends in water quality before and after a fire event (Wright 1976; Lathrop 1994; Theriot et al. 1997). Drought conditions may reduce nutrients by limiting atmospheric inputs, temperature, water level, light penetration, lake productivity, vegetation around the lake, and also watershed nutrients being carried into the lake through precipitation runoff (Theriot et al. 1997; Gresswell 1999).

From the Seibold data, nutrients appear to play a role in the abundance of fish and gastropods. Fish abundance is positively correlated with gastropod abundance. We chose gastropods as a proxy for nutrients because of their dependence on periphyton, and thereby nutrients. However, the relative nutrient levels vary throughout the record and are punctuated with a series of droughts. We speculate that the amount of charcoal deposited in each of the layers would be positively correlated with the intensity of the drought associated with the charcoal layer. We hypothesize this relationship because fish abundance is lower prior to the charcoal layer being deposited and because gastropod abundance associated with charcoal layers negatively responds to the amount of charcoal deposited, which is inferred to be correlated with the intensity of the drought.

Second, nutrient input increased as the vegetation shifted from spruce to deciduous woodland as a result of climatic warming. As we previously discussed, gastropod abundance, as a proxy for system nutrient levels, is correlated with fish abundance. The greatest increases in fish abundance occurred after the vegetation in the riparian area had converted to a deciduous forest and fire frequency increased. As the climate warmed, drought, deciduous trees, and fire became more common, thereby changing the landscape. We have already discussed the potential effects of the limitation of

nutrients due to drought, but we have not discussed the implications of allochthonous inputs from a deciduous-dominated riparian area on fish abundance. Nutrients from deciduous trees may have increased eutrophication by elevating nutrient levels in the lake higher than those of the spruce-dominated watershed, thereby permitting a trend of increasing total fish abundance until the system senesced. Enright (2001) found that nutrients (i.e., nitrogen and phosphorus) from deciduous litter were significantly higher than those from conifers, thus permitting increases in system productivity to support higher fish abundance. In addition, soil nutrients were found to be the highest among hardwoods and lowest among spruce in the boreal forests of North America (Pastor et al. 1987, 1988).

Only two of the five species occur in the uppermost lake sediments, brassy minnow and banded killifish. From the species richness and abundance data, we interpret that fish species richness and abundance declined in the system because the postglacial lake turned into an isolated wetland like many of the prairie potholes today. We speculate that the system ceased to support significant numbers of fish because the streams and rivers, which interconnected many of the prairie potholes, dried up from a lack of meltwater and rain. As a result, no more fish were able to colonize the system and fish populations declined because of a fall in lake levels due to evaporation.

Third, a warming climate may influence fish population structure and overall productivity through a complex series of biological and climate-related effects. Research conducted to examine the effects of a warming climate on fishes, using information from population dynamics and bioenergetics studies, has produced hypotheses concerning the effects of climatic warming on fishes. For example, Hill and Magnuson (1990) suggested that changes in bioenergetics due to climate change might modify yearling growth and prey consumption, thereby greatly influencing the food-web dynamics. Shuter and Post (1990) suggested that an increase of 4 °C may increase the northern distributional limit of yellow perch and, depending on lake morphometry and productivity, may also greatly influence survival, relative year-class strength, and system carrying capacity. Fossil fish deposited during a time of warming climate have the potential to be used to test Shuter and Post's (1990) hypotheses to examine fish growth and shifts in modal year classes.

Temperature probably has an influence on Seibold fish abundance cycles because temperature and other climate-related conditions could alter population dynamics and fishery productivity (Pauly 1980; Beamish and Bouillon 1993; Finney et al. 2002). Pauly (1980) examined many fish populations from polar to tropical regions and from fresh water to salt water, and he derived a mathematical relationship for mortality, growth, and temperature. Beamish and Bouillon (1993) identified similar trends between production of salmon and copepods with the pressure patterns of the Aleutian Low. Finney et al. (2002) used diatoms as a proxy for estimating sockeye salmon (*Oncorhynchus nerka*) productivity because they were correlated with climatic forcing. Nevertheless, there remains a need to consider the additional dynamic effects of temperature and drought on the dispersion and population dynamics of fishes in the light of climate change.

In summary, this research provides a snapshot of fish colonization and abundance patterns during a time of climatic warming. In this study, we conclude that appearances of fishes in the lake can be explained in terms of differences in life-history characteristics. Yellow perch and brassy minnow, species with tolerances for moderate water velocities, appeared early during a cool-climate period. Fishes with preferences for slow-moving and warmer water appeared later. In a dynamic landscape, like that of the Missouri Coteau at the end of the ice age, fish colonization was controlled by the dispersal potential of the species. Independent of colonization, changes in abundance were probably the result of changes of productivity rather than representing a series of mass fish kills. Further, changes in productivity appear to be linked to the occurrence of drought and climate change, but the relationships are uncertain.

From our perspective, climate change is complex in its effects on aquatic systems, which are more easily detectable in long-term data sets. We showed that fish colonization and populations could be affected by climate change by responding to factors such as changes in nutrients, changes in drought frequency and intensity, and changes in rivers incorporating various lacustrine systems. The resolution of our data is low, but our results provide a conceptual framework of the ecology based on observations, which is useful in developing testable hypotheses in other studies examining the effects of climate change on contemporary and fossil fishes. The complex relationships that we have outlined in our paleoecological study emphasize the need for study of longer data sets in examining the causal relationships between productivity, nutrient cycles, fire frequency, and climate change (Gresswell 1999).

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