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Effects of introduced fish on macroinvertebrate communities in historically fishless headwater and kettle lakes

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ABSTRACT

Widespread fish introductions have led to a worldwide decline in the number of fishless lakes and their associated communities. Studies assessing effects of fish stocking on native communities in historically fishless lakes have been limited to high-elevation headwater lakes stocked with non-native trout. Little is known about the effect of fish stocking in historically fishless and hydrologically isolated lowland kettle lakes. We compared the effects of introduced fish on macroinvertebrate communities in kettle lakes stocked with centrarchids, salmonids, and cyprinids, and headwater lakes stocked with brook trout (*Salvelinus fontinalis*) in Maine, USA. Fish had significant effects on macroinvertebrate community structure in both lake types, with reduced species richness and abundances of taxa characteristic of fishless lakes. The effects of introduced fish were more pronounced in headwater lakes despite a less diverse fish assemblage than in kettle lakes. We attribute this to abundant submerged vegetation providing refuge from fish predation and reduced stocking frequency in kettle lakes. We assessed effects of stocking duration on macroinvertebrates in a subset of headwater lakes with known dates of trout introduction. Species richness and abundance of most taxa declined within 3 years following trout introduction; however, richness and abundance were least in lakes with long stocking histories (⩾40 years). Macroinvertebrates previously identified as fishless bioindicators were absent from all stocked lakes, indicating that trout rapidly eliminate these sensitive taxa. Conservation of this historically undervalued ecosystem requires protecting remaining fishless lakes and recovering those that have been stocked.

1. Introduction

Widespread fish introductions have led to a worldwide decline in the number of fishless lake communities (Donald, 1987; Bahls, 1992; Pister, 2001; Schilling et al., 2008). This study assesses the need for urgent management strategies ensuring their conservation in eastern North America, a region where little is known about fishless lake communities. Naturally fishless lakes represent a unique freshwater ecosystem. Such lakes enhance regional aquatic species diversity by providing unique freshwater habitat conditions along a gradient of waterbody permanence and predator presence, ranging from temporary vernal pools lacking large dragonfly and fish predators to permanent lakes where fish are top predators (Wellborn et al., 1996; Stoks and McPeek, 2003). The potential conservation value of fishless lakes extends beyond the boundaries of the waterbody; fishless lakes provide important prey items for migrating and breeding waterfowl (Bouffard and Hanson, 1997), passerines (Epanchin, 2009) and reptiles (Matthews and Knapp, 2002).

Historically, humans have undervalued the ecological importance of naturally fishless lakes, viewing them primarily as potential sport fish habitat or sites for rearing bait fish. Rarefaction of this unique habitat type due to the introduction of predatory fish has led to landscape-scale losses of native prey species, such as zooplankton (Stoddard, 1987; Bradford et al., 1998; Knapp et al., 2001), amphibians (Fisher and Shaffer, 1996; Bradford et al., 1998; Knapp et al., 2001; Pilliod and Peterson, 2001; Denoel et al., 2005; Orizaola and Brana, 2006) and macroinvertebrates (Bradford et al., 1998; Carlisle and Hawkins, 1998; Knapp et al., 2001). In addition to direct predatory effects, introduced fish disrupt in lake ecosystem processes (e.g., nutrient cycling and primary productivity; Schindler et al., 2001) and sever trophic connections between aquatic and terrestrial food webs with cascading effects on riparian plants (Knight et al., 2005) and vertebrates (Matthews and Knapp, 2002; Finlay and Vredenburg, 2007; Knapp et al., 2007).

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Studies documenting the detrimental effects of fish stocking in historically fishless lakes have focused on high-elevation headwater lakes stocked with non-native trout, primarily in western North America where fishless lakes historically were common (Donald, 1987; Bahls, 1992). This research is part of a larger body of work that questions traditional fish management practices (Stanley, 1995; Rahel, 1997, 2000). Recent research, also in western North America, demonstrates the potential for native headwater lake fauna to recover following fish removal (Donald et al., 2001; Hoffman et al., 2004; Knapp et al., 2005, 2007). Recognizing the ecological value of fishless lakes and their potential for recovery has spurred state and federal agencies to take a more holistic management approach. Stocking has been halted in many high-elevation fishless lakes in national parks and wilderness areas in western North America, and some lakes are being restored to their natural fishless condition (Milliron, 1999; Yosemite National Park, 2006; Bunn et al., 2007).

There have been no similar attempts to evaluate or mitigate the effects of stocking historically fishless lakes in eastern North America, a region where fish faunas are greatly altered due to widespread introductions. While the predominant geographical trend of fish introductions in North America has been westward invasions of species native to the East, northeastern states contain some of the most altered fish faunas in the USA due to the few species considered desirable as game fish in northeastern waters (Whittier and Kincaid, 1999; Rahel, 2000; Whittier, 2002). Fish have been moved liberally within their native ranges among eastern lakes, with many instances of translocations of "native" fish to waterbodies that have not previously contained these species (Whittier and Kincaid, 1999; Whittier, 2002). Many naturally fishless lakes in northeastern North America now contain fish (Schilling et al., 2008). These include headwater lakes stocked primarily with brook trout (*Salvelinus fontinalis*) and kettle lakes (lakes formed in depressions left by glacial ice blocks) stocked with a more diverse fish assemblage, including centrarchids, salmonids, and cyprinids (Schilling et al., 2008). The ecological effects of stocking have never been studied in fishless kettle lakes, a physiographic lake type that occurs throughout formerly glaciated regions of North America.

Despite differences in lake physical characteristics, fishless kettle and headwater lakes in Maine, USA support similar macroinvertebrate communities (Schilling et al., 2009). Fishless lake macroinvertebrate communities in Maine are distinct from those in similar lakes containing fish, with several unique species occurring in fishless lakes (Schilling et al., 2009). It is estimated that ~50% of the naturally fishless lakes in Maine have been stocked with game or baitfish (Schilling, 2008). This study was developed with the goal of informing conservation planning for this resource. Our primary objective was to assess differences in macroinvertebrate communities between currently and historically (but now stocked) fishless kettle and headwater lakes in Maine to aid understanding of how these unique communities are affected by introduced fish. We hypothesized that effects of introduced fish on macroinvertebrate communities would differ between the two physiographic lake types, headwater and kettle, due to differences in lake habitat structure, stocking regime, and fish species composition. Our second objective was to assess whether the effect of introduced fish on native macroinvertebrate communities in repeatedly stocked lakes varies with the amount of time since the original fish introduction. We hypothesized that the effect of introduced fish on native macroinvertebrate communities would be more pronounced in lakes with long histories of repeated stocking than in recently stocked lakes. Understanding the reduction in natural fishless lake macroinvertebrate biodiversity that occurs with repeated stocking will help managers establish conservation goals for these lakes.

2. Methods

2.1. Study lake selection

We identified two physiographic types of naturally fishless lakes in two biophysical regions in Maine, USA: headwater lakes in the central and western mountains and kettle lakes in the eastern lowlands and foothills (Schilling et al., 2008). Prior to being stocked, fish were naturally absent from these lakes since the last glaciation (~10,000 years BP) created natural physical barriers to fish colonization. Fishless lakes in western Maine are high-elevation headwater cirques isolated from fish colonization by steep outlets impassable to fish. Fishless lakes in eastern Maine are kettle lakes formed in depressions left by glacial ice blocks. Many kettles have no surface water connections to other waterbodies and thus lack routes for fish movement. Additionally, many kettles are bog lakes with naturally low pH, which limits fish species richness (Rahel, 1984).

We identified 16 currently fishless (eight headwater, eight kettle) and 14 historically fishless but now stocked (eight headwater, six kettle) lakes for study (Fig. 1) by consulting fish survey records (Maine Department of Inland Fisheries and Wildlife (MDIFW), unpublished data) and a geographic information systems (GIS) analysis identifying lakes inaccessible to fish (Schilling et al., 2008). These represent approximately half of the known fishless lakes in the state of Maine (Schilling et al., 2008; MDIFW, unpublished data) and were selected primarily based on their accessibility and availability of landowner permits for overnight sampling. Historical fish survey records indicated that five of the stocked headwater lakes were fishless prior to state-authorized brook trout stocking (MDIFW, unpublished). The remaining three stocked headwater lakes and all six stocked kettle lakes were selected based on GIS analyses that demonstrated that physical characteristics of these lakes were similar to other known fishless lakes in the region (Schilling et al., 2008). Historical fishless status of these lakes was verified with paleolimnological analyses of *Chaoborus* remains in lake sediment cores (DeGoosh, 2007). The original dates of fish introductions in these lakes were unknown, but sediment cores indicated fish absence 14–61 years before present (Davis et al., 1994; DeGoosh, 2007).

Field surveys to verify fish absence (fishless lakes) and fish species composition (stocked lakes) and describe habitat characteristics were conducted during single site visits during the summers of 2002–2005. We surveyed the lakes for fish with gillnets and minnow traps following MDIFW fish survey protocols (Tim Obrey, MDIFW, personal communication). One four-panel (19 mm, 25 mm, 33 mm, 38 mm mesh) monofilament gillnet (40 m × 1.5 m) was bottom-set perpendicular to shore for two, 15 min sets and checked for fish between sets. If no fish were caught after two sets, the net was deployed overnight and checked the following morning. Three minnow traps baited with dog biscuits were placed at equal distances around the lake perimeter and checked for fish after 12 h. If no fish were captured during this survey, we considered the lake to be fishless. We qualitatively assessed habitat structure (visual assessment of the approximate proportion of lake perimeter rimmed with littoral vegetation and distance it extended from shore), measured maximum lake depth with a depth finder, and collected one water sample for closed cell pH analysis. Lake surface area and elevation were estimated with GIS (Schilling et al., 2008). We assessed differences in measured physical variables between fishless and stocked lakes within each physiographic lake type, as well as between stocked headwater lakes and stocked kettle lakes, with Student's t-tests ($\alpha = 0.1$).