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Late glacial impacts on dispersal and colonization of Atlantic Canada and Maine by freshwater fishes

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Abstract

Late glacial scenarios of ice retreat and biogeography databases constrain the dispersal routes of obligate freshwater fishes into Atlantic Canada and Maine. Evidence indicates glacial ice covered the present-day mainland and offshore islands at 18,000 ^{14}C yr before present. Possible refugia for extirpated freshwater fishes were the exposed outer edge of the Grand Banks (east), exposed Georges Bank (south-Atlantic Refugium), and the Mississippi Refugium in the west. It is improbable that the region was recolonized from the offshore refugia. Rather, fishes recolonized from the east via the upper St. Lawrence River valley into the upper Saint John River, Maine (Lake Madawaska) from 11,000 to 12,000 ^{14}C yr BP. The short period of entry resulted in the low diversity of obligate freshwater species in the region. Lake Madawaska was breached and dispersal continued into the remainder of the region after 8000 ^{14}C yr BP. By 6000 ^{14}C yr BP, access routes to the east along low-lying coastal zones were blocked by rising sea levels, which isolated Prince Edward Island, Cape Breton Island, and most probably Nova Scotia. Natural dispersal across the region appeared complete by this time.

Keywords: Biogeography; Fishes; Recolonization; Freshwater habitats; Refugia; Ice retreat; Eastern North America

Introduction

Geological evidence strongly indicates that from 18,000 to 22,000 ^{14}C yr BP, all of present-day Maine (ME, USA), Maritime Canada (Gaspé, Quebec—QC, New Brunswick—NB, Prince Edward Island—PEI, and Nova Scotia—NS), and Newfoundland (NF) were covered by sheets of glacial ice (e.g., Stea et al., 1998; Dyke et al., 2002; Shaw et al., 2002). Freshwater organisms would have been extirpated from the region, most probably inhabiting refugia south of the ice margins. As the ice retreated to the north and east, freshwater habitats were created by meltwater, stagnant ice, and crustal rebound. The spatial and temporal locations of these habitats are critical factors that controlled the dispersal and recolonization by obligate freshwater fishes into the eastern region. Only 23 obligate freshwater, and non-introduced species occur east of Maine in the region (R.A. Curry, unpublished data). Such low biodiversity (e.g., Pielou, 1991) is hypothetically related to the physical and temporal barriers to dispersal. This paper reviews regional geological records of glacier retreat and ice positions, biogeographic information, and updated distribution data for fishes to propose a new dispersal route for obligate freshwater fishes into the eastern region.

Maximum extent of glacier advances

Our best evidence indicates that during the last glacial advance of the late Wisconsinan, the maximum extent of glacial ice in the east occurred about 18,000 ^{14}C yr BP (Fig. 1). The southern margin of the Laurentide ice sheets extended from the continent south of Cape Cod, Massachusetts (MA), along the outer edge of the continental shelf to the Grand Banks off present-day NF (Stea et al., 1998; Shaw and Courtney, 2002). At that time, the continental landmass extended out to the Georges Bank (southwest of present-day NS), the outer Grand Banks was above sea level, and there was no exposed land between these areas (Fig. 1; Stea et al., 1998; Shaw and Courtney, 2002).

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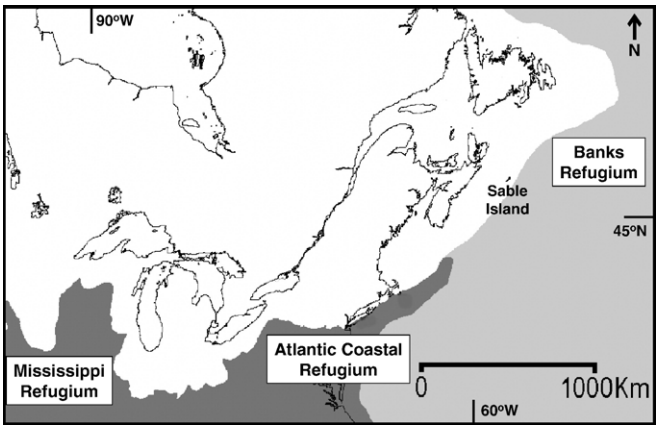

Figure 1. Maximum extent of ice sheet coverage in eastern North America (18,000 ^{14}C yr BP). White areas represent glacial ice, dark areas are terrestrial environments, and light grey areas are marine environments. The three hypothesized refugia for freshwater fishes are identified (adapted from Fig. 1 in Dyke et al., 2002).

Organisms evading the ice, particularly freshwater fishes, are hypothesized to have inhabited three major refugia during this period. First, the upper Mississippi River valley is well established as a refugium for freshwater fishes, crustaceans, and dipterans (Fig. 1; Dadswell, 1974; Carter et al., 1980; Bailey and Smith, 1981; Mandrak and Crossman, 1992). Second, an Atlantic Coastal or Upland refuge along the east coast of the continent has also been documented (Fig. 1; Schmidt, 1986; Pigeon et al., 1997). The third refugium is the outer, presently submerged banks of the continental shelf, for example the Grand and Sable Island Banks, where evidence suggests terrestrial environments persisted at the maximum extent of the glaciers' advances (Fig. 2A; Munroe, 1956; Dyke et al., 2002; Shaw et al., 2002). Each of these hypotheses and their predictions for the modern distribution of freshwater fishes are examined in turn.

Grand Banks Refugium

From 18,000 ^{14}C yr BP to about 5000 ^{14}C yr BP, glacial ice lingered across the eastern region of North America. The retreating and wasting ice, sea-level changes, and isostatic rebound effects combined to create terrestrial and freshwater environments that were different from present-day conditions. As the ice began to recede, two island groups formed by present-day, shallow banks were created off the south coasts of NF and NS (Fig. 2A, Fig. 4). These island groups have been proposed as the connections to the mainland for organisms

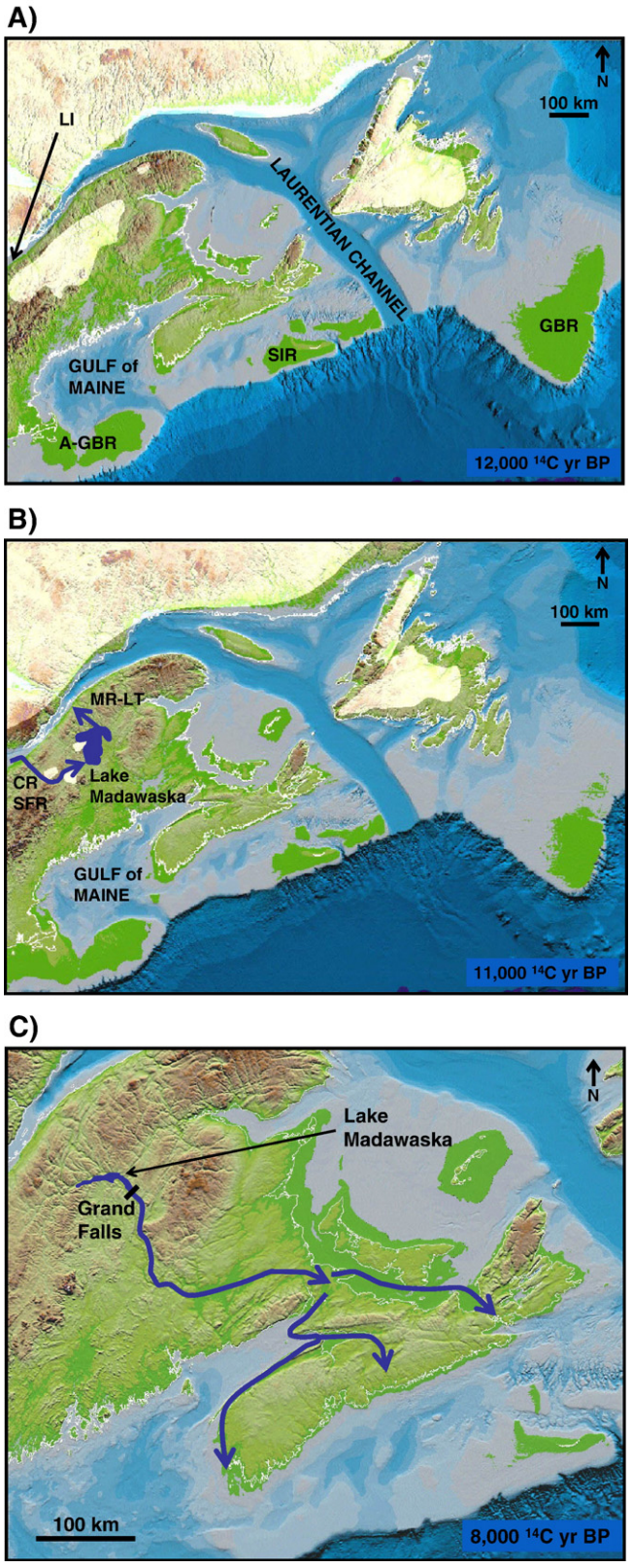

Figure 2. Paleo-coastlines of eastern North America from 12,000 to 8000 ^{14}C yr BP after Shaw and Courtney (2002). White areas are glacial ice, green areas are terrestrial environments, and white lines are present-day coastlines. Arrows represent proposed recolonization routes for obligate freshwater fishes (see text). (A) 12,000 ^{14}C yr BP. Hypothesized refugia are the Grand Banks (GBR) and Sable Island (SIR); the Georges Bank was initially connected to the known Atlantic Coastal Refuge (A-GBR). The upper St. Lawrence River valley of present-day was freshwater Lake Iroquois (LI) blocked from the sea by glacial ice across the valley at approximately the location of present-day Quebec City, QC. Present-day southern Maine remained inundated by the sea. (B) 11,000 ^{14}C yr BP. Arrows indicate the hypothesized flow of fresh water and access routes for fishes from the Chaudière River (CR) and St. François River (SFR) to Lake Madawaska forming in the river valley of the present-day Saint John River in northern Maine and New Brunswick. The Lake Madawaska outflow was north through the present-day Madawaska River-Lake Temiscouata valley (MR-LT). The St. Lawrence River valley was eventually inundated by marine waters to become the Champlain Sea. (C) 8000 ^{14}C yr BP. The proposed colonization routes from Lake Madawaska (arrows) are indicated.