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Range Extension, Present and Potential Distribution, and Possible Effects of Rainbow Smelt in Hudson Bay Drainage Waters of Northwestern Ontario, Manitoba, and Minnesota

WILLIAM G. FRANZIN

Canada Department of Fisheries and Oceans, Central and Arctic Region Freshwater Institute 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada, and Zoology Department, University of Manitoba Winnipeg, Manitoba R3T 2N2, Canada

BRUCE A. BARTON[1]

Department of Biology, University of North Dakota Grand Forks, North Dakota 58202, USA

RICHARD A. REMNANT[2]

Natural Resources Institute, University of Manitoba Winnipeg, Manitoba R3T 2N2, Canada

DUNCAN B. WAIN

Zoology Department, University of Manitoba Winnipeg, Manitoba R3T 2N2, Canada

SHIRLEY JO PAGEL

Department of Biology, University of North Dakota Grand Forks, North Dakota 58202, USA

Abstract.—Rainbow smelt *Osmerus mordax*, introduced into the Great Lakes watershed (Crystal Lake, Michigan) in about 1912, began colonizing the Great Lakes in the 1920s. The species now is found throughout much of the Great Lakes watershed of Ontario and in the Mississippi–Missouri drainage as a result of inadvertent or intentional introductions. Gill-net and trawling surveys in 1989 and 1990 of 79 lakes (92 separate times or sites) in the Winnipeg River system of the Hudson Bay drainage in northwestern Ontario, southeastern Manitoba, and northeastern Minnesota revealed or confirmed the presence of rainbow smelt in 19 lakes and extended the species' known range in the Rainy, English, and Wabigoon river systems. Rainbow smelt also were discovered in Lake Winnipeg late in 1990 and in Lake of the Woods in early 1991. Elsewhere, the establishment of rainbow smelt in new water bodies often has been associated with changes in native fish populations. The potential now exists for further spread of rainbow smelt in this watershed as far as Hudson Bay.

The rainbow smelt *Osmerus mordax* is an invasive species considered a pest by some and a boon to fisheries by others. Undesirable effects of exotic species, such as rainbow smelt, on indigenous fish faunas include reduction in growth, elimination of native species, and changes in the community structure of the affected waters (Moyle et al. 1986). Many retrospective studies have been written on the effects of rainbow smelt invasions, most recently those of Evans and Loftus (1987), Evans and Waring (1987), and Nellbring (1989). These studies identified the potential threat posed by rainbow smelt to existing sport and commercial fisheries and attempted to define some of the interactions that have occurred in lakes where rainbow smelt have become established. Evans and Waring (1987) identified a basic problem: the success of rainbow smelt colonization and the ecological effects of the species in a lake ecosystem are not always predictable from physical and biological data.

Evans and Loftus described the distribution of rainbow smelt in Ontario as of 1986. The species

[1] Present address: Department of Biology, University of South Dakota, Vermillion, South Dakota 57069, USA.

[2] Present address: North/South Consultants, Inc., 202-1475 Chevrier Boulevard, Winnipeg, Manitoba R3T 1Y7, Canada.

reached Ontario after it was deliberately introduced from landlocked native Maine populations into the Great Lakes as early as 1912. Several intentional and accidental introductions of rainbow smelt have occurred outside the Great Lakes basin, particularily in the upper Mississippi River system and in the headwaters of the Rainy River in Minnesota and northwestern Ontario. The Rainy River drains, via the Winnipeg and Nelson rivers, to Hudson Bay.

The following account of the spread of rainbow smelt in the Missouri–Mississippi drainage after a point introduction illustrates the potential of the species as a colonist. Gravid female rainbow smelt were introduced into a Missouri River reservoir—Lake Sakakawea, North Dakota—from Lake Superior in the spring of 1971 by the North Dakota Game and Fish Department to serve as a forage base for sport fishes (Dyke 1989). A self-sustaining population of rainbow smelt established itself within a few years. Rainbow smelt appeared in Lake Oahe, South Dakota, the first reservoir downstream of Lake Sakakawea, by 1974 and large numbers of the species are now present in both of these reservoirs (Mayden et al. 1987). Rainbow smelt also are found in the next three downstream reservoirs but are not as well established there, apparently because of inferior habitat (Mayden et al. 1987). This species also has been recorded from several locations further downstream in the mainstem Missouri and Mississippi rivers, and it was collected as far south as Louisiana in 1979 (Suttkus and Connor 1979). Rainbow smelt have been collected in the Missouri River upstream of Lake Sakakawea as far as just below Fort Peck Dam and in the Yellowstone River, Montana, in 1979 (Gould 1981). Most Mississippi and all Missouri River occurrences are presumed to have resulted from the Lake Sakakawea introduction (Mayden et al. 1987). Rainbow smelt found in the Illinois River (and some in the Mississippi River) are assumed to have arrived there from Lake Michigan via the Chicago Sanitary Canal, but a single specimen taken from the Ohio River in 1986 is of unknown origin (Mayden et al. 1987).

The first record of rainbow smelt from the Hudson Bay drainage basin was from Little Eagle Lake near Dryden, Ontario, in about 1962 (Campbell et al. 1991). This small closed-basin lake was poisoned in 1978 and the population of rainbow smelt was eradicated (Campbell et al. 1991). It is not known whether other populations of rainbow smelt in the basin were established via dispersal from Little Eagle Lake. Rainbow smelt also have been present in the upper portion of the Rainy River system since 1972—in Burntside Lake, Minnesota, and Eva Lake, Ontario (Campbell et al. 1991).

Our study documented the current distribution of rainbow smelt in Hudson Bay drainage waters of northwestern Ontario, southeastern Manitoba, and northern Minnesota, waters that eventually drain into Manitoba's large lakes, which have important commercial fisheries. In this paper, we present the new survey data and, in combination with existing information on rainbow smelt, use them to examine the potential for further spread of this species in the Hudson Bay watershed and to assess some of the consequences of the species' presence.

Methods

Two study teams surveyed Hudson Bay drainage waters near the mutual borders of Ontario, Manitoba, and Minnesota during the summers of 1989 and 1990 to establish or confirm the presence of rainbow smelt. Initially, biologists from Ontario Ministry of Natural Resources (OMNR) and Minnesota Department of Natural Resources (MNDNR) were consulted to list those lakes that were known or suspected to contain rainbow smelt populations. Sampling programs were focused on lakes either reported to contain rainbow smelt or to possess habitat suitable for rainbow smelt. For example, deep water that thermally stratifies and maintains adequate levels of dissolved oxygen was one habitat criterion. Additional lakes sampled, although considered to contain marginal rainbow smelt habitat, were selected because they were along important drainage routes. Seventy-nine lakes (92 separate collection sites or times) were sampled over the two summers (Table 1).

Sampling for rainbow smelt was done mainly with small-mesh gill nets set overnight. This sampling method was verified before the survey in lakes known to contain rainbow smelt (Pakwash Lake, Ontario, and Lake Audubon, North Dakota). Sampling in Ontario and Manitoba included overnight sets of gill nets with 8-, 10-, and 13-mm-bar mesh in 1989 and with 6.25-, 8-, 10-, 12.5-, and 16-mm-bar mesh in 1990. Nets were set perpendicular to depth contours on steep slopes near points of land, islands, or reefs. Nets often were suspended with floats at an angle from the surface to the bottom to sample different depths within the pelagic zone. Most of the net gang was suspended at depths where fish had been located with an electronic fish finder or at depths in the temperature range (8–13°C) preferred by rainbow smelt. A 6-m otter trawl also was used but was restricted to waters with depths less than 16.5 m and with flat stretches of silt or sand bottom. Trawling was effective in catching yearling rainbow smelt, but its use was limited because many of the lakes surveyed were either riverine or reservoirs with unsuitable substrates.

Rainbow smelt were sampled in Minnesota with overnight sets of gill nets of 10- and 13-mm-bar mesh in 1989 and of 8-, 10-, and 13-mm mesh in 1990. An electronic thermistor thermometer was used first to determine the thermocline depth in all Minnesota lakes. Nets were then set on the bottom, with the aid of an electronic depth finder, such that the top of the net was below the thermocline.

Results and Discussion

Present Distribution in Northwestern Ontario and Eastern Manitoba

The presence of rainbow smelt was confirmed in Pakwash, Red, and Gullrock lakes, Ontario (sample numbers 1, 3, and 4: Table 1; Figure 1). The species also was discovered in Keg and Two Island lakes (5 and 6, immediately upstream and downstream from Gullrock Lake) in the Chukuni River drainage just above its confluence with the English River. Gullrock, Keg, and Two Island lakes had high relative abundances of rainbow smelt, even though they were poorly stratified and had limited hypolimnetic volumes. Later in the summer when these three lakes were resampled, the water columns were isothermal with temperatures up to 20°C. Large numbers of rainbow smelt were caught again, suggesting that temperature may not be as important a barrier to downstream migration and colonization as previously thought.

Rainbow smelt also were confirmed in Sandybeach Lake (43) and were detected in Abram Lake (38), both English River headwaters above Lac Seul. Our survey did not detect rainbow smelt in Minnitaki Lake (39, between Sandybeach and Abram lakes) but OMNR confirmed their presence there in summer 1991 (P. McMahon, ONMR, personal communication). There are no barriers to rainbow smelt movement from these lakes into Lac Seul, where there is an important regional fishery and ideal rainbow smelt habitat.

The presence of rainbow smelt was confirmed in Favel Lake (33), but the species was not found immediately downstream in Canyon Lake (35); both are in the Canyon River, a tributary of the Wabigoon River. No rainbow smelt were found in Wabigoon (53) or Eagle (54) lakes in the upper Wabigoon River or in Clay Lake (52), a main-stem lake in the Wabigoon River downstream of the outlet of Canyon River.

No rainbow smelt were caught in most lake basins of the lower English River downstream of Manitou Falls Dam (7, 10, 12, 13, 14). Many of these lakes are widened, thermally unstratified channels of the river and may not be suitable for rainbow smelt. Several lakes flowing into the lower English River, notably Clear (8), Johnson (9), Unexpected (11), and Dumpy (49) lakes, appeared suitable for rainbow smelt, but the species was not caught in them. Similarly, Oak Lake (46, 47), a main-stem lake downstream of a series of falls, has a deep basin off the main channel that is stratified and thus suitable for rainbow smelt, but none were caught there. Below yet another series of falls, a single rainbow smelt was caught in Tide Lake (16) and in Indian (18) Lake (upstream and downstream of Ball Lake at the confluence of the Wabigoon and English rivers), even though these were highly turbid, unstratified basins with bottom temperatures of 21°C at the time. Umfreville Lake (24–29, 56, 57), a large reservoir on the English River, was sampled in both 1989 and 1990 because of its apparently suitable habitat and its position downstream of known rainbow smelt populations, but no rainbow smelt were caught. Rainbow smelt were not caught in any of the remaining lakes sampled in the English River system.

Gillnetting in Tetu (30), Big Sand (31), and Lulu (32) lakes in the Winnipeg River system above its confluence with the English River and in Silver Lake (34) in the Black Sturgeon River system did not yield rainbow smelt. Similarly, rainbow smelt were not detected in Eaglenest Lake (55), Nutimik Lake (51), or Lac du Bonnet (50) on the main stem of the Winnipeg River in Manitoba or in the south basin of Lake of the Woods (60).

Rainbow smelt were not detected in Berens Lake, Ontario (58, 59), a headwater lake on the Berens River that drains to the east side of Lake Winnipeg. Berens Lake is accessible by road from the town of Red Lake, Ontario.

Stomachs of Lake Winnipeg walleyes *Stizostedion vitreum* collected immediately after the beginning of the 1990 spring commercial fishery on Lake Winnipeg and examined by Remnant (1991) provided the earliest record of rainbow smelt from that lake. Rainbow smelt also were captured in Lake Winnipeg (61) during the fall commercial fishery in October 1990 (Campbell et al. 1991).

TABLE 1.—Lakes in western Ontario, southeastern Manitoba, and northeastern Minnesota sampled for rainbow smelt during 1989 and 1990.

Date	Sample number	Lake name[a]	Latitude	Longitude	Temperature (°C) Surface	Temperature (°C) Bottom	Maximum depth (m)	Fishing effort (number of gang-nights)[b]	Rainbow smelt caught?
			Ontario lakes: 1989						
Jun 6–10	1	Pakwash	50°45'N	93°30'W	17.0	11.0	15.0	10	Yes
Jun 11	2	Bruce	50°49'N	93°20'W	18.5		3.0	2	No
Jun 15	3	Red	51°03'N	93°57'W	14.0	7.0	31.0	3	Yes
Jun 18	4	Gullrock	50°58'N	93°40'W	19.0	11.0	13.5	1	Yes
Jun 17	5	Keg	51°00'N	93°41'W	20.0	12.0	12.0	1	Yes
Jun 19	6	Two Island	50°55'N	93°35'W	18.0	12.5	9.5	1	Yes
Jun 29	7	Barnston	50°35'N	93°30'W	18.5	18.5	8.5	1	No
Jun 30	8	Clear	50°34'N	93°35'W	21.0	4.5	16.3	1	No
Jun 30	9	Johnson	50°34'N	93°35'W	22.5	10.0	11.0	1	No
Jul 1	10	Wegg	50°34'N	93°35'W	24.5	18.5	11.0	1	No
Jul 2	11	Unexpected	50°30'N	93°52'W	22.0	13.5	13.5	3	No
Jul 2	12	Goose	50°32'N	93°40'W	21.5	18.5		1	No
Jul 2	13	Wilcox	50°31'N	93°47'W	21.5	18.5		1	No
Jul 4	14	Camping	50°36'N	93°25'W	22.5	20.5	7.0	1	No
Jul 8	15	Grassy Narrows	50°09'N	94°02'W	23.0	8.5	15.0	3	No
Jul 9	16	Tide	50°20'N	93°58'W	21.5	21.0	18.5	1	Yes
Jul 9	17	Ball	50°18'N	94°00'W	21.0	20.5	12.5	1	No
Jul 9	18	Indian	50°14'N	94°05'W	21.5	19.5	18.5	1	Yes
Jul 10	19	Little Fox	50°11'N	94°09'W	21.0	20.5	15.0	1	No
Jul 10	20	Shoe	50°08'N	94°10'W	23.5	12.0	6.0	1	No
Jul 10	21	Big Fox	50°11'N	94°13'W	21.5	20.5	9.5	1	No
Jul 11	22	Lount	50°10'N	94°19'W	21.5	20.5	13.0	1	No
Jul 11	23	Separation	50°14'N	94°24'W	21.5	21.0	17.0	2	No
Jul 21	24	UR: Twelnor Lake	50°23'N	94°57'W	27.0	5.5	29.5	1	No
Jul 21	25	UR: Gib Lake	50°21'N	94°57'W	26.0	8.0	21.5	1	No
Jul 21	26	UR: main basin	50°18'N	94°58'W	24.5	10.5	22.0	1	No
Jul 22	27	UR: Powerline Bay	50°18'N	95°03'W	26.0	4.5	30.5	1	No
Jul 22	28	UR: Goshawk Lake	50°15'N	94°48'W	18.5	8.5	18.5	1	No
Jul 22	29	UR: Oneman Lake	50°18'N	94°48'W	24.0	9.5	26.0	1	No
Jul 23	30	Tetu	50°11'N	95°02'W	23.0	21.0	15.0	2	No
Jul 24	31	Big Sand	50°06'N	94°37'W	25.0	6.0	40.0	3	No
Jul 25	32	Lulu	49°47'N	94°42'W	27.0	9.5	12.5	2	No
Jul 31	33	Favel	50°00'N	94°00'W	23.0	7.0	24.5	3	Yes
Aug 1	34	Silver	49°53'N	94°11'W	24.0	6.5	28.0	3	No
Aug 1	35	Canyon	49°58'N	93°40'W	24.0	10.0	16.5	3	No
Aug 8	36	Namakan	48°27'N	92°35'W	22.0	9.5	23.0	3	No
Aug 9	37	Rainy	48°42'N	93°10'W	25.5	10.5	31.0	3	No
Aug 14	38	Abram	50°04'N	91°57'W	21.0	7.5	29.0	3	Yes
Aug 15	39	Minnitaki	49°58'N	92°00'W	21.0	9.0	25.0	3	No
Aug 16	40	Pelican	50°07'N	91°58'W					No
Aug 16	41	LSR: Italian Bay	50°07'N	92°07'W	23.0	5.0	19.5	1	No
Aug 16	42	LSR: Keewatin Bay	50°07'N	92°07'W	23.0	7.0	18.0	2	No
Aug 17	43	Sandybeach	49°49'N	92°21'W	21.0	7.0	35.0	3	Yes
Aug 18	44	Two island	50°55'N	93°35'W	21.5	20.0	10.0	1	Yes
Aug 19	45	Gullrock	50°58'N	93°40'W	21.0	20.0	13.0	3[c]	Yes
Aug 28	46	Oak west	50°26'N	93°50'W	20.0	6.0	21.0	1	No
Aug 28	47	Oak east	50°26'N	93°50'W	20.0	5.0	30.5	1	No
Sep 1	48	Maynard	50°22'N	93°54'W	20.0	14.0	16.5	1	No
Sep 2	49	Dumpy	50°19'N	94°04'W	20.5	4.3	25.0	1	No
			Ontario lakes: 1990						
Jun 20	52	Clay	50°03'N	93°30'W	19.0	8.0	19.0	3	No
Jun 21	53	Wabigoon	49°44'N	92°44'W	17.0	15.0	13.0	3	No
Jun 22	54	Eagle	49°51'N	93°24'W	18.5	11.0	20.0	4	No
Jun 24	56	UR: Gib Lake	50°21'N	94°57'W	20.0	6.3	21.0	1	No
Jun 24	57	UR: main basin	50°18'N	94°58'W	20.0	8.5	25.0	3	No
Jul 31	58	Berens south	51°47'N	93°45'W	21.5	5.5	9.5	1	No
Jul 31	59	Berens main	51°47'N	93°45'W	22.0	7.5	7.5	2	No
Aug 28–29	60	Lake of the Woods	49°05'N	94°26'W	22.5	22.5	8.0	6	No[d]

TABLE 1.—Continued.

Date	Sample number	Lake name[a]	Latitude	Longitude	Temperature (°C) Surface	Temperature (°C) Bottom	Maximum depth (m)	Fishing effort (number of gang-nights)[b]	Rainbow smelt caught?
			Manitoba lakes: 1990						
Jun 18	50	Lac du Bonnet	50°22'N	95°55'W	20.0	11.0	14.0	3	No
Jun 19	51	Nutimik	50°09'N	95°41'W	17.0	17.0	11.0	1	No
Jun 23	55	Eaglenest	50°06'N	95°23'W	22.0	16.0	8.0	1	No
Oct 9	61	LWS: near Arnes	50°48'N	96°52'W			8.0	8	No[e]
Oct 16	61	LWS: near Arnes	50°48'N	96°52'W			10.0	4	No
Oct 21	61	LWS: near Arnes	50°48'N	96°52'W			10.0	4	No
			Minnesota lakes: 1989[b]						
Aug 8	36	Namakan	48°27'N	92°36'W	20.5	16.0	12.0	6	No
Aug 10	37	Rainy	48°38'N	93°00'W	20.5	19.0	10.0	3	No
Jun 20(?)	62	Hanson	47°58'N	91°56'W					Yes[d]
Jun 20	63	Burntside	47°56'N	92°00'W	9.0	6.0	38.0	5	Yes
Jun 21	64	Little Long	47°56'N	91°53'W					Yes[d]
Jun 22	65	Fall	47°57'N	91°42'W	19.0	15.0	9.0	2	No
Jun 22	66	Shagawa	47°55'N	91°53'W	19.0	13.5	10.5	2	No
Jun 23	67	Eagles Nest 1	47°50'N	92°06'W	19.0	5.5	10.5	2	Yes
Jun 23	68	Eagles Nest 2	47°49'N	92°07'W	20.0	7.5	8.0	3	Yes
Jun 24	69	Eagles Nest 3	47°49'N	92°05'W	21.0	8.5	9.0	2	No
Jun 24	70	Eagles Nest 4	47°50'N	92°04'W	21.0	5.0	12.0	2	No
Jun 26	71	Basswood	48°03'N	91°29'W	18.5	7.5	17.0	4	No
Jun 27	72	Snowbank	47°59'N	91°25'W	18.5	10.5	13.5	4	No
Jun 27	73	White Iron	47°52'N	91°49'W	19.5	10.0	12.0	2	No
Jun 29	74	Vermilion	47°52'N	92°19'W	19.5	14.5	10.0	6	No
Jul 13	75	Saganaga	48°13'N	90°55'W	20.0	8.5	12.0	6	Yes
Jul 14	76	Gunflint	48°06'N	90°42'W	20.0	11.0	10.5	4	No[f]
Jul 14	77	North	48°06'N	90°35'W	21.5	9.4	13.0	1	No
Jul 15	78	Magnetic	48°06'N	90°46'W	20.5	7.5	11.5	2	No[f]
Jul 15	79	Loon	48°04'N	90°42'W	21.0	10.5	7.0	4	No
Jul 17	80	North Star	47°33'N	93°40'W	25.0	5.5	13.5	4	No
Jul 17	81	Bello	47°40'N	93°43'W	24.0	6.0	12.0	2	No
Jul 18	82	Jessie	47°35'N	93°49'W	20.5	14.0	10.0	3	No
Jul 18	83	Big Deer	47°50'N	93°23'W	24.5	11.5	12.0	3	No
Jul 19	84	Turtle	47°37'N	93°42'W	24.5	6.5	13.5	6	No
Jul 20	85	Sand	47°37'N	94°01'W	25.0	9.5	15.0	6	No
Aug 2	86	Crane	48°16'N	92°30'W	23.5	8.5	15.5	6	No
Aug 3	87	Sandpoint	48°20'N	92°27'W	25.0	8.5	15.0	6	No
Aug 4	88	Lac la Croix	48°20'N	92°17'W	23.5	11.0	10.5	3	Yes
Aug 7	89	Kabetogama	48°28'N	93°01'W	21.5	18.0	12.0	6	No
			Minnesota lakes: 1990[b]						
Jul 22	90	Namakan	48°27'N	92°36'W	22.0	13.0	15.0	4	Yes
Jul 24	91	Rainy	48°38'N	93°00'W	23.0	12.0	16.5	4	Yes
Jul 22	92	Crane	48°16'N	92°30'W	21.2	8.0	17.0	4	No

[a] UR denotes an Umfreville Reservoir subbasin, LSR denotes a Lac Seul Reservoir subbasin, and LWS denotes the Lake Winnipeg south basin.

[b] Gill nets were set overnight unless footnoted differently. In Ontario in 1989, one gang comprised three 1.5-m × 15-m panels of 8-, 10-, and 13-mm-bar mesh. In both Ontario and Manitoba in 1990, one gang comprised five 1.5-m × 15-m panels of 6-, 8-, 10-, 13-, and 16-mm-bar mesh. In Minnesota in 1989, one gang comprised four 2-m × 38-m panels of 13-mm-bar mesh, to which usually was added one 2-m × 46-m panel of 10-mm-bar mesh and (or) one 2-m × 61-m panel of 10-mm-bar mesh. In Minnesota in 1990, one set each of two 2-m × 38-m panels of 13-mm-bar mesh, one 2-m × 46-m panel of 10-mm-bar mesh, and one 2-m × 38-m panel of 8-mm-bar mesh was made in each lake.

[c] Gangs were set for 2.5 h.

[d] Sample was taken by the Minnesota Department of Natural Resources.

[e] Sample was taken by the Manitoba Department of Natural Resources.

[f] Previous records indicate the presence of rainbow smelt in the lake.

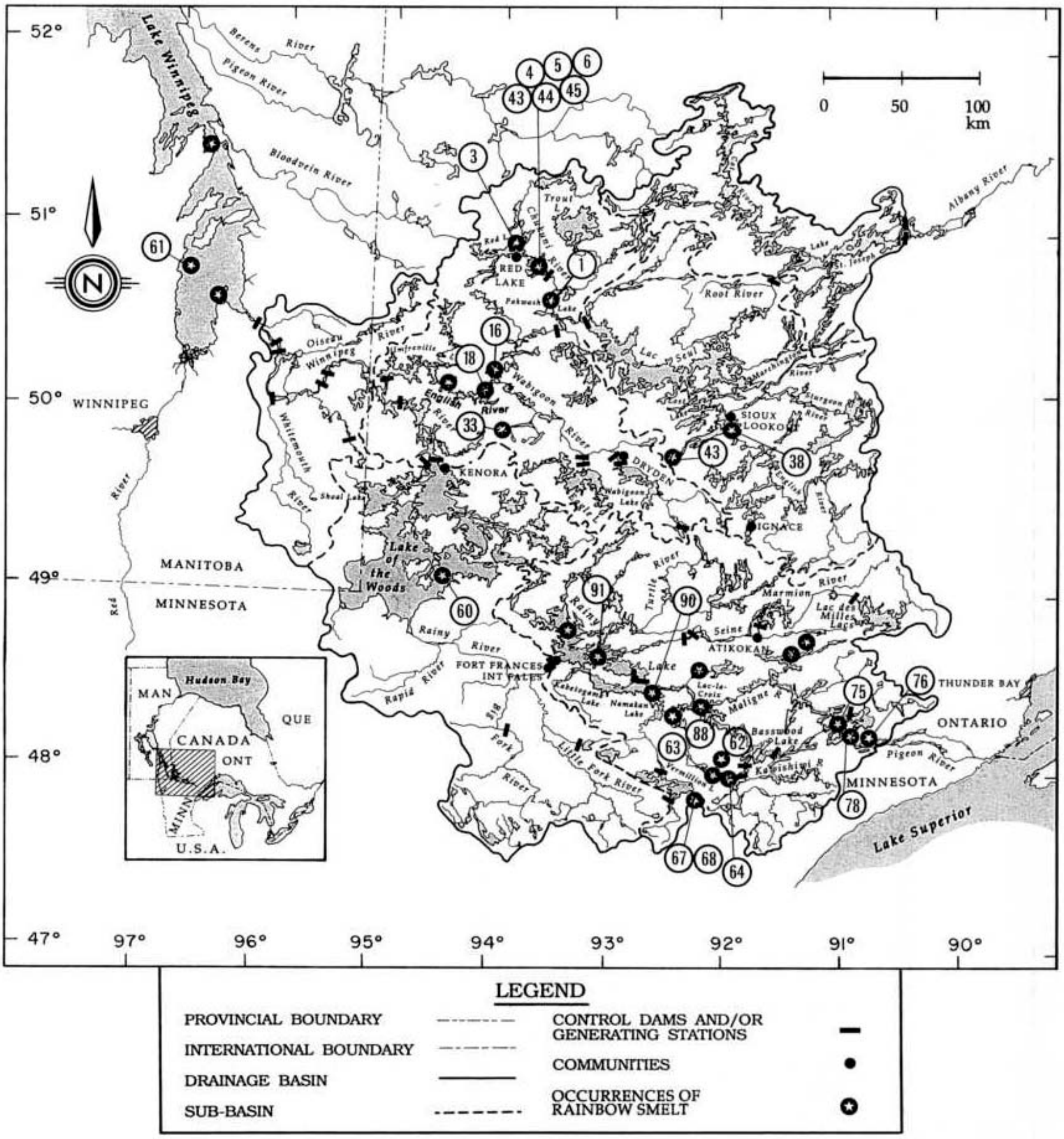

FIGURE 1.—Known occurrences of rainbow smelt in the Hudson Bay drainage basin of Manitoba, northwestern Ontario, and northeastern Minnesota as of December 1991. Numbered stars indicate locations where rainbow smelt were discovered or confirmed during the study period; unnumbered stars indicate occurrences that were known but not confirmed. Circled numbers are sample numbers (see Table 1). Adapted from Remnant (1991).

Present Distribution in Northern Minnesota

Rainbow smelt were found in Lac la Croix (88) in 1989 and in Namakan (36, 90) and Rainy (37, 91) lakes in 1990. These new records represent substantial range extensions for this species in the main-stem portion of the Rainy River. Rainbow smelt were found at depths of 7–8 m in 14.5°C water in Snow Bay at the west end of Lac la Croix, in 10.5°C water at a 20-m depth in Rainy Lake, and in 13°C water 15 m deep in Namakan Lake. The occurrence of rainbow smelt in these lakes could be explained by accidental introductions by anglers, downstream migrations from Trout, Beaverhouse, Eva, and Pickerel lakes in Ontario, or downstream movements in the Rainy River system from Saganaga Lake. The failure to detect rainbow smelt upstream of Lac la Croix in Bayley Bay (71) of Basswood Lake suggests that the last alternative is the least plausible of the three.

The presence of rainbow smelt also was confirmed in most of the lakes in which they previously had been reported by MNDNR: Burntside Lake (63), Eagles Nest lakes 1 and 2 (67, 68), and Saganaga Lake (75). Samples of rainbow smelt captured in 1989 from Hanson (62) and Little Long (64) lakes were provided by MNDNR. Rainbow smelt were not caught in Gunflint (76) or Magnetic (78) lakes, although they have been found previously in these waters. The failure to find rainbow smelt in those lakes may have been due to the relatively low sampling effort applied. Rainbow smelt were not detected in any lakes of the Big Fork River system (80–85).

Since the collection of rainbow smelt in the eastern end of Rainy Lake in 1990, additional specimens have been taken, including a single large specimen from the North Arm of the lake in early July 1991 (R. Wepruck, OMNR, personal communication). Rainbow smelt apparently have migrated down the Rainy River into Lake of the Woods; several specimens of young-of-year rainbow smelt were caught in bottom trawls at two locations along the south shore of Big Traverse Bay in August 1991 (D. Topp, MNDR, personal communication).

Figure 1 shows all known rainbow smelt occurrences in the investigated area as of December 1991.

Factors Affecting the Distribution of Rainbow Smelt

Important correlative biological and physical characteristics of lakes and their suitability for successful invasion by rainbow smelt have been reviewed by Evans and Loftus (1987) and Nellbring (1989). We found no significant differences in means of surface and bottom temperatures or means of maximum depths between lakes with and without rainbow smelt in our surveys.

An assessment of the potential for the spread of rainbow smelt beyond their presently documented distribution is subject to assumptions about the relative importance of two processes: continued colonization by fish moving unaided, and spread of the species by human activities, which have played a very large role in the modern distribution of the species. We may be able to do very little to contain the species if unaided colonization predominates, but educational programs and public information can help shape the result if humans remain the predominant vector.

Natural Dispersal

Significant rainbow smelt populations probably will develop without human assistance in Namakan Lake, Rainy Lake, and Lake of the Woods (including Shoal Lake) and in the larger, deeper, off-current main-stem lakes in the Winnipeg River below Lake of the Woods that meet habitat requirements (e.g., Sand, Gun, Swan, and Cygnet lakes).

Namakan Lake, Rainy Lake, and Lake of the Woods offer habitats to support all life stages of rainbow smelt and large populations are possible in these waters. A large rainbow smelt population in Lake of the Woods would provide a source for continual downstream colonization of the Winnipeg River system. Despite large populations of the species in Chukuni River lakes, large-scale colonization of downstream English River lakes apparently has not yet occurred. However, it is possible that a large population will build up in Lac Seul over the next few years, providing a larger source and more direct route for rainbow smelt movement downstream than has hitherto been available. If a large population develops in Umfreville Lake, the last large reservoir on the English River, the Winnipeg River system in Manitoba would have two large sources from which rainbow smelt could colonize lower main-stem lakes and reservoirs, from Tetu Lake to Lac du Bonnet. Many of these lakes will not provide ideal habitat for all life stages of rainbow smelt and thus may not support large populations. The potential for upstream movement of rainbow smelt from the Winnipeg River is limited by rapids or falls on some tributaries (e.g., Whiteshell River) and by dams on others (e.g., Black Sturgeon River). A third route by which rainbow smelt may colonize Manitoba is transportation by humans from Red Lake into the headwater lakes of the Berens River, a short distance north of Red Lake by road.

If rainbow smelt had not found their way to Lake Winnipeg already, they probably would appear there shortly, given the upstream sources and the rapid, recent movement of the species downstream in the Rainy River. Campbell et al. (1991) reviewed the possible routes that rainbow smelt may have used to reach Lake Winnipeg.

It is worth considering the potential future distribution of rainbow smelt in the Lake Winnipeg basin. Remnant (1991) considered the likelihood that a large rainbow smelt population will become established in Lake Winnipeg and what might limit the species' dispersal from the lake. He concluded that rainbow smelt eventually will colonize Lake Winnipeg, but that suitable thermal habitat, particularily for adult fish, is limited. Lake Winnipeg is shallower, more turbid, and warmer in summer than other large lakes (e.g., Lake Erie) where rainbow smelt have become abundant. Also, Lake Winnipeg remains thermally unstratified during most of the open-water period, precluding development of cool hypolemnetic refugia usually sought by adult rainbow smelt in most lakes where they are abundant (e.g., the eastern, stratified basin of Lake Erie). Lake whitefish *Coregonus clupeaformis* are abundant only in the north basin of Lake Winnipeg (Davidoff et al. 1973), indicating the existence of potentially suitable habitat for rainbow smelt there. Remnant (1991) concluded, in view of these factors, that a rainbow smelt population in Lake Winnipeg would favor the north basin of the lake but that such fish may be expected to exhibit early maturation, short life spans, high summer mortality, and fluctuating population size, as seen in other shallower lakes with stressed rainbow smelt populations.

The natural dispersion of rainbow smelt that may occur if a large population develops in Lake Winnipeg is more speculative than dispersion to the lakes between Lake of the Woods and Lake Winnipeg. Remnant (1991) concurred with Loch et al. (1979) that rainbow smelt may colonize, in a limited way, Lakes Manitoba and Winnipegosis via Dauphin and Fairford rivers, but that habitat for adult rainbow smelt in these lakes is limited. Lake whitefish are taken in summer commercial fisheries only in the very northern area of Lake Manitoba (Department of Fisheries and Oceans, Freshwater Fish Marketing Corp., unpublished data), suggesting that most of the lake is unsuitable for all but young-of-year rainbow smelt. Bajkov (1930) indicated that summer conditions suitable for lake whitefish in Lake Winnipegosis were limited to the deeper northern portion of the lake. This suggests that only limited areas of the lake may be suitable for all life stages of rainbow smelt. Downstream movement in the Nelson River is expected, but apparently suitable thermal habitat for all life stages of rainbow smelt is limited to Split and Stephens lakes (Remnant 1991).

The natural outcome of downstream movement in the Nelson River, of course, is that rainbow smelt, for the first time since the Wisconsinan glacial period, will have access to Hudson Bay. This access will complete the cycle of their introduction from marine Atlantic coast to freshwater and back to the marine system. Rainbow smelt on the Atlantic coast are restricted, apparently by cold sea temperatures, to the area south of Hamilton Inlet, Labrador (Scott and Scott 1988). The distribution of capelin *Mallotus villosus* and rainbow smelt overlaps along Canada's east coast, but only capelin extend their distribution around northern Labrador and Quebec and along the Arctic coast (Scott and Scott 1988). There is every reason to expect that once rainbow smelt are introduced into Hudson Bay, they will thrive there. The large estuary at the mouth of the Nelson and Hayes rivers in Hudson Bay, as well as several smaller estuaries around the southern end of Hudson and James bays, should provide areas of warmer water necessary for rainbow smelt to overwinter in Hudson Bay. Also, rainbow smelt probably will establish anadromous populations in tributary rivers.

Human-Assisted Dispersal

Humans have been by far the most important agent in the spread of rainbow smelt, whether their actions have been deliberate or accidental. Because this activity is not likely to halt immediately, many more lakes in northwestern Ontario, central and northern Manitoba, eastern Saskatchewan, and northern Minnesota are at risk of rainbow smelt introduction.

Ontario sportfishing regulations state "It is illegal to possess live or dead smelt for use as bait or while sport fishing in Divisions 22, 24, 30 and 31 in Northwestern Ontario" (OMNR 1990). This area includes most of northwestern Ontario west of 89°W, from Rainy Lake in the south to Big Trout Lake in the north to the Manitoba border. Manitoba sportfishing regulations (1991) prohibit possession of live rainbow smelt or use of live or fresh dead rainbow smelt for angling. Both provinces have begun public information programs aimed at reducing the risk of further spread of rainbow smelt. Despite these efforts, most lakes in both provinces that contain lake trout *Salvelinus namaycush* and that are accessible by road or have substantial cottage developments on them are at great risk of rainbow smelt introduction. These lakes include many in the Red Lake, Dryden, Kenora, and Fort Frances districts of northwestern Ontario, the Whiteshell, Nopiming, and The Pas–Flin Flon–Thompson areas of Manitoba, and lake trout lakes in east-central Saskatchewan.

Minnesota sportfishing regulations (1991) forbid possession or transport of live rainbow smelt in Minnesota and warn of the consequences of depositing fresh rainbow smelt or their eggs in lakes. However, allowing the use of fresh rainbow smelt as bait may encourage their continued spread to accessible, suitable waters in northern Minnesota (e.g., lakes in the Big Fork River system and in the headwaters of the Mississippi River system in the Bemidji area). A large factor in the spread of rainbow smelt by anglers is the coincidence in time of rainbow smelt spawning, recreational fishing for the species as food and bait, and the spring lake trout fishery. Viable, fertilized rainbow smelt eggs can be obtained from a bucket of fresh, iced, mixed-sex rainbow smelt taken during the spawning run, even many hours after capture (W. G. Franzin, personal observation).

Ecological Impacts of Rainbow Smelt Introductions

Rainbow smelt are opportunistic feeders and can occupy the roles of prey, predator, and competitor. They are used as food by virtually all coexisting predators, including larger conspecifics. A frequent result of rainbow smelt introduction or colonization is increased growth rates of salmonids (McCaig and Mullan 1960; Bridges and Hambly 1971; Ryan and Kerekes 1988) and possibly other predator species.

There are indications that changing to a diet of rainbow smelt increases mercury levels in the white muscle of piscivorous fishes, particularly those in soft-water areas. Three studies support these conclusions. MacCrimmon et al. (1983) observed a pronounced acceleration in growth rate of and an increase in mercury accumulation in lake trout after the trout switched from an invertebrate diet to one of rainbow smelt. Akielaszek and Haines (1981), as well as MacCrimmon et al. (1983), found that lake trout taken from lakes containing rainbow smelt exhibited higher mercury levels than did those taken from nearby lakes where rainbow smelt were absent. Mathers and Johansen (1985) found that walleyes in Lake Simcoe, Ontario, which fed mainly on rainbow smelt, accumulated higher levels of mercury than did northern pike *Esox lucius*, which fed mainly on other species; they also found higher levels of mercury in Lake Simcoe rainbow smelt than in other forage fish. However, it remains to be shown that mercury levels in a single piscivorous fish population increase after a change from an indigenous forage fish diet to one of rainbow smelt.

Lake whitefish is perhaps the most frequently cited example of a species that is negatively affected by the introduction of rainbow smelt. Frequently, lake whitefish recruitment declines after invasion of a lake by rainbow smelt. This suggests a cause–effect relationship. Whether the mechanism of the interaction is predation or competition or a combination of factors cannot be determined retrospectively, however. Loftus and Hulsman (1986) documented extensive predation on larval lake whitefish by postspawning rainbow smelt over a 7-week period in a small Ontario lake.

The evidence for competition between rainbow smelt and indigenous species has been more circumstantial. A presumption of competition between rainbow smelt and native fishes is based on habitat and diet overlaps and on comparisons of change in growth, survival, and abundance of native species before and after rainbow smelt introductions. Rainbow smelt and lake whitefish overlap in their uses of space and food at each life history stage, and rainbow smelt have been implicated in the successive recruitment failures of lake whitefish in Lake Simcoe (Evans et al. 1988), failures that eventually led to classification of this stock as "threatened" by the Committee on the Status of Endangered Wildlife in Canada. Data collected in a study of a recently invaded, small northwestern Ontario lake suggest that rainbow smelt displace juvenile lake whitefish and cisco *Coregonus artedi* from preferred habitats and compete with both species for preferred food; they also negatively affect the distribution of juvenile yellow perch *Perca flavescens* (D. B. Wain, personal observations). In contrast, Evans and Waring (1987) found that both cisco and yellow perch numbers in Lake Simcoe increased as rainbow smelt number rose and lake whitefish abundance declined. Other examples in the literature show harmonious coexistence of both lake whitefish and ciscoes with rainbow smelt, so the evidence for a detrimental effect of rainbow smelt introductions is not universally conclusive. Rainbow smelt in Lake Superior, for example, fed on larval ciscoes but not to a level that had significant effects on cisco populations (Selgeby et al. 1978).

Management Implications

The effects of rainbow smelt introductions on sport fisheries are mixed. Salmonid and other predatory species often exhibit increased growth following a switch to a diet consisting mainly of rainbow smelt. However, evidence of detrimental effects includes the potential of rainbow smelt for increasing the mercury contents of their predators and for competing with and preying on the juveniles of important sport fishes (Evans and Loftus 1987).

The potential impact of rainbow smelt on Manitoba's commercial fishery resources was addressed previously by Loch et al. (1979). These authors examined the potential effects of exotic species, including rainbow smelt, that were expected to gain access to Manitoba waters from the upper Missouri River via a fully developed Garrison Diversion Unit irrigation project. They speculated that rainbow smelt would cause the collapse of cisco populations in Lakes Winnipeg, Manitoba, and Lake Winnipegosis and have a major negative impact on the lake whitefish fishery in the north basins of Lakes Winnipeg and Manitoba. Loch et al. (1979) also predicted negative impacts on the walleye fisheries in certain areas of these three large lakes. Remnant (1991), in his reexamination of potential effects of rainbow smelt on Lake Winnipeg's fisheries, concurred with Loch et al. (1979) in most respects, but cautioned that the extent of potential effects of rainbow smelt will depend greatly on the species' success in a lake, a factor that presently cannot be estimated with any precision. Increased mercury levels in walleyes are probable, but the importance that rainbow smelt attain in walleye diets will affect the degree of increased contamination. Mathers and Johansen (1985) found about a fourfold increase in mercury content of 8-year-old walleyes relative to that of their rainbow smelt prey in Lake Simcoe. Northern pike in Lake Simcoe had few rainbow smelt in their diets and had mercury concentrations about 50% lower than walleyes did at the same age. This suggests that a switch by walleyes from a diet mainly of cyprinids and coregonids to one predominantly of rainbow smelt does not equate to a complete additional trophic step in the walleye food chain. Mercury levels in commercially caught Lake Winnipeg walleyes presently are quite low (mostly <0.2 mg/kg: Department of Fisheries and Oceans, Inspection Service, data); walleyes in the commercial catch range in weight from about 0.7 to 1.1 kg. If rainbow smelt become the dominant dietary species for Lake Winnipeg walleyes, as they have in some other lakes, a doubling of walleye mercury levels probably will occur. An increase of twofold in Lake Winnipeg walleye mercury concentrations would bring them close to the maximum acceptable for domestic markets (0.5 mg/kg) and necessitate increased monitoring activities. Sport-caught walleyes, which tend to be larger and older than those in the commercial catch, could be expected to have higher mercury levels, possibly high enough to require consumption advisories.

If rainbow smelt become abundant throughout Lake Winnipeg (and possibly in Lakes Manitoba and Winnipegosis), a decrease in commercial income due to the reduced abundance of native species and replacement by the less-valued rainbow smelt also could be expected. In the Great Lakes, the shift from the historic fishery for coregonids and lake trout to fisheries for yellow perch, rainbow smelt, and alewife *Alosa pseudoharengus* resulted in higher associated capture costs and lower market values for the catch. The general affect of the species composition changes in the Great Lakes on commercial fisheries has been a reduction in gross revenue and failure of many fishing ventures (Christie 1974). Lake Winnipeg has been spared the introduction of the many exotic species that have appeared in the Great Lakes; novel species have been limited to common carp *Cyprinus carpio*, black crappie *Pomoxis nigromaculatus*, white bass *Morone chrysops*, and now rainbow smelt. Lake Winnipeg also largely has been spared the cultural eutrophication that shaped ecological changes in Lake Erie. However, with ever-increasing human populations and exotic species introductions, it now seems that the Lake Winnipeg basin is approaching the threshold of ecological threats that were so dramatically illustrated in the lower Great Lakes 30 years ago.

Early detection of the presence of rainbow smelt (and other exotics) allows management agencies time to adapt fishery management plans to potentially changing circumstances. The most cost-effective method to do this may be examination of predator stomachs at commercial fish plants (or, in the absence of commercial fisheries, at creel censuses) in early spring. Remnant (1991) discovered smelt remains in walleye stomachs well ahead of the first capture of a rainbow smelt in Lake Winnipeg. Commercial fishers, by virtue of their closeness to the resource, the quantity of gear used, and the sheer volume of fish handled, offer a large, valuable sampling effort. Indeed, as Campbell et al. (1991) reported, a curious fisherman provided the first intact specimen of rainbow smelt from Lake Winnipeg. Anglers and commercial fishers alike require information, before the next fishing season, on management agency interest in new species and they must be provided clues to identification. Such information was successfully provided by staff of the Manitoba Department of Natural Resources, who used a poster campaign at commercial fishery facilities on Lake Winnipeg, and who received several specimens captured around the lake over the last 2 years. Surveys such as ours provide evidence of rainbow smelt when they have become abundant, but they provide less confidence in the species' absence if populations are small and specimens are not caught. For example, survey gill nets used in the vicinity of capture of the first specimen in Lake Winnipeg yielded no rainbow smelt. Bottom-trawling surveys in suitable areas provide better quantitative assessment of abundance than gill nets, but much effort is required to sample a substantial proportion of all but very small lakes.

Summary

Rainbow smelt now are known to be present in 32 lakes of the Lake Winnipeg drainage in Manitoba, northwestern Ontario, and northeastern Minnesota. Thirteen new records resulted from our 1989 and 1990 surveys and specimens from an additional three lakes were reported after our surveys. Rainbow smelt originating from the headwaters of the Rainy River system are presumed to be the source for Lac la Croix, Namakan, and Rainy lakes and Lake of the Woods. Rainbow smelt probably will move downstream in the main-stem Winnipeg River, which presents relatively few barriers, once expected large populations build up in Rainy Lake and Lake of the Woods. Lac Seul probably also will develop a large rainbow smelt population and become a major source for lakes downstream in the English River mainstem. Both of these routes feed directly to the lower Winnipeg River, probably ensuring a constant supply of immigrants to the several reservoirs in the river and to Lake Winnipeg. Even with regulations on the use of rainbow smelt as bait, it is reasonable to expect that the species will continue to spread to accessible lake trout lakes throughout the populated parts of the drainage basin. The invasion of rainbow smelt in the drainage basin presents the opportunity to carry out before-and-after research to determine definitively the effects of a colonizing fish species in a variety of lake settings.

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