Maine Landlocked Salmon: Life History, Ecology, and Management

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Division of Fisheries and Hatcheries

A fine landlocked salmon from the Magalloway River in western Maine. (Paula J. Kasprzak)

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DEDICATION

We dedicate this publication to Keith A. Havey, Sr., former Regional Fishery Biologist and Research Biologist for the Maine Department of Inland Fisheries and Wildlife. During his 35-year career, Keith co-authored two previous editions of this paper, and authored or co-authored many key papers on Maine's unique landlocked salmon and brook trout resources. He was a true friend and mentor to many biologists and students, and he is sorely missed.

David P. Boucher
Kendall Warner
February 2006

Keith A. Havey, Sr. 1926-1990. (MDIFW)

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INTRODUCTION

The landlocked Atlantic salmon has long been closely associated with Maine and remains one of the state's most highly prized sport fishes. Indeed, recent questionnaire surveys conducted by the Maine Department of Inland Fisheries and Wildlife show that landlocked salmon are sought by more Maine anglers than any other coldwater sportfish, excepting brook trout. Among the landlocked salmon's many positive attributes as a sport fish are its high catchabilty, its outstanding sporting qualities, its potential for good growth and longevity, and the ease with which it can be cultured in hatcheries. These factors, along with its tolerance of a moderately broad range of environmental conditions, make the landlocked salmon highly responsive to intensive management.

The objectives of this report are to document the status of this important fishery resource in Maine, and to update our understanding of landlocked salmon life history and management since publication of Life History, Ecology and Management of Maine Landlocked Salmon (Warner and Havey 1985). Specifically, our intent is to use the data consolidated here to refine existing management techniques, to develop new techniques, and to identify future research needs to keep pace with the changing desires and expectations of salmon anglers and other resource users. It is our hope that this document will be useful to professional fishery managers and others in their continuing work to maintain and enhance landlocked salmon populations, wherever they occur.

The development of a computerized database of key habitat, biological, and regulatory variables associated with salmon ecology and management has been central to this effort. Presently, this file contains over 70,000 records of individual salmon sampled in about 170 lakes from 1939 to 2003. Examples of new or expanded assessments made possible with the large database include performance comparisons of hatchery fish with wild fish, and comparison of fisheries provided by salmon originating from West Grand Lake and Sebago Lake. Food habits data have expanded significantly since 1985, permitting detailed analysis of forage use based on salmon size and season. Angler use and success data from riverine salmon fisheries have also increased dramatically since 1985 and those are summarized as well.

In compiling this report, we have drawn heavily on research already completed or in progress in Maine, although data from neighboring states and provinces have been utilized where appropriate and pertinent. Where administrative management reports have been published by Fishery Division staff, we have cited these under References, but where no reports have been written, unpublished field data have been used and cited as such. This paper is the third edition of bulletins authored by Havey and Warner (1970) and Warner and Havey (1985). Although much has been revised and re-written, some original portions of the earlier documents have been included without substantial changes.

THE LANDLOCKED SALMON IN MAINE

Origins of landlocked salmon

There have been many theories and opinions expressed on the origin of landlocked salmon. Some early workers (Hamlin 1874) believed that these salmon were of recent origin and were sea-run Atlantic salmon that had become physically landlocked by man-made dams. The majority was of the opinion, however, that landlocked salmon originated from sea-run Atlantic salmon and that the landlocking process was a gradual "voluntary" or physiological one. Perhaps the general opinion of early workers was most appropriately stated by Atkins (1884) who wrote, "*I do not think we have any evidence that landlocking of the species under consideration has occurred during recent geological periods. There is nothing at present to prevent any of these salmon from going to sea from any of those waters where they are now found...I think it possible, also, that the change in their habits and instinct occurred gradually.*" Kendall (1935) believed landlocked salmon originated from sea-run Atlantic salmon through "physiological adaptation and heredity", and he further stated "*it is manifestly impossible that the fish should have originated in those fresh waters, which they now inhabit, for the region was once covered by a field of ice thousands of feet thick over a period of thousands of years. The fact that lake salmon now flourish in certain cold period 'glacial lakes' indicates that their present physiological requirements are the culmination of thousands of years of adaptation to changing conditions.*"

There is now little doubt that landlocked salmon populations arose from sea-run Atlantic salmon following the most recent glacial retreat, about 10,000 years ago (Power 1958, Behnke 1972, Berg 1985, Verspoor 1994, and Behnke 2002). Landlocked salmon populations merely represent a variant life history form of the sea-run fish. Recent genetic evidence suggests that Maine sea-run and landlocked fish share a common, post-glacial ancestry (Spidle et al. 2003).

There is considerable variation in appearance, ecology, and habits among populations of landlocked salmon, but differences in morphometric or physiological criteria do not warrant taxonomic separation, even on a subspecific basis (Wilder 1947, Nyman 1966, Gray and McKenzie 1970, Westman 1970, Legendre 1973, MacCrimmon and Gots 1979, and Berg 1985). Power (1958), in writing of the myriad forms or "races" of landlocked salmon in eastern North America, stated, "*It appears that a gradual transition exists between the forms found in the extreme northern part of the area and those found in the southern part. The apparently different growth patterns are the result of the differences in length of the growing season and in the amount and types of food available. The numerous isolated populations of freshwater salmon, distributed over the entire range from north to south, form a cline and therefore ought not to be considered as two separate subspecies, but rather to represent an assemblage of variable forms which can be distinguished from the parent form by loss of the marine phase of the life cycle...It seems that mere physical isolation does not suffice as explanation of the present distribution and characteristics of the fresh water salmon of eastern North America. Physical isolation has occurred in some cases that no one would dispute; however, since many of the freshwater populations now have access to the sea, but do not take advantage of it, a physiological as well as physical cause is necessary to explain all the facts.*"

Distribution

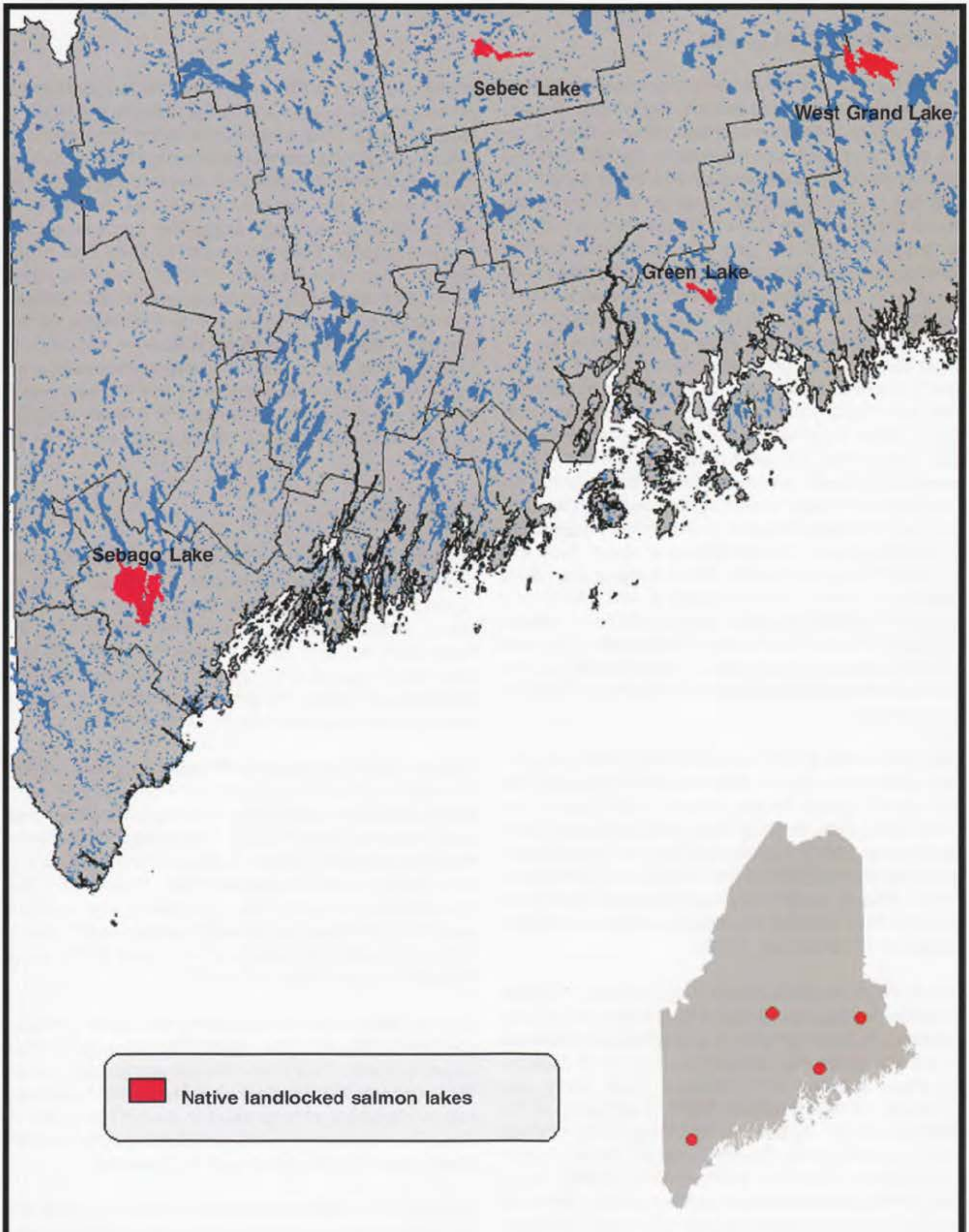
In Maine, landlocked salmon were known to originally occur in four river basins (Figure 1): the St. Croix, including West Grand Lake in Washington County; the Union, including Green Lake in Hancock County; the Penobscot, including Sebec Lake in Piscataquis County; and the Presumpscot, including Sebago Lake in Cumberland County. The presence of salmon in the four lakes was well documented by Kendall (1935).

A recent review of historical literature suggests that native stocks of landlocked salmon were perhaps more widely distributed within these four river basins than originally reported. Merrill (1903) commented on the presence of landlocked salmon in West Grand Lake as well as in Junior Lake, Scraggley Lake, Pocumcus Lake, Sysladobsis Lake, and West Musquash Lake. It seems likely that all or most of the latter waters, which prior to dam construction flowed freely with West Grand Lake, harbored original stocks of salmon.

Sea-run Atlantic salmon apparently were able to negotiate Grand Falls and other natural obstacles on the East Branch of the St. Croix River (Stillwell and Stanley 1874b). This suggests that landlocked salmon may have been native inhabitants of large lakes in the portion of the St. Croix River drainage that includes Spednic Lake and East Grand Lake, but this is not well documented.

A report from Stillwell and Stanley (1874b) suggests that landlocked salmon may have been native to Onawa Lake and other lakes upstream of Sebec Lake: "*These fishes,*

Figure 1. Original distribution of landlocked salmon in Maine as reported by Kendall (1935).



in all the Grand Lake and Schoodic waters, as well as in the whole line of lakes of which Sebec is the lower, are identical in appearance and more closely resemble a grilse than any other fish." Hamlin (1903) angled salmon in Onawa and Ship Pond Stream, the outlet of Onawa and an inlet to Sebec Lake.

There is also evidence that landlocked salmon occurred in the West Branch of the Pleasant River drainage, a major tributary of the Penobscot River. In their discussion of landlocked salmon, Stillwell and Stanley (1874b) wrote: "*We have caught these fishes high up on the Pleasant river at Katahdin Iron Works; we have caught them still higher up in the mountains, at a place known as the Gulf, which approaches within a mile of Long pond and the Sebec head waters on the other side of the mountain.*"

The original presence of landlocked salmon in the upper West Branch of the Penobscot River was possible because sea-run Atlantic salmon apparently were able to pass the many natural obstacles to these waters. Regarding the possibility of sea-run Atlantic salmon being present above Chesuncook Lake, Atkins (1870) wrote, "*Above this point* {Big Ambejackmockamus Falls} *I only know from others that there is a long succession of falls, rapids, and dead waters, to Chesuncook lake. Salmon are known to ascend further than this. Joel M. Lane of Oldtown informs me that twenty-eight years ago, one blustering night in November, he speared nine large salmon on Ripogenus falls. This place is a few miles below Chesuncook lake, and the fall is so difficult that Mr. Johnston thought that no salmon could pass. But Mr. Lane has seen them in October at the mouth of Hall brook, and my guide, Joe Francis, has seen them in Penobscot brook near the head of the river.*" Also writing of sea-run Atlantic salmon, Stillwell and Stanley (1874a) stated "*Mr. Manley Hardy of Brewer, one of our largest fur buyers, who has an extensive acquaintance with all our guides and trappers, informs us that a smolt or salmon in its second year was taken on the West Branch this last autumn, thirty-five miles above Chesuncook lake*", and in discussing landlocked salmon, Stillwell and Stanley (1874b) reported "*We have heard of a pond emptying into the West branch of the Penobscot where these fishes are said to abound, but have never had time to explore and investigate the matter in person.*"

Lakes in other parts of eastern North America included in the native range of the salmon are located in New Brunswick and Nova Scotia along the fringe of presumed maximum extent of Pleistocene glaciation (Power 1958). Landlocked salmon, known in Canada as ouananiche, are also distributed throughout the more remote areas of Quebec, Labrador, and Newfoundland (Leggett and Power 1969). Salmon formerly inhabited Lake Ontario (Kendall 1935) and possibly Lake Champlain (Behnke 2002). The geographical distribution in North America is detailed by MacCrimmon and Gots (1979). Freshwater forms of Atlantic salmon in Europe are also native to a small number of waters in Norway, Sweden, Finland, and in northwestern Russia (Behnke 2002).

The landlocked salmon was one of the first game fish species in Maine to be widely disseminated for the purpose of generating a sport fishery (Foster and Atkins 1868). The first lake to be artificially stocked with landlocked salmon was probably Cathance Lake in Washington County. In 1868, a tributary of Cathance was stocked with 800 salmon eggs resulting from the first successful egg collection at Grand Lake Stream. As techniques of fish culture improved, salmon were introduced into many well-known Maine lakes, including the Rangeley Lakes (1875), Cold Stream Pond (1876), the Belgrade Lakes (1878), Moosehead Lake (1879), and the Fish River Lakes (1894). Records of the more prominent early salmon introductions are given in Table 1.

Introductions of salmon fry continued through the years, primarily on a trial and error basis. Successful establishment was achieved in those lake systems that provided suitable spawning and rearing conditions. Temporary fisheries were provided in many waters with satisfactory water quality, but populations soon diminished in those with inadequate spawning and nursery habitat. Early fish cultural activities were responsible for widespread distribution of landlocked salmon not only in Maine, but also to many states in the United States and to several foreign countries. For example, Smiley (1884) reported that from 1874 to 1880, landlocked salmon from Maine were planted in 22 states, ranging from New England to South Carolina and California. Despite widespread distribution, most of these introductions were unsuccessful, probably because of inadequate spawning area, unsuitable water quality conditions, lack of suitable forage, or lack of a sustained stocking program. In the eastern United States, landlocked salmon fisheries are presently being provided in a limited number of waters in New Hampshire, Vermont, Massachusetts, and New York. Details of attempted and successful introductions of landlocked salmon in waters around the world were presented by MacCrimmon and Gots (1979).

Population and fishery status

A total of 303 Maine lakes comprising 641,207 acres presently support salmon populations (Boucher 2001). Salmon provide a principal fishery in 176 of these lakes comprising 484,791 acres, which is nearly 50% of the total freshwater acreage in Maine. Salmon provide incidental or relic fisheries in 127 lakes (156,416 acres). These latter lakes are those where stocking has been discontinued and a few survivors remain, where small populations remain

Table 1. Records of early introductions of landlocked salmon in Maine lakes.

Water	County	Year of introduction
Cathance Lake	Washington	1868
Rangeley Lake	Franklin	1875
Webb Lake	Franklin	1876
Howard Pond	Oxford	1876
Cold Stream Pond	Penobscot	1876
Wilson Pond	Androscoggin	1876
Drews Lake	Aroostook	1878
Keenes Lake	Washington	1878
Belgrade Lakes	Kennebec	1878
Cobbosseecontee Lake	Kennebec	1878
Pushaw Lake	Penobscot	1879
Moosehead Lake	Piscataquis	1879
Nash Lake	Washington	1879
Maranacook Lake	Kennebec	1881
Molunkus Lake	Aroostook	1883
Nicatous Lake	Hancock	1884
Peabody Pond	Cumberland	1885
Thompson Lake	Oxford	1887
Patten Pond	Hancock	1888
Alligator Lake	Hancock	1888
Embden Pond	Somerset	1889
Auburn Lake	Androscoggin	1889
Tunk Lake	Hancock	1889
Schoodic Lake	Piscataquis	1889
Moose Pond	Somerset	1889
Floods Pond	Hancock	1890
Squapan Lake	Aroostook	1890
Eagle Lake	Hancock	1890
Toddy Pond	Hancock	1892
Craig Pond	Hancock	1892
Long Pond	Hancock	1893
Donnell Pond	Hancock	1893
Parlin Pond	Somerset	1893
Beech Hill Pond	Hancock	1893
Phillips Lake	Hancock	1893
China Lake	Kennebec	1893
Fish River Lakes	Aroostook	1894

through limited natural reproduction, or where direct connections exist to waters in which salmon are abundant. These lakes provide anglers with an opportunity to catch an occasional salmon while fishing for more abundant species.

The number of lakes classified as principal fisheries for salmon has declined slightly since 1981. Most of the decline is attributable to a careful re-examination of the status of salmon populations in individual lakes. Better data, as well as a more rigorous application of criteria that describe a principal fishery, resulted in several waters being placed in the "relic" category. In addition, salmon management was abandoned in several waters, at least temporarily, in favor of splake or brown trout due to chronic poor performance of salmon (Boucher 2001).

This decline notwithstanding, the overall distribution of salmon has increased substantially since publication of the first edition of this paper (Havey and Warner 1970). Today, salmon lakes are so well distributed that few anglers live far from one (Figure 2). Salmon are present in at least one lake in all Maine counties, but are most prevalent in Piscataquis, Aroostook, Somerset, and Washington Counties (Table 2). A complete listing of Maine's salmon lakes is presented in Appendix 1.

Of those lakes with salmon principal fisheries, 127 (72%) are supported wholly or in part by hatchery stocks, and natural reproduction supports fisheries in 49 lakes (28%). Most wild fisheries are located in northern and western Maine where spawning and nursery habitat for salmon is most abundant (Boucher 2001).

Salmon provide fisheries in 64 known river segments comprising 635 miles. About 289 miles on 44 river segments provide moderate-to-high quality fisheries (Table 3). River fisheries for salmon are generally confined to western and northern Maine, but there are notable exceptions. Grand Lake Stream in Washington County has gained national fame for its fishery, and biologists in southern Maine have generated a popular fishery for hatchery-reared salmon in the Presumpscot River, the outlet of Sebago Lake.

River fisheries are usually associated with spawning runs from large lakes and provide only seasonal fisheries. However, where river habitat is suitable and salmon are denied access to large lake systems, or where stocking occurs, riverine populations can support fisheries throughout the fishing season. Examples of year-long salmon fisheries include the Kennebec River below Indian Pond, the Rapid River, and the Presumpscot River near the Eel Weir Bypass.

Table 2. Population status of landlocked salmon in Maine lakes, 2000.

County	Number of lakes	Population status (number of lakes)	
		Principal fishery[1]	Relic population
Piscataquis	47	30	17
Aroostook	40	28	12
Somerset	38	21	17
Washington	37	18	19
Hancock	34	17	17
Penobscot	24	11	13
Franklin	22	16	6
Oxford	21	18	3
Kennebec	14	4	10
Cumberland	11	7	4
Waldo	5	2	3
Knox	3	1	2
Androscoggin	2	1	1
Lincoln	2	0	2
York	2	2	0
Sagadahoc	1	0	1
Totals:	**303**	**176**	**127**
Percent of totals:	**100%**	**58%**	**42%**

[1] A principal fishery denotes a lake where salmon are regularly sought by anglers, and they make up a significant portion of the total catch of all species in that water.

Figure 2. Present distribution of landlocked salmon in Maine lakes.

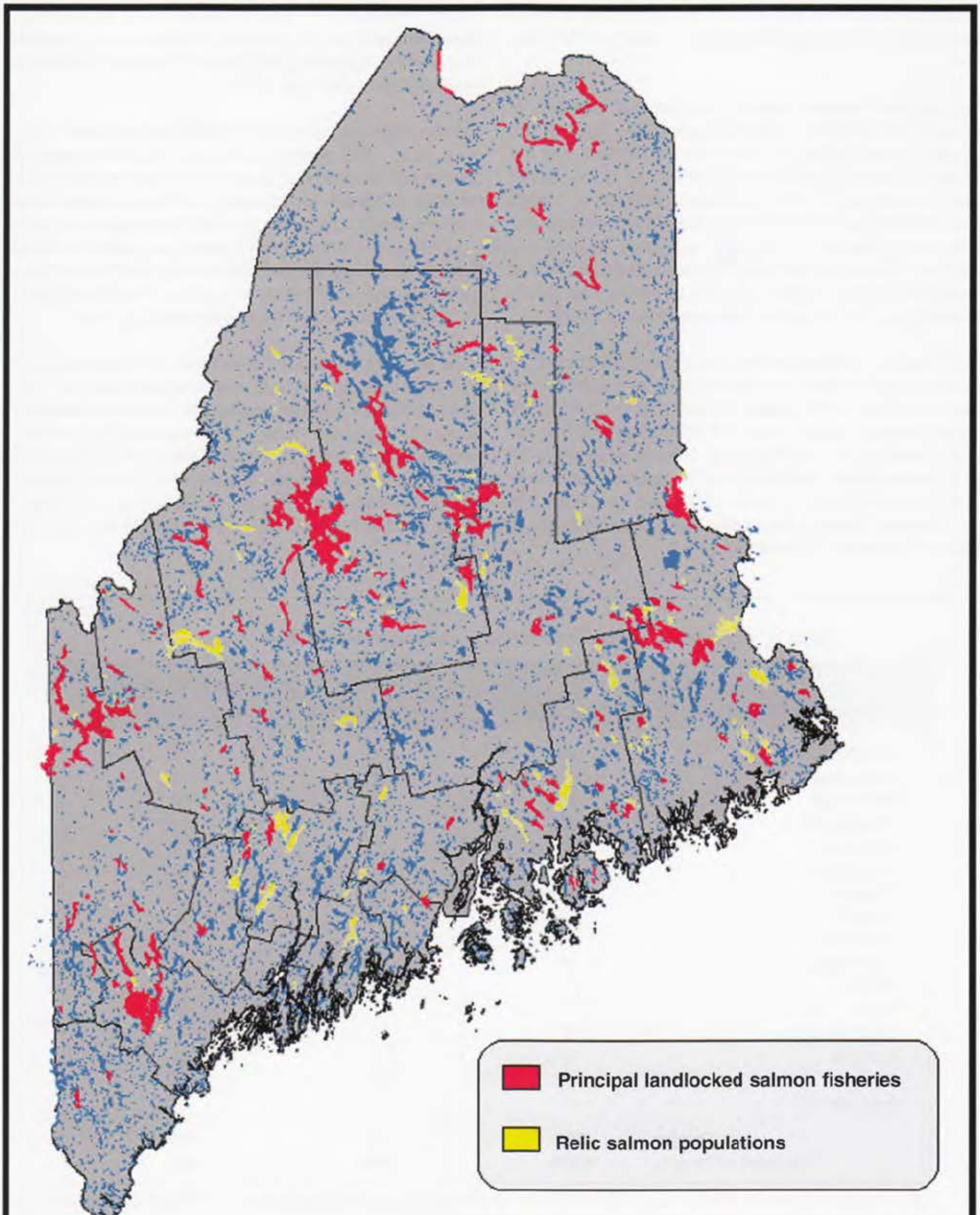
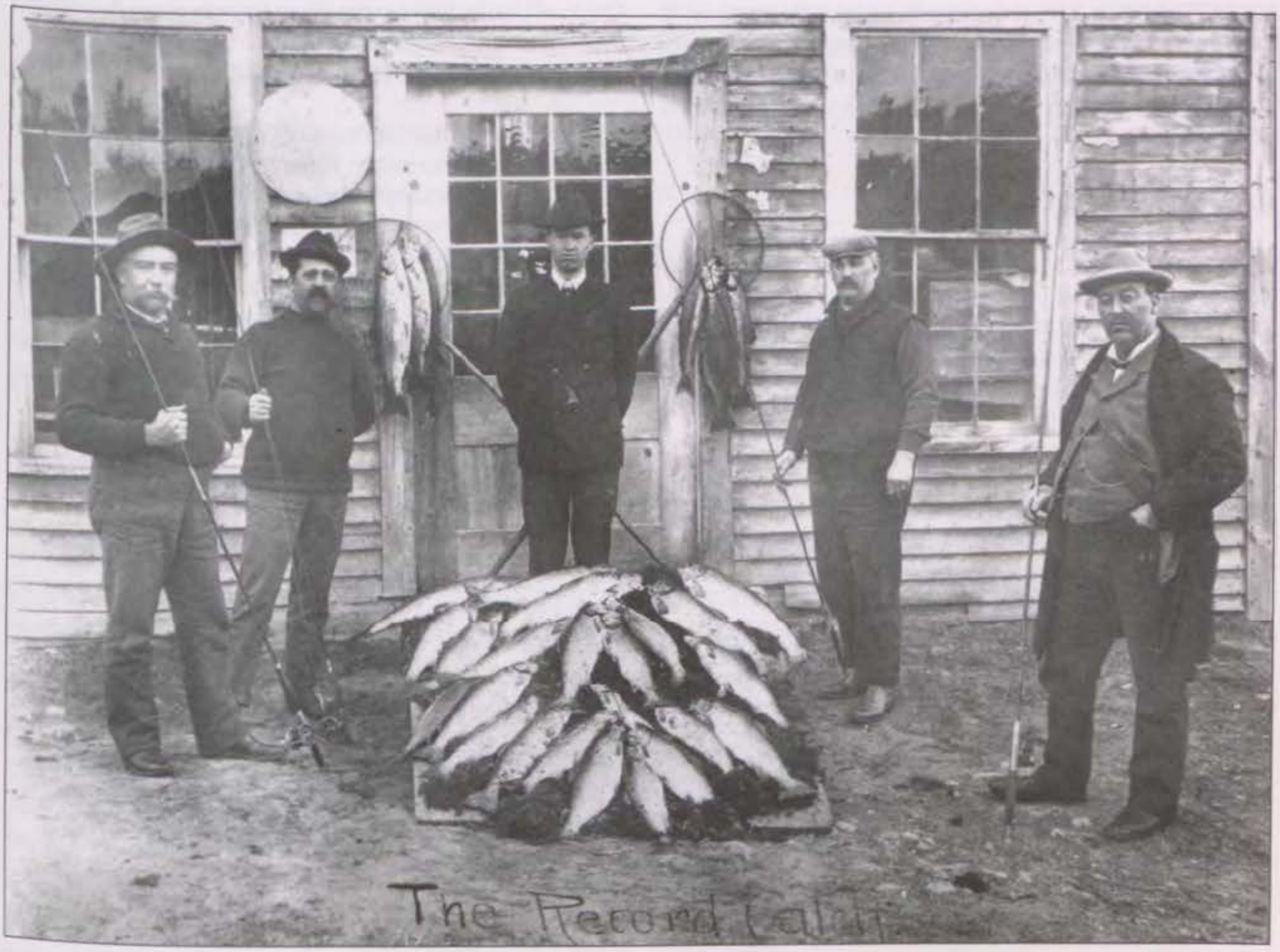


Table 3. Distribution of riverine salmon fisheries with moderate-to-high fishing quality, 2000.

County	Number of miles	Number of river segments
Piscataquis	113.9	19
Aroostook	53.8	11
Somerset	50.3	3
Cumberland	21.3	2
Oxford	18.7	3
Franklin	14.0	2
Penobscot	9.8	2
Waldo	3.9	1
Washington	3.2	1
Statewide totals:	**288.9**	**44**



"The Record Catch". An early example of the Maine landlocked salmon sport fishery in Sebago Lake. This photograph was probably taken prior to 1900.

LIFE HISTORY AND ECOLOGY OF MAINE LANDLOCKED SALMON

Life history traits of landlocked salmon in Maine were well documented in the two previous editions of this bulletin (Havey and Warner 1970, Warner and Havey 1985). In this edition, we have updated much of the data that formed the basis of earlier discussions. We also report new information obtained since 1985 from work completed primarily, but not exclusively, in Maine. In some cases we have drawn on work conducted on sea-run Atlantic salmon, as their life history in freshwater closely parallels that of landlocked salmon.

Landlocked salmon life history usually includes two distinct phases in self-sustaining populations – stream life and lake life. Where populations are maintained solely through lake stocking, the stream phase is usually lacking. Some naturally reproduced populations of salmon spend their entire lives in rivers with no lake life involved in their life history. Reproduction and post-spawning behavior are considered lake life for the purpose of the discussion, because adult occupation of the stream spawning areas is usually transitory.

Stream Life

During their first year of life, young salmon are variously termed young-of-the-year, fingerlings, under-yearlings, or fry; in this paper we refer to them as fry. We use the term parr for landlocked salmon that continue to live in their natal streams after their first year of life.

Habitat

Salmon prefer lake outlets or large inlets for spawning and rearing. Salmon sometimes use small inlets for spawning, but the resulting contribution to the population is usually minor because many of these inlets normally become dry during the summer months. Highest production is probably from outlet streams or from large inlets with natural or artificial impoundments at their sources, because summer flows are often of greater volume. Where these conditions are absent salmon may spawn in lakes, although production is generally poor. Where lake spawning occurs, it is usually associated with moving water above outlets, near the mouths of inlets, or on windswept shoals.

Not surprisingly, the majority of Maine's naturalized salmon populations (those that became self-sustaining following their initial introduction) are in lakes associated with large streams, either outlets or inlets, that have ample spawning and nursery habitat. Most are located in western and northern Maine in large systems such as the Rangeley Chain of Lakes, lakes in the West Branch of the Penobscot River drainage, lakes in the upper Aroostook River drainage, and the Fish River Chain of Lakes.

Late summer water chemistry of several salmon nursery streams is summarized in Table 4. Chemical characteristics of these streams show that they are dilute, poorly buffered, and infertile with regard to their biological productivity. Except for a few isolated areas (northeastern Aroostook County for example), Maine's bedrock and soil geology are derived from granite or granitic rocks, which are of an infertile nature (Davis et al. 1978). In general, Maine's surface waters, including streams harboring salmon, reflect this infertility.

Temperature characteristics have been described for several major salmon nursery streams (Table 5). Average daily water temperatures during the peak growing season for young salmon rarely exceeded 70°F and were within the

Table 4. Late summer water chemistry characteristics of several Maine salmon nursery streams. Values reported for streams where multiple years were sampled are averages.

Stream	County	Year	Dissolved oxygen (mg/l)	pH	Total alkalinity (mg/l $CaCO_3$)	Specific conductance (µmhos/cm)
Long Pond S.	Franklin	2002	7.4	6.4	6	49
Kennebago R.	Franklin	1996	6.0	6.8	6	35
Magalloway R.	Oxford	2000	7.0	6.8	10	56
North Branch Dead R.	Franklin	2002	8.4	6.9	11	50
Bigelow B.	Somerset	1990-1999	10.6	6.7	8	30
Squaw B.	Piscataquis	1990-1997	11.6	6.8	10	24
McConnell B.	Aroostook	1992-1996	8.6	7.5	35	69

Table 5. Summer water temperatures in several Maine salmon nursery streams.

Stream (site)	County	Lake system	Year	Average daily water temperature (°F) May	June	July	August	September
Crooked River	Cumberland	Sebago Lake	1999	*	69	72	69	64
Rapid R. (Middle Dam)	Oxford	River residents	1994	46	59	70	70	61
			2002	44	56	67	71	64
			2003	48	60	69	71	65
Long Pond S. (lower reach)	Franklin	Rangeley Lake	2002	46	56	63	67	62
Long Pond S. (upper reach)	Franklin	Long Pond	2002	48	59	67	70	61
Dodge Pond S.	Franklin	Rangeley L./Dodge P.	2003	53	65	72	72	64
Round Pond Outlet	Franklin	Dodge Pond	2003	53	65	71	71	64
Kennebago R.	Franklin	Mooselookmeguntic L.	1994	*	62	69	63	57
Magalloway R.	Oxford	Parmachenee Lake	2001	*	66	62	67	58
Magalloway R.	Oxford	Aziscohos Lake	2001	*	69	67	70	65
North Branch Dead R.	Franklin	Chain of Ponds	2003	52	63	70	68	62
Horseshoe S.	Franklin	Chain of Ponds	2002	*	64	71	69	60
Kennebec R. (East Outlet)	Somerset	Moosehead Lake	2003	*	56	66	68	62
		Monthly averages for all streams:		**50**	**62**	**68**	**69**	**62**

range of 59° to 66°F reported by DeCola (1970) as optimal for growth and production for sea-run Atlantic salmon.

Daily maximum stream temperatures during July and August often exceeded 68°F, and in some rivers exceeded 77°F for short time periods (Table 6). None exceeded the upper incipient lethal temperature of 82°F for 7 days, a tolerance zone within which sea-run Atlantic salmon survived (Elliot 1991). Temperature regimes in these stream nurseries suggested that they provided nearly ideal conditions for salmon production.

Several stream surveys have documented the location, types, and abundance of habitat for juvenile salmon. These surveys, which varied in level of detail, categorized a variety of stream habitat features including substrate types and the amount and distribution of riffles, runs, and pools. Riffles and runs are utilized by young salmon as nursery areas and by adults for spawning. Pools provide cover, resting areas, and wintering habitat for both adults and larger juveniles.

Grand Lake Stream in Washington County, which supports one of Maine's native landlocked salmon populations, provides superb spawning and nursery habitat. Jordan's (1985) survey of this stream showed it was comprised of 61% riffles, 19% runs, and 20% pools and deadwaters. Boulders and rubble were the predominant substrates, accounting for over 50% of the stream bottom. Gravel substrate suitable for salmon spawning comprised 6% of the total stream area, while 61% of the stream was considered suitable nursery habitat. This survey, as well as those described below, was conducted during minimum flow conditions.

Table 6. Temperature regimes during July and August for several Maine salmon nursery streams (minimum, mean, and maximum values are daily averages).

Stream (site)	Year	Daily mean temperature (°F)	Minimum temperature No. days ≥68°F	Mean temperature No. days ≥68°F	Maximum temperature No. days ≥68°F	Maximum temperature No. days ≥77°F
Crooked R.	1999	70	40	52	55	4
Rapid R. (Middle Dam)	1994	70	41	48	56	0
	2002	68	17	24	41	0
	2003	70	37	50	58	0
Long Pond S. (lower reach)	2002	65	6	12	30	0
Long Pond S. (upper reach)	2002	67	10	25	41	2
Dodge Pond S.	2003	72	51	55	59	10
Round Pond Outlet	2003	71	47	52	56	12
Kennebago R.	1994	66	5	23	54	11
Magalloway R. (above Parmachenee L.)	2001	65	0	2	24	0
Magalloway R. (above Aziscohos L.)	2001	69	17	35	51	10
North Branch Dead R.	2003	69	24	39	53	7
Horseshoe S.	2002	70	20	40	59	21
Kennebec R. (East Outlet)	2003	67	0	15	29	0

The Kennebago River below Kennebago Falls in northwestern Maine, considered an excellent salmon nursery stream, was comprised of 57% riffles, 35% runs, and 8% pools (DeSandre and Bonney 1984). Gravels, rubble, and boulders were the predominant substrates, and were well distributed throughout the river.

The Rapid River, which forms the outlet of the Rangeley Lakes in northwestern Maine, was dominated by riffles (50%) and pools (40%); run habitat comprised only 10% of the river (DeSandre 1986). Substrate materials were largely composed of boulders and rubble; spawning gravel was notably scarce. Mean water depth in the riffle areas was 2.5 feet, while most pools exceeded 5 feet in depth.

In the upper Magalloway River, also in northwestern Maine, riffles and runs accounted for about 75% of the total river (Bonney 2002). Pools and dead water areas comprised

Grand Lake Stream, the outlet of West Grand Lake, provides ideal nursery habitat for young landlocked salmon. (Dave Boucher, MDIFW) about 23% of the remaining area. A variety of substrate types was present, and spawning gravel was distributed throughout the reach.

Stream banks were well vegetated and relatively stable in the three aforementioned streams. Spring seepages, which provide cool water refuges during exceptionally warm periods, were common in the Kennebago and Magalloway Rivers, but rare in the Rapid River.

Spawning and incubation

Landlocked salmon eggs spawned and fertilized in October and November lie buried beneath the gravel surface of the redd where they develop and hatch the following spring. To survive and develop, incubating eggs require a good flow of well-oxygenated water percolating through the gravels.

Characteristics of salmon spawning habitat in Grand Lake Stream were examined in detail by Nemeth (2001). On average, salmon redds (a total of 45 were measured) were constructed at a depth of 18.1 inches in water flowing at a rate of 1.1 ft/second. These values were similar to those reported by Beland et al. (1982) for sea-run Atlantic salmon in four Maine rivers (15 inches and 1.7 ft/second). About 50% of gravels used by spawning salmon was between 0.4 and 1.0 inches in diameter, and substrate particles were moderately embedded (average of 3.6 on a scale of one to five). Nemeth (2001) concluded that water velocity, average substrate size, and substrate embeddedness were consistent predictors of redd site selection by salmon in Grand Lake Stream and in three New York streams. Groundwater upwelling did not significantly influence redd site selection in this study.

In northern Maine, Warner (1963) analyzed the size composition of redd materials used by salmon in the large thoroughfares connecting the Fish River Lakes. Analyses of the size composition of redd materials showed that 72% (by weight) was gravel larger than 0.25 inches in diameter, while 16-17% was sand (0.006 to 0.24 inches). Silt and clay comprised less than 0.5% of redd materials.

Studies in these same northern Maine spawning areas (Warner 1963) indicated that in 22 redds measured, salmon eggs were buried an average of 8 inches below the surface, with a range of 4 to 12 inches in depth. Depth of egg deposition below the gravel surface was limited mainly by depth of compact gravel, ledge, or clay substrate. In many cases, eggs were found deposited directly on these impenetrable layers. Most of the salmon eggs were localized in egg pockets within each redd; most redds contained from 1 to 3 egg pockets. There was an average of 749 eggs in each redd.

Incubation time depends on water temperature – the period of incubation is longer with colder water temperatures. In the thoroughfares of the Fish River Lakes, salmon eggs hatch in about 6 months at water temperatures ranging from 32-35°F. The thoroughfares remain mostly free of ice during this period because of the warming influence of outflowing lake water. In many lake inlets in northern and western Maine, the incubation period is longer because of lower water temperatures resulting from persistent snow and ice cover. In southern Maine spawning areas, incubation time for salmon eggs is probably somewhat less because of an earlier spring and resultant earlier warming of the water.

In two Maine hatcheries during 1999 and 2000, the incubation periods of salmon eggs from spawning to swim-up ranged from 164 to 211 days (Table 7). Geographically, Grand Lake Stream is the northernmost of the two hatcheries. Both have lakes as a water source, but only the Casco Hatchery has deep-water pipes permitting warmer incubation temperatures. The longer incubation periods were at Grand Lake Stream Hatchery, where water was taken from relatively shallow depths (about 18 feet). Incubation periods at this station were probably the nearest to that of natural incubation conditions in lake outlets, an example of which is the Rapid River (Table 7).

Eggs held at the Grand Lake Stream Hatchery took over twice as long to hatch as those from Casco, but the period from hatching to swim-up (yolk sac absorption) was somewhat longer at Casco.

During April 1959, 1960, and 1961, a total of 33 landlocked salmon redds was excavated in two spawning areas of the Fish River Lakes to evaluate survival of naturally spawned eggs. Egg survival to the late-eyed stage, just before hatching, averaged 93.2% (Warner 1963). Mortality due to nonfertilization was less than 1%. Loss of eggs averaged 4.2% in the pre-eyed stage and 1.7% in the eyed stage.

Landlocked salmon redd in Munsungan Stream, the outlet of Munsungan Lake and a headwater of the Aroostook River. (Randy Spencer, ASRC)

Table 7. Mean water temperatures and incubation periods of landlocked salmon eggs in two Maine hatcheries, 1999-2001, and incubation temperatures recorded in a natural stream (Rapid River).

	Hatchery and Year				
	Casco		Grand Lake Stream		Rapid River
	1999-2000	2000-2001	1999-2000	2000-2001	2002-2003
Mean water temperature (°F) in:					
November	45	46	44	45	41
December	36	39	38	35	34
January	36	34	35	35	34
February	37	35	34	35	33
March	38	36	36	35	34
April	41	36	40	37	37
Date spawned:	Nov. 7	Nov. 7	Nov. 2	Nov. 2	
Date eyed:	Jan. 11	Jan. 15	Dec. 28	Jan. 9	
No. days from spawning to eyeing:	65	69	56	68	
Date hatched:	Feb. 21	Mar. 2	Apr. 3	Apr. 25	
No. days from eyeing to hatching:	41	46	97	106	
Date of swim-up:	Apr. 20	May 6	May 18	June 1	
No. days from hatching to swim-up:	58	65	45	37	
Total days from spawning to swim-up:	164	180	198	211	

Working with sea-run Atlantic salmon in tributaries of the Machias River, Washington County, Jordan (1976) found that survival to the eyed-egg stage ranged from 84.8 to 94.6% in 1975, and from 90.5 to 98.8% in 1976.

We have shown that under ideal incubating conditions, about 93% of landlocked salmon eggs survived to a period just before hatching. The high survival of naturally spawned salmon eggs in the two spawning areas studied in the Fish River Lakes indicated that those environments were nearly ideal for natural reproduction of salmon. Egg survival was favored by relatively stable stream flow, lack of severe ice conditions, and suitable gravel size to allow adequate aeration. Up to 18% sand, silt, and clay in the redd materials apparently had little adverse effect on survival of salmon eggs.

These survival data are probably representative of many spawning areas in Maine with comparable flow patterns, gravel sizes, and water temperatures. Conditions for egg survival in other types of stream habitat, however, may be much more severe. For example, in small lake tributaries where flows become extremely low during winter, some redds may be exposed to freezing. Efficient aeration of incubating eggs is probably reduced in some spawning areas because of low stream flows or excessive amounts of fine materials in the redds.

In spawning areas of the Fish River Lakes, salmon hatch in late April and remain in small crevices among the gravel particles for about 6 weeks. During this period, young salmon are nourished by absorption of nutritive material from their yolk sacs. When the yolk sac is absorbed, the fry work their way upward through interstices and emerge at the gravel surface. Presence of an adequate amount of coarse gravel in the redd is important, not only to provide living spaces for the young salmon during the sac-fry stage, but also to allow passage from depths of the redd to the gravel surface.

No data are available on mortality of landlocked salmon eggs between hatching and fry emergence at the gravel surface, but studies of sea-run Atlantic salmon suggest mortality increases quite dramatically at this stage. Gustafson-Marjanen (1982), working in Old Stream, Washington County, showed survival to emergence of eggs planted in artificial redds ranged from about 1 to 7%. MacKenzie and Moring (1988), also working with sea-run Atlantic salmon, reported survival from egg deposition to fry emergence ranged from 0 to 7% and averaged 1.7%. Data for this latter study were obtained from Whitlock-Vibert egg boxes buried in the gravel substrate of Northern Stream, Washington County. Survival to emergence for landlocked salmon eggs under favorable circumstances is probably quite similar.

LIFE AS FRY

Upon emergence from the gravel, which usually occurs during late May and early June, young landlocked salmon begin their lives as free-swimming fish that must protect themselves and seek and acquire their own food to survive.

A social behavioral trait common to members of the salmon family is that of choosing and defending home territories. Kalleberg (1958) and other workers have described territoriality among sea-run Atlantic salmon. Fenderson et al. (1968) have shown that this behavior is also strongly exhibited by Maine landlocked salmon.

Salmon fry occupy nursery areas with a wide variety of bottom types, but they are often found in abundance over gravel spawning material where older and larger juvenile salmon are seldom found. Salmon fry often occupy gravel spawning areas where the bottom is barely covered with water, and they are often the only fish present in such habitat. The ability of salmon to occupy such shoals may ensure perpetuation of at least a remnant stream population during critical low water periods or in the presence of predators. Optimum growth and survival of salmon fry, however, can probably be expected only when the nursery area is supplied with ample stream flow.

Density

Density of salmon fry in nursery areas is highly variable among different streams and within the same stream from year-to-year (Table 8). Variability is apparently normal among wild salmon populations and is related to such factors as egg density, food supply, competition from other species or other salmon cohorts, stream flows and temperatures, stream size, and streambed types. Nursery areas range from small brooks to river-like thoroughfares between lakes.

Meister (1962), working with sea-run Atlantic salmon at Cove Brook in Winterport, Waldo County, Maine, obtained a 2-year average density of 26.5 fry per 100 square yards. Elson (1957a) pointed out that for certain sea-run Atlantic salmon rivers in New Brunswick, 20 fry per 100 square yards of nursery area is necessary to ensure maximum smolt production. Density estimates from these two studies compare favorably with the average density of 21.4 landlocked salmon fry per 100 square yards from 20 nursery streams in Maine (Table 8).

Havey (1974a) obtained an average density of 9.7±2.9 salmon fry per 100 square yards at Barrows Stream, Washington County, Maine between 1960 and 1971 (10 different years). Corresponding weight standing stock was 2.27±0.68 pounds per acre. Boucher (MDIFW, unpublished data) estimated an average standing stock of 7.5±1.6 pounds per acre of fry from five western Maine streams during the period from 2001 to 2003 (Table 9).

Growth

Seasonal growth of salmon fry at four nursery areas associated with the Fish River Lakes is shown in Table 10. Total lengths attained by early October 1959 probably represented a nearly completed season's growth. These lengths (2.4-3.0 inches) agreed well with calculated lengths (2.6-2.8 inches) of age I salmon from the respective nurseries. Size attained by salmon fry in these ideal nursery areas is close to that attained in other Maine salmon nurseries. For example, length at age I for 69 naturally reared fish from Love Lake was 2.7 inches, and length at age I for 1,281 wild salmon sampled from nine lakes in western Maine averaged 2.9 inches (Table 11).


Landlocked salmon fry (left) and parr (right) from Long Pond Stream, a tributary of Rangeley Lake in Franklin County. (Dave Boucher, MDIFW)

Table 8. Density of salmon fry (age 0+) in representative Maine nursery streams, 1957-2003.

Stream	Lake system	County	Date	Number/100 square yards
Long Lake Thoroughfare	Long/Mud Lakes	Aroostook	Sept. 1959	63.8
Cross Lake Thoroughfare	Cross/Mud Lakes	Aroostook	Sept. 1959	90.0
Square Lake Outlet	Square/Eagle Lakes	Aroostook	Oct. 1957	43.6
Portage Lake Inlet	Portage Lake	Aroostook	Oct. 1969	0.6
St. Froid Lake Outlet	St. Froid/Eagle Lakes	Aroostook	Sept. 1960	15.8
Eagle Lake Outlet	Eagle Lake	Aroostook	Sept. 1960	13.7
Pollywog Stream	Nahmakanta Lake	Piscataquis	Aug. 1996	8.9
Long Pond Stream	Long Pond	Piscataquis	Oct. 1959	2.7
Long Pond Stream	Long Pond	Piscataquis	Aug. 1995	5.1
Long Pond Stream	Long Pond	Piscataquis	Aug. 1996	9.2
Long Pond Stream	Long Pond	Piscataquis	Aug. 1998	5.8
Long Pond Stream	Long Pond	Piscataquis	Aug. 1999	6.1
Davis Stream	Sebec Lake	Piscataquis	Aug. 1990	5.4
Davis Stream	Sebec Lake	Piscataquis	Aug. 1991	2.1
Davis Stream	Sebec Lake	Piscataquis	Aug. 1992	14.7
Davis Stream	Sebec Lake	Piscataquis	Aug. 1993	0
Davis Stream	Sebec Lake	Piscataquis	Aug. 1994	0
Davis Stream	Sebec Lake	Piscataquis	Aug. 1995	15.8
Davis Stream	Sebec Lake	Piscataquis	Aug. 1996	14.8
Davis Stream	Sebec Lake	Piscataquis	Aug. 1997	0.4
Davis Stream	Sebec Lake	Piscataquis	Aug. 1998	24.2
Davis Stream	Sebec Lake	Piscataquis	Aug. 1999	10.3
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1990	9.2
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1991	13.1
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1992	21.1
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1993	0.4
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1994	0.2
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1995	11.6
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1996	8.8
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1997	3.5
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1998	25.7
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1999	8.5
Barrows Stream	Love Lake	Washington	Oct. 1961	7.9
Barrows Stream	Love Lake	Washington	Oct. 1962	6.7
Barrows Stream	Love Lake	Washington	Oct. 1963	4.9
Barrows Stream	Love Lake	Washington	Oct. 1964	5.5
Barrows Stream	Love Lake	Washington	Oct. 1967	21.5
Barrows Stream	Love Lake	Washington	Oct. 1968	17.6
Barrows Stream	Love Lake	Washington	Oct. 1969	1.2
Barrows Stream	Love Lake	Washington	Oct. 1970	6.2
Barrows Stream	Love Lake	Washington	Oct. 1971	11.7
Wood Stream	Big Wood Pond	Somerset	Aug. 1999	5.4
Bigelow Brook	Mayfield Pond	Somerset	Oct. 1959	140.0
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1990	29.9
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1991	20.6
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1992	21.1
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1993	6.9
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1994	13.3
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1995	17.9
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1997	0.9
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1998	17.2
Horseshoe Stream	Chain of Ponds	Franklin	Sept. 2001	7.7
Dead River (N. Branch)	Chain of Ponds	Franklin	Oct. 2001	11.7
Dead River (N. Branch)	Chain of Ponds	Franklin	Sept. 2002	29.6
Long Pond Stream	Rangeley Lake	Franklin	Aug. 2002	44.7
Long Pond Stream	Rangeley Lake	Franklin	Aug. 2003	48.5
Dodge Pond Stream	Rangeley Lake	Franklin	Sept. 1972	170.0
Dodge Pond Stream	Rangeley Lake	Franklin	Aug. 1973	168.0
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1965	11.6
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1966	24.9
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1971	3.1
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1972	0.9
Kennebago River	Mooselookmeguntic Lake	Oxford	Aug. 1977	4.3
Kennebago River	Mooselookmeguntic Lake	Oxford	Aug. 1978	4.9
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1983	4.2
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1990	19.8
Nason Brook	Sebago Lake	Cumberland	Aug. 1963	58.6
Northwest River	Sebago Lake	Cumberland	Aug. 1961	45.4
Northwest River	Sebago Lake	Cumberland	Oct. 1963	8.5
			Mean±standard error:	**21.4±4.1**

Table 9. Estimated standing stocks of juvenile salmon from western Maine streams. Confidence limits (±) were computed at the 95% probability level.

Stream (reach)	Year	Fry standing stock Number/100 yd²	Fry standing stock Pounds/acre	Parr standing stocking stock Number/100 yd²	Parr standing stocking stock Pounds/acre
Long Pond S. (lower)	2002	44.7±4.0	9.3±0.8	18.1±1.2	18.9±1.3
Long Pond S. (lower)	2003	48.5±4.7	8.8±0.9	3.6±0.2	4.1±0.2
Long Pond S. (upper)	2002	46.0±2.5	7.9±3.7	3.8±0.6	4.6±0.7
Horseshoe S.	2001	7.7±1.7	1.9±0.4	0.42±0.2	1.0±0.5
North Branch Dead R.	2001	11.7±3.4	5.3±1.5	9.2±1.0	2.7±0.3
North Branch Dead R.	2002	29.6±5.0	11.7±2.0	6.9±2.0	19.8±5.9
	Means:	**31.4±7.4**	**7.5±1.6**	**7.0±2.5**	**8.5±1.5**

Table 10. Seasonal growth of landlocked salmon fry in five Maine nursery streams.

Stream and mean fish size	June	July	August	September	October
Long Lake Thoroughfare					
Length (inches)	*	1.3	1.7	2.1	2.4
Monthly increment (inches)	*	*	0.4	0.3	0.3
Sample size	*	82	59	60	51
Cross Lake Thoroughfare					
Length (inches)	1.2	1.6	1.9	2.2	2.4
Monthly increment (inches)	*	0.4	0.3	0.3	0.2
Sample size	60	80	42	54	60
Eagle Lake Outlet					
Length (inches)	*	1.7	2.1	2.8	3.1
Monthly increment (inches)	*	*	0.4	0.7	0.3
Sample size	*	14	42	34	57
St. Froid Lake Outlet					
Length (inches)	*	1.5	1.9	2.4	2.7
Monthly increment (inches)	*	*	0.4	0.5	0.3
Sample size	*	53	36	33	58

Typically, salmon fry weigh between 1.5 and 2.5 grams at the end of their first growing season.

As a matter of interest, scalation in landlocked salmon is probably always completed during their first year of life. Warner and Havey (1961) found that scales first appear on these fish at a total length of about 1.2 inches and that scalation is essentially complete at lengths of 1.8-2.0 inches.

Movements

The speed and manner in which fry disperse from the area of the redd are not well documented for Maine landlocked salmon. We have observed them lying passively along the edge of the stream in shallow backwaters and stream channel margins soon after emergence, and fry have been collected both upstream and downstream of known spawning sites within a few days or weeks following emergence.

Table 11. Back-calculated lengths of salmon fry from western Maine lakes, 1986-2003.

Water	County	Sample size	Calculated length at age I (inches)
Beaver Mountain Lake	Franklin	112	2.79
Rangeley Lake	Franklin	330	2.91
Dodge Pond	Franklin	109	3.02
Kennebago Lake	Franklin	28	2.84
Mooselookmeguntic Lake	Oxford	367	2.62
Richardson Lake	Oxford	35	2.71
Parmachenee Lake	Oxford	64	2.93
Aziscohos Lake	Oxford	193	3.08
Chain of Ponds	Franklin	43	2.96
	Mean and standard error:		**2.85±0.01**

Recent laboratory experiments conducted in New York by Nemeth et al. (2003) examined the rheotactic response (directional response to water currents) of Maine-origin salmon. Newly hatched fry (0 to 3 weeks old) exhibited a strong upstream response – this was particularly evident with the strain from Sebago Lake, which are known to be inlet spawners. Nemeth et al. observed that upstream movements declined with increasing age of the fry, downstream movements increased as fry densities were increased, and higher flow velocities resulted in declining movements in either direction.

Nemeth et al. (2003) suggested that the strong propensity of newly hatched fry to move upstream might be a strategy for dispersing from local hatching areas. This could have adaptive value for fish that must utilize a stream nursery for one to several years prior to emigrating to a lake. For inlet-spawning salmon (e.g. Sebago Lake), strong upstream movements immediately after emergence also may prevent premature entry of fry into a lake environment where their survival could be compromised.

Atkinson et al. (2002) studied post-stocking dispersal of unfed fry of sea-run Atlantic salmon in the Dennys River, Washington County. During the period from May 19 to June 14, 81% of the fry remained within 50 meters (164 feet) of the release sites. The study suggested that fry movements were restricted to low-light periods – no fry were captured during daylight hours.

Survival

Survival from egg deposition to fry about 11 months later can be estimated from work done by Havey (1974a) at Barrows Stream in Washington County (Table 12). The weighted average survival (5.4%) is less than that reported by Meister (1962) for sea-run Atlantic salmon at Cove Brook (9.0-11.0%), but approximates that reported by Elson (1957a) for sea-run Atlantic salmon on the Miramichi and Pollet Rivers in New Brunswick, Canada. Havey's fry were taken mostly in October, while Elson's were sampled in late summer.

Stream Associates

Juvenile salmon (fry and parr) are often the dominant fish in stream nurseries (Table 13). The most frequent associates with salmon include brook trout, blacknose dace, white sucker, slimy sculpin, creek chub, and lake chub. In general, these same species are also the most abundant fish present other than salmon. Brook trout are more commonly associated with salmon in cool tributary nurseries. In lake outlets, brook trout are found only seasonally because they do not tolerate high summer temperatures (70-75°F) that are common in these environments.

A total of 28 fish species are known to occur with salmon in Maine nursery streams. The role of several of these species as potential competitors with salmon in nursery streams is discussed in a later section.

Brook trout are common associates with salmon. (Toby Bonney)

Table 12. Survival of salmon from egg deposition to early autumn fry at Barrows Stream, Washington County, Maine.

Brood year	Female spawners No. per acre	Female spawners Weight (lb) per acre	Estimated egg deposition per acre	Estimated fry per acre	Percent survival
1959	28.9	53.4	17,000	1,468	8.6
1961	6.0	20.0	6,500	322	4.9
1963	58.9	55.6	18,000	268	1.5
1966	16.9	34.0	10,500	1,040	9.9
1967	23.0	29.2	9,500	854	9.0
1968	24.9	28.0	9,000	62	0.7
1969	33.9	32.0	10,000	302	3.0
1970	16.9	33.5	10,500	568	5.4
	Total or weighted mean:		**91,000**	**4,884**	**5.4**

Table 13. Fish species (percent occurrence) associated with juvenile salmon in several Maine nursery streams.

Species	Stream and year(s) Long Pond S. (2002-2003)	Magalloway R. (2000)	N.Branch Dead R. (2001-2002)	Horseshoe S. (2001)	Bigelow B. (1990-1999)	Squaw B. (1990-2002)	Lily Bay B. (2003)	McConnell B. (1992-1996)
Landlocked salmon	74.2	16.4	41.6	13.0	76.6	30.6	11.6	6.4
Brook trout	2.2	7.5	0.6	3.1	18.6	41.4	25.6	20.1
Slimy sculpin	0.2	28.9	8.2			3.3	34.9	41.0
Burbot						0.9	4.7	8.6
Blacknose dace	15.7	41.8	41.0	72.8		5.0	6.9	15.3
White sucker	0.5	0.5	0.3	1.2	0.7	0.1		0.3
Longnose sucker			1.0			0.5		
Chain pickerel					0.7			
Redbreast sunfish					1.5			
Sunfish species					1.7			
Creek chub	3.4		0.6	4.3	<0.1	7.5	16.3	
Lake chub		4.5	6.6			1.3		7.0
Finescale dace						8.0		
Fallfish		0.5				0.1		
Yellow perch						1.3		
Common shiner	3.8			5.6				1.3

Other species observed in statewide surveys of salmon nursery areas, but not enumerated: sea-run alewife, brown trout, round whitefish, muskellunge, northern redbelly dace, pearl dace, American eel, banded killifish, threespine stickleback, ninespine stickleback, white perch, pumpkinseed, smallmouth bass.

Early annual fall standing stocks of bony fishes, excluding salmon, in Barrows Stream, Washington County from 1960-1971 (Havey 1974a) are tabulated below. White suckers and creek chubs were usually the most numerous associates of salmon fry at Barrows Stream, with fallfish being less abundant but present in significant numbers.

Year	Estimated number (no. per acre)[1]	Estimated weight (lb. per acre)[1]
1960	1,149±214	12.75±2.29
1961	780±236	11.35±1.37
1962	422±227	4.88±2.59
1963	3,639±400	30.07±3.68
1964	1,873±114	24.20±1.39
1965	1,246±232	18.22±3.39
1966	2,368±348	19.21±3.68
1967	2,061±494	14.04±3.38
1968	4,339±510	22.80±2.79
1969	2,789±205	16.63±1.89
1970	1,759±144	25.29±2.09
1971	3,191±469	17.82±2.59

[1]± values denote 95% confidence limits

Predators

Several of the fish species listed above are potential predators as well as competitors with salmon fry. American eels are extremely abundant and of large size in some salmon nursery areas, but most other potential predators (e.g. chain pickerel or smallmouth bass) are rare or of small size. Elson (1957a) discussed the adverse effect of eel predation on survival of sea-run Atlantic salmon fry in certain New Brunswick Rivers. Eels are absent in the thoroughfares of the Fish River Chain of Lakes where salmon fry are very abundant (Table 8). Juvenile salmon have been observed in the stomachs of burbot in one northern Maine stream (D. Cote, MDIFW, personal communication).

Mergansers and kingfishers are known predators on juvenile sea-run Atlantic salmon (Elson 1957b). Mergansers and kingfishers probably prey commonly on landlocked salmon fry – we have often seen broods of mergansers actively feeding in salmon nursery areas. Cormorants frequent some landlocked salmon lakes but their role as a predator is unknown. Likewise, otter and mink are common around many Maine salmon nursery streams, but their effects on salmon production are undocumented.

Food habits of salmon fry

Gut contents of a sample of salmon fry collected in September 1981 from the West Branch of the Penobscot River are summarized in Table 14. To the best of our knowledge, these are the only data available on feeding habits of landlocked salmon fry in Maine. Mayfly (Ephemeroptera) or caddis fly (Trichoptera) species were the most common food items. We suspect that some choice is involved in the feeding behavior of even these tiny salmon, but that availability of food items of appropriate size largely dictates utilization. A study of Maine-origin landlocked salmon fry conducted in Argentina supports this idea; Dipteran (true flies) species were the dominant group found in the study streams, as well as in the stomachs of salmon fry (Sakai et al. 1993).

Life as parr

Landlocked salmon parr, like fry, choose, occupy, and defend home territories (Fenderson et al. 1968). Flow velocities and water depths selected by parr are generally greater than that for fry; consequently they are often found mid-stream, whereas fry are more closely associated with shoreline areas. Segregation of the two age groups may reduce competitive interactions (Gibson et al. 1993). Parr occupy a wide range of substrates, but they clearly prefer course material such as cobbles, rubble, and boulders.

Density

Densities of parr in representative landlocked salmon nurseries are summarized in Table 15. Estimated densities are not always precise because fry and parr have usually not been separated by aging, but rather by length frequencies. Densities may be underestimated because some parr may already have emigrated to lakes prior to sampling in late summer or early fall.

Parr density in waters listed in Table 15 averaged 6.2 fish per 100 square yards of nursery habitat. As with fry (Table 8), the density of salmon parr is highly variable between streams and annually within the same stream. At Wilson Stream, a tributary to Sebec Lake, production ranged from 0.2 to 15.2 parr per 100 square yards during a recent 10-year period (T. Obrey, MDIFW, unpub. data). Annual variability was also high at Bigelow Brook, tributary to Mayfield Pond, during the same period (4.9 to 23.3 parr per 100 square yards). These examples of fluctuating production are apparently normal among wild salmon populations.

Twelve tributaries to Moosehead Lake supported an average of 7.7 parr per 100 square yards (range 5.7-14.7) during a study by AuClair (1982). In a 12-year study at Barrows Stream, Washington County, Havey (1974a) obtained an average of 2.0±0.5 parr per 100 square yards. Corre

Table 14. Gut contents of landlocked salmon fry collected from three sites on the West Branch of the Penobscot River, Piscataquis County, Maine, mid-September 1981.[1]

	Site					
	Little Ambejackmockamus Deadwater (six fish; total lengthrange:55-72 mm)		Nesownehunk Deadwater (four fish; total length range:60-69 mm)		Abol Bridge (four fish; total length range:66-71 mm)	
TAXA	**Total number of food items**	**Mean number per fish of items**	**Total number of food items**	**Mean number per fish of items**	**Total number of food items**	**Mean number per fish of items**
Harpacticoid copepod					1	0.25
Gastropoda	2	0.33				
Adult Insecta heads	3	0.50			5	1.3
Immature Insecta heads	2	0.33	5	1.3	14	3.5
Lepidoptera	1	0.17				
Ephemeroptera						
Unidentified larvae					53	13.3
Ephemerellidae						
Ephemerella sp.	1	0.17				
Tricoptera						
Unidentified larvae	16	2.7	10	2.5	1	0.25
Hydropsychidae	3	0.50				
Chematopsyche sp.	1	0.17				
Hydropsche sp.	9	1.5				
Hydroptilidae						
Hydroptilia sp.	8	1.3	1	0.25		
Lepeoceridae						
Ceraclea sp.	9	1.5				
Diptera						
Pupae					1	0.25
Chironomidae					1	0.25
Chironomidae heads						
Simuliidae			2	0.50	5	1.3
All food items:	**55**	**9.2**	**18**	**4.5**	**81**	**20.3**

[1] Data provided by G. M. Lander and E. Spear.

Table 15. Density of salmon parr (age I+ and age II+) in representative Maine nursery streams, 1957-2003.

Stream	Lake system	County	Date	Number/100 square yards
Square Lake Outlet	Square/Eagle Lakes	Aroostook	Oct. 1957	2.4
Pollywog Stream	Nahmakanta Lake	Piscataquis	Aug. 1996	6.0
Long Pond Stream	Long Pond	Piscataquis	Aug. 1995	3.3
Long Pond Stream	Long Pond	Piscataquis	Aug. 1996	5.2
Long Pond Stream	Long Pond	Piscataquis	Aug. 1998	7.8
Long Pond Stream	Long Pond	Piscataquis	Aug. 1999	1.8
Davis Stream	Sebec Lake	Piscataquis	Aug. 1990	1.9
Davis Stream	Sebec Lake	Piscataquis	Aug. 1991	7.2
Davis Stream	Sebec Lake	Piscataquis	Aug. 1992	1.4
Davis Stream	Sebec Lake	Piscataquis	Aug. 1993	5.1
Davis Stream	Sebec Lake	Piscataquis	Aug. 1994	1.9
Davis Stream	Sebec Lake	Piscataquis	Aug. 1995	0
Davis Stream	Sebec Lake	Piscataquis	Aug. 1996	1.3
Davis Stream	Sebec Lake	Piscataquis	Aug. 1997	3.9
Davis Stream	Sebec Lake	Piscataquis	Aug. 1998	1.0
Davis Stream	Sebec Lake	Piscataquis	Aug. 1999	7.4
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1990	1.7
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1991	3.9
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1992	2.2
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1993	8.8
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1994	1.8
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1995	0.2
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1996	4.4
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1997	5.4
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1998	1.8
Wilson Stream	Sebec Lake	Piscataquis	Aug. 1999	15.2
Barrows Stream	Love Lake	Washington	Oct. 1961	2.0
Barrows Stream	Love Lake	Washington	Oct. 1962	2.9
Barrows Stream	Love Lake	Washington	Oct. 1963	4.4
Barrows Stream	Love Lake	Washington	Oct. 1964	1.5
Barrows Stream	Love Lake	Washington	Oct. 1967	0.5
Barrows Stream	Love Lake	Washington	Oct. 1968	5.4
Barrows Stream	Love Lake	Washington	Oct. 1969	3.5
Barrows Stream	Love Lake	Washington	Oct. 1970	0.2
Barrows Stream	Love Lake	Washington	Oct. 1971	1.3
Bigelow Brook	Mayfield Pond	Somerset	Oct. 1959	20.0
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1990	21.7
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1991	21.8
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1992	23.3
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1993	13.6
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1994	5.6
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1995	6.5
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1997	22.0
Bigelow Brook	Mayfield Pond	Somerset	Aug. 1998	4.9
Horseshoe Stream	Chain of Ponds	Franklin	Sept. 2001	2.0
Dead River (N. Branch)	Chain of Ponds	Franklin	Oct. 2001	9.2
Dead River (N. Branch)	Chain of Ponds	Franklin	Sept. 2002	6.9
Long Pond Stream	Rangeley Lake	Franklin	Aug. 2002	18.1
Long Pond Stream	Rangeley Lake	Franklin	Aug. 2003	3.6
Long Pond Stream	Beaver Mountain Lake	Franklin	Aug. 2002	3.8
Dodge Pond Stream	Rangeley Lake	Franklin	Sept. 1972	25.0
Dodge Pond Stream	Rangeley Lake	Franklin	Aug. 1973	10.0
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1965	12.6
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1966	10.1
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1971	4.5
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1972	3.7
Kennebago River	Mooselookmeguntic Lake	Oxford	Aug. 1977	3.6
Kennebago River	Mooselookmeguntic Lake	Oxford	Aug. 1978	2.5
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1983	3.7
Kennebago River	Mooselookmeguntic Lake	Oxford	Sept. 1990	4.6
Nason Brook	Sebago Lake	Cumberland	Aug. 1963	4.9
Northwest River	Sebago Lake	Cumberland	Oct. 1962	5.4
Northwest River	Sebago Lake	Cumberland	Sept. 1967	4.7
Northwest River	Sebago Lake	Cumberland	Sept. 1972	5.9
Northwest River	Sebago Lake	Cumberland	Sept. 1973	8.3
			Mean±standard error:	**6.2±0.7**

sponding weight standing stock was 3.6± 0.8 pounds per acre. Standing stock of parr in four western Maine nursery streams (Table 9) averaged 8.5±1.5 pounds per acre (D. Boucher, MDIFW, unpublished data).

Growth

Parr that have spent 2 years in stream nursery areas show considerable variation in growth (Table 16). Except for Cold Stream Pond, figures given are calculated lengths. Calculated length for age II parr (average of 5.9 inches) probably reflects the approximate size of salmon just prior to migration to lakes. Aroostook County data are from Warner and Fenderson (1963); data from Washington County are from Havey (1974b); Piscataquis County data are from AuClair (1982); and Franklin and Oxford County data are from Boucher (MDIFW, unpublished data).

Survival

Utilizing density figures from Tables 8 and 15 for fry and parr salmon, respectively, we can estimate survival from age 0+ to age I+. Assuming that about 80% of the salmon migrate from the natal streams at age II (from Havey [1974a], DeSandre et al. [1977] and Auclair [1982]), and that migration as fry is minimal, survival from late summer or early fall age 0+ salmon to late summer or early fall age I+ salmon is approximately 29%. Annual survival for nine brood years at Barrows Stream, Washington County was 19% (Havey 1974a). In streams subject to drastic flow fluctuations, water control dams may increase survival (Havey 1974a).

Food habits of salmon parr

Information on food habits of landlocked salmon parr remains very limited. The usual food of landlocked salmon parr is thought to be primarily crustaceans and insects. However, stomachs of 5 of 25 parr living in the outlet of Long Pond, Hancock County, contained juvenile anadromous alewives, and 20 contained insects. These parr averaged about 6.5 inches in total length. Four parr examined from Cross Lake Thoroughfare, Aroostook County in 1956 had all fed on aquatic insect nymphs and larvae.

Table 16. Size attained by age II parr in Maine salmon nursery areas.

Water	County	Sample size	Calculated length at age II (inches)	Year(s)
Long Lake	Aroostook	367	6.7	1957-1959
Eagle Lake	Aroostook	356	7.0	1957-1959
St. Froid Lake	Aroostook	185	6.4	1957-1959
Portage Lake	Aroostook	153	5.9	1957-1959
Square Lake	Aroostook	1,058	7.3	1957-1959
Cross Lake Thoroughfare	Aroostook	310	6.6	1955
Cross Lake Thoroughfare	Aroostook	300	5.9	1960
Moosehead Lake	Piscataquis	369	5.3	1967-1975
Cold Stream Pond	Penobscot	32	6.1	1952
Love Lake	Washington	113	5.3	1954-1963
Arnold Pond	Franklin	61	6.9	2003
Chain of Ponds	Franklin	43	6.1	1996,1998-1999
Beaver Mountain Lake	Franklin	112	5.6	1994,1997,2000
Dodge Pond	Franklin	92	6.0	2001
Mooselookmeguntic Lake	Franklin	527	4.5	1986-2003
Richardson Lake	Oxford	35	5.1	2001
Parmachenee Lake	Oxford	64	5.6	1999
Aziscohos Lake	Oxford	193	5.5	1993-2002
	Unweighted mean±standard error:		**5.9±0.2**	

Transition from stream life to lake life

Among sea-run Atlantic salmon, emigration from fresh to salt water is preceded by striking physical and physiological changes in the young fish. Several of the changes in physical characteristics described for sea-run Atlantic salmon have been noted in landlocked salmon, but to a lesser degree. Perhaps the most noticeable change is the tendency toward loss of parr marks and the appearance of the silvery sheen so evident among sea-run Atlantic salmon smolts. However, among landlocked salmon, the silvering is much less pronounced and parr marks are more persistent.

Landlocked salmon showing partial smoltification prior to moving from the nursery stream to lake habitat. (Dave Boucher, MDIFW)

Young landlocked salmon typically remain in the nurseries for 1 to 3 years before movement into lakes. This important life history event is easily identified by growth patterns on scales – salmon that have become lake-dwellers show rapid growth upon leaving the stream environment. Boucher (MDIFW, unpublished data) analyzed stream residence time of wild salmon from 22 lakes and found the majority (75%) had spent at least two full growing seasons in stream nurseries (Table 17). The proportion of salmon spending only one year in nursery streams prior to emigrating averaged 22% and ranged from 4 to 94%. Very few 3-stream year salmon were observed from any water. Several 4-stream year fish and a single 5-stream year fish have been observed from Mooselookmeguntic Lake in western Maine.

These data show there is considerable variation in the ratio of stream years among waters and to a lesser degree within the same water from year-to-year. Factors associated with the timing of migration from streams have not been clearly defined, but may include the amount and quality of habitat for older juveniles, density of young salmon, and growth rates. In the thoroughfares linking the Fish River Lakes, 51 to 74% of young salmon emigrate at age I (in their second year of life). In some of these thoroughfares, the boulders and pools that typically characterize habitat for large juvenile salmon are scarce. Thus, as salmon reach a certain size at age I, they may wander around to locate suitable territories, and in so doing move out into the lakes. It is possible that some salmon fry, particularly larger individuals, also emigrate from these nurseries into the lakes.

Irrespective of the factors influencing the timing of migration, knowledge of lake-specific stream life patterns is important in the management of wild salmon. AuClair (1982) described an inverse relationship between time spent in the tributaries and later lake growth rates and size quality of salmon from three northern Maine lakes. This same relationship was apparent for a larger group of lakes from western and northern Maine (Table 17 and Figure 3).

In general, 1-stream year salmon grow faster (Figure 4), are recruited into the fishery at younger ages, and exhibit lower survival to older ages because they are exploited by anglers earlier (see below). Conversely, populations in waters with a high proportion of 2 and 3-stream year fish are slower growing but exhibit greater longevity than those where 1-stream year fish are predominant.

Stream years	% age V+ and older	% age VI+ and older
1	28	8
2	59	24
3	84	50

Landlocked salmon smolts emigrate to lakes during both spring and fall, but the major movement appears to be in the spring. At Barrows Stream, 8 of 87 captured smolts surviving from the 1958 year class moved into the lake in late fall 1959 at age I+, while the remainder emigrated the next spring at age II. Spring emigrants averaged 6.4 inches in total length and 1.25 ounces in weight. Peak spring emigration was in April and May at water temperatures of 40-45°F. During April and May 1962, 25 spring emigrants at Barrows Stream averaged 6.2 inches in total length and 1 ounce in weight; there was no known autumn emigration in 1961. Barrows Stream is a small nursery area (average width 22 feet) and possibly autumn emigration takes place only when a year class is large. Subsequent trapping at Barrows Stream (1963 through 1966) indicated that the fall 1959 and spring 1960 smolt runs from the stream were from a relatively large year class.

At the East Outlet of Moosehead Lake, which has extensive habitat for older juvenile salmon, the predominant movement into the lake occurs at age II (P. Johnson, MDIFW, personal communication). Growth of juvenile salmon is excellent in the East Outlet; from 1971-1975, salmon that emigrated during their second, third, and fourth year had attained lengths of 4.1, 3.9 and 3.5 inches, respectively, after their first full year of stream life (Auclair 1982). Observed average lengths of salmon moving up in their second, third, or fourth year of life were 6.9, 9.7, and 11.2 inches, respectively.

Table 17. Stream residence time and size of wild salmon from Maine lakes, 1958-1999. (Includes fish sampled by all methods during all seasons).

Water	County	% of fish sampled spending: 1 year	2 years	3 years	Mean length (inches)[1]	No. fish sampled
Beaver Mountain Lake	Franklin	4	96	0	15.4	132
Mooselookmeguntic Lake	Oxford	2	92	6	16.4	536
Aziscohos Lake	Oxford	12	87	1	15.7	337
Baker Pond	Somerset	10	87	3	15.2	32
Richardson Lakes	Oxford	8	85	7	16.6	61
Embden Pond	Somerset	7	85	8	17.1	129
Sebec Lake	Piscataquis	14	83	3	16.9	220
Big Kennebago Lake	Franklin	11	82	5	15.1	62
Parmachenee Lake	Oxford	13	80	7	14.2	60
Onawa Lake	Piscataquis	19	78	3	15.6	62
Long Pond	Piscataquis	21	75	4	15.3	21
Caucomgomoc Lake	Piscataquis	29	71	0	15.6	21
Lower Hudson Pond	Piscataquis	29	71	0	15.3	40
Pond in the River	Oxford	29	65	6	16.3	15
Chesuncook Lake	Piscataquis	36	62	2	17.9	332
Pierce Pond	Somerset	43	55	2	17.7	118
Lobster Lake	Piscataquis	38	55	7	18.7	69
Chain of Ponds	Franklin	65	35	0	14.8	111
Rangeley Lake	Franklin	66	33	2	18.5	300
Kingsbury Pond	Somerset	63	32	5	19.3	13
Munsungan Lake	Somerset	75	25	0	17.2	128
Eagle Lake	Aroostook	76	21	3	16.2	426
	All waters	**22**	**75**	**3**		

[1] Size data from fish with stream-years recorded.

Figure 3. Stream residence and size of wild landlocked salmon from Maine lakes.

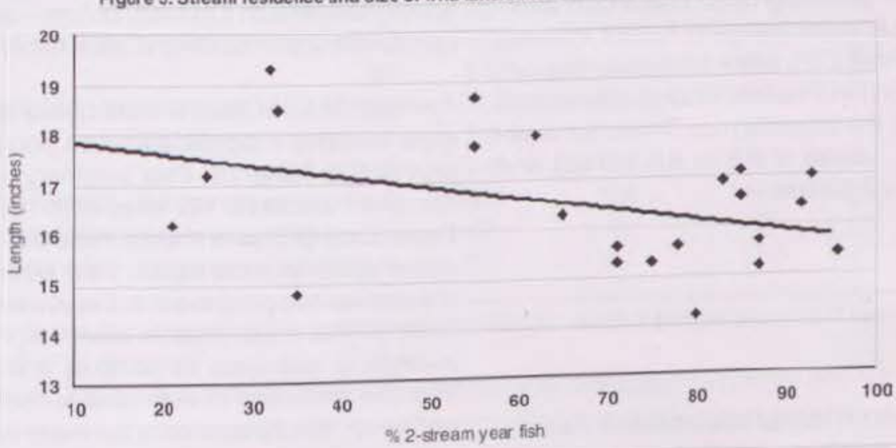
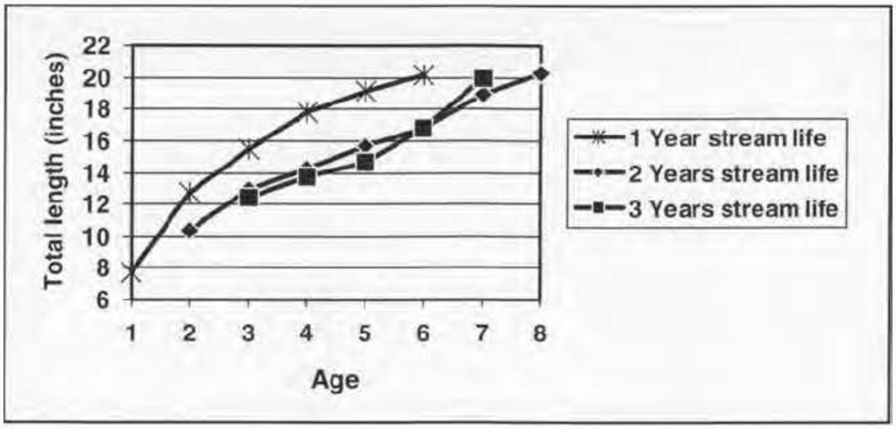


Figure 4. Variations in growth of wild salmon exhibiting one, two, and three years of stream residence. Data from spawning run surveys, 1963-2002.



Survival from late fall parr to smolts at Barrows Stream averaged about 5.1%, based on four annual determinations. Meister (1962), working with sea-run Atlantic salmon at Cove Brook, estimated survival of the 1955 year class to be 8.9% from mid summer parr to smolts. The Barrows Stream data are minimal because some smolts were able to bypass the trapping facilities. Havey (1974b) showed that catch per unit effort of adult wild salmon by trap netting in Love Lake varied little, despite fairly large fluctuations in the pre-smolt population.

Age at maturity among landlocked salmon is discussed in detail in another section of this paper. However, it can be pointed out here that some male salmon mature and spawn at age I+. Precocious males are commonly observed in all our studies dealing with salmon maturity. During salmon spawning migrations in 1953 at Cross and Long Lake Thoroughfares in Aroostook County, age I+ male salmon participated in spawning runs. These parr averaged 5.8 inches in total length (range of 4.3-9.7 inches), and they comprised about 7.5% of the total spawning run. In 2001, at Dodge Pond in Franklin County, precocious parr comprised 17% of the spawning run. These fish averaged 5.5 inches long (range of 4.6 to 8.3 inches) and weighed an average of 2 ounces.

Lake Life

Habitat

The earliest statements on habitat requirements for landlocked salmon were probably made by Stillwell and Stanley (1891) in an early report of the Maine Fish and Game Commissioners (1889-1890). Trial and error plantings prior to 1889 indicated that for a salmon introduction to be successful, "*ponds must be of good size and of clear, pure water, with streams flowing in, of swift running current, clean gravelly bottom, to which the fish can have free access to deposit their eggs, must also contain plenty of freshwater smelts or spring spawning minnows for food.*"

The habitat requirements of landlocked salmon were first described in detail by Dr. Gerald P. Cooper in his biological surveys of Maine lakes (Cooper 1940). Cooper's reports gave 70-75°F as the maximum temperature for salmon lakes, with a dissolved oxygen content of at least 5 ppm, and a pH above 6.0. Other requirements listed were adequate food supply and suitable spawning and nursery areas.

These early descriptions of salmon habitat – a large, deep, clear lake with rocky shores, cool well-oxygenated water in its depths, an abundance of smelts, and fed by a swiftly flowing stream with a gravelly bottom – are consistent with our current understanding of ideal habitat.

Average values of several water quality and trophic parameters for lakes supporting salmon principal fisheries are provided in Table 18. This summary was derived from samples collected in 152 lakes from 1970 to 2003 (Maine Department of Environmental Protection {MDEP}, unpublished data). In most cases, data were obtained during one annual sampling event in the late summer or early fall months. The mean column values represent the overall average of estimates for all lakes and years combined. With the exception of estimates for color, chlorophyll *a*, and secchi disk transparency, the mean minimum and maximum columns represent minimums and maximums of the annual averages for all lakes. Mean minimum and maximum column values for color, chlorophyll *a*, and transparency are the absolute lower and upper ranges in the raw dataset. Metalimnion (thermocline) and hypolimnion temperature and dissolved oxygen values are means of late-summer readings taken below the 30-foot level. They are from 142 salmon lakes sampled from 1935 to 1995 (MDIFW, unpublished data).

These indicators show that, as a group, Maine salmon lakes are among Maine's most unproductive (oligotrophic) – they are low in phosphorous, chlorophyll *a* production is low, and summer dissolved oxygen values are generally high in the deeper regions of the lakes. The majority (53%) of Maine's salmon populations currently exist in these oligotrophic lakes (Table 19).

A significant number of salmon populations are also present in the more productive mesotrophic and eutrophic lakes (Table 19), indicating that salmon are capable of tolerating less stringent water quality conditions. Experimental stockings have shown that salmon may grow well and provide attractive fisheries in homothermous lakes (those with little or no summer temperature stratification), especially if forage fish are abundant (Warner and Havey 1985). The fact that nearly one-half of the state's salmon populations occur in lakes once thought poorly suited to them indicates their ability to often thrive and provide viable sport fisheries in a diversity of habitats. However, optimum development of salmon fisheries, including management for certain types of fisheries such as those emphasizing "trophy-size" fish, is best achieved in large lakes with excellent water quality, and where competition for food (smelts) and space from other species is negligible (Boucher 2001).

Adult male landlocked salmon sampled from Lower Hudson Pond, T10 R16, Piscataquis County. (Dave Boucher, MDIFW)

Table 18. Chemical and trophic state parameters for Maine lakes with principal salmon fisheries.

Parameter	Mean of annual averages for salmon lakes[1]: Mean	Minimum	Maximum	Mean (range) for all lakes surveyed[2]
Color (SPU)	20	14	70	28 (0-250)
Total alkalinity (mg/l $CaCO_3$)	10.8	2.9	46.5	*
pH	6.8	5.9	8.0	6.7 (4.5-9.4)
Specific conductance (*u*MHOS/cm)	37.3	14.0	99.0	*
Total phosphorous (ppb)	7.3	1.0	20.0	14.0 (1.0-110.0)
Chlorophyll *a* (ppb)	2.9	0.8	14.3	4.7 (1.1-51.5)
Secchi disk transparency (feet)	20.6	5.6	44.6	16.1 (1.5-67.0)
Metalimnion/hypolimnion water temperature (°F)	52	42	68	*
Metalimnion/hypolimnion dissolved oxygen (mg/l)	6.9	0.7	13.0	*

[1] Data provided by Maine Department of Environmental Protection, except temperature and dissolved oxygen data, which are from MDIFW files.
[2] Statewide data from Public Educational Access to Environmental Information in Maine (PEARL 2003).

Table 19. Occurrence of principal salmon fisheries by lake trophic type.

	Lake trophic type					
	Oligotrophic		Mesotrophic		Eutrophic	
County	No. lakes	No. acres	No. lakes	No. acres	No. lakes	No. acres
Piscataquis	19	137,525	10	5,058	1	570
Aroostook	12	44,466	9	13,046	7	8,165
Somerset	10	16,060	10	16,323	1	684
Washington	8	23,761	10	43,111	0	0
Hancock	14	16,918	3	2,460	0	0
Penobscot	7	34,887	4	6,433	0	0
Franklin	10	27,282	6	1,568	0	0
Oxford	7	15,880	3	7,509	8	12,630
Kennebec	2	2,668	2	2,993	0	0
Cumberland	2	29,082	0	0	5	8,218
Waldo	1	1,095	1	1,370	0	0
Knox	0	0	1	1,305	0	0
Androscoggin	1	2,260	0	0	0	0
York	0	0	0	0	2	1,464
Totals:	**93**	**351,884**	**59**	**101,176**	**24**	**31,731**
Percent of totals:	**52.9**	**72.6**	**33.5**	**20.9**	**13.6**	**6.5**

The majority of Maine's salmon populations are supported in lakes managed solely for coldwater species, usually with lake trout and brook trout (Table 20). In 72 lakes (42%), salmon are managed in combination with various warmwater species, including smallmouth bass, largemouth bass, and white perch. In the southern and eastern regions where warmwater sport fish species are widely distributed, virtually all salmon management is in conjunction with warmwater species.

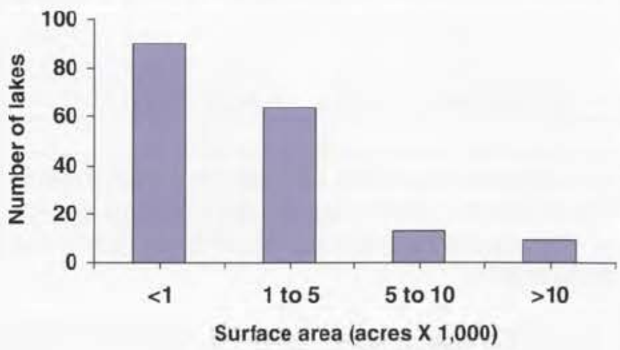
Table 20. Occurrence of principal salmon fisheries by lake management type.

	Lake management type			
	Coldwater species only		Coldwater/warmwater species	
County	No. lakes	No. acres	No. lakes	No. acres
Piscataquis	21	95,562	9	47,591
Aroostook	26	60,515	2	5,162
Somerset	19	32,537	2	530
Washington	2	3,100	16	63,772
Hancock	8	7,030	9	12,348
Penobscot	5	7,109	6	34,211
Franklin	14	27,536	2	1,314
Oxford	7	16,120	11	19,899
Kennebec	0	0	4	5,661
Cumberland	0	0	7	37,300
Waldo	0	0	2	2,465
Knox	0	0	1	1,305
Androscoggin	0	0	1	2,260
York	0	0	2	1,464
Totals:	**102**	**249,509**	**74**	**235,282**
Percent of totals:	**58**	**51.5**	**42**	**48.5**

Combination management lakes often provide conditions that encourage faster salmon growth rates than those lakes managed strictly for coldwater species (MDIFW, unpublished data). The growing season in southern and eastern Maine, where most combination management waters are located, is up to a month longer than in northern Maine, and lake trout, significant competitors with salmon for smelts, are more abundant in northern and western Maine where coldwater management lakes prevail. That salmon can co-exist and thrive in the presence of at least some warmwater fishes attests again to its adaptability.

The size distribution (surface area) of lakes currently supporting principal salmon fisheries is depicted in Figure 5. Most salmon lakes have a surface area of less than 5,000 acres, and they range in size from 58 to 74,890 acres. Average and median lake size for all lakes is 2,755 and 955 acres, respectively. If Moosehead Lake is excluded, average lake size is 2,342 acres.

Figure 5. Size distribution of Maine lakes supporting principal salmon fisheries, 2001.



Mean depth is a broad indicator of productivity; lakes with high average depth tend to show lower productivity because they often lack extensive littoral areas. Most salmon lakes have mean depths of less than 40 feet, with lakes in the 11 to 30 feet range predominating.

Cooper and Fuller (1945), in an intensive biological survey of Moosehead Lake, found that salmon seldom inhabit the deepest water. Landlocked salmon were found exclusively in depths ranging from 15 to 75 feet, with the majority distributed in depths shallower than 60 feet. There was relatively little difference in salmon abundance in the 16 to 30 and 45 to 60-foot zones. Gill netting with nets suspended at various depths revealed that salmon were more abundant at mid-depths than near the bottom.

Maine salmon lakes are located in a rather wide range of climatic conditions, ranging from Sebago Lake in the extreme south to the most northerly, Long Lake, in the Fish River Lakes. The variations in latitudes, elevations, and climatic conditions have some effect on the physical characteristics of the lakes. Those lakes located in southern Maine or at lower elevations may become warmer in the epilimnion during the summer, and are covered by ice for a shorter period during the winter. Extremes in duration of ice cover are represented by Sebago Lake and Long Lake. Due to its large volume of water, Sebago Lake seldom freezes completely before late January or early February, and in some years it does not freeze completely. When complete freezing does occur, ice-out is usually during early April. In contrast, Long Lake usually freezes over during early December, and ice cover leaves the lake during early May. Thus, both length of the open water fishing season and length of the salmon growing season are affected by climatic differences.

Growth

Seasonal salmon growth proceeds in the following sequence: Growth begins in the spring at a rapid rate; as spring yields to summer, growth declines at a fairly constant rate; in fall, the rate of growth speeds up slightly; and growth in winter is negligible. Warner and Fenderson (1963), working with wild salmon populations from Square Lake, Aroostook County in 1954 and 1961, found that about 80% of Square Lake salmon had started their current season's growth by the end of May. By mid-June, over 90% had commenced a new season's growth. The Square Lake salmon population is one of the northernmost in Maine, and it is likely that populations in southern Maine begin to grow slightly earlier.

Lengths attained at different ages by salmon from many of Maine's most important lakes are presented in Tables 21 and 22, and Tables 24 and 25. Samples were obtained on fall spawning run surveys during the period from 1985 to 2002. The data are separated by origin of the fish (wild or hatchery). Hatchery fish are further segregated by strain to compare the growth performance of Maine's two principal brood sources (Sebago Lake and West Grand Lake). The lakes are arranged hierarchically by length at age IV+ and III+ for wild and hatchery-reared fish, respectively. Unweighted means of lengths at age are reported for salmon from all lakes by origin and strain.

Individual lake summaries demonstrate the range in growth potential of salmon among Maine waters. Large differences in growth between lakes occur among both wild populations and those supported by hatchery fish (Tables 21 and 22). These differences can be attributed to a number of factors, including presence and abundance of co-predators on smelts, habitat quality and quantity, climate (e.g. length of the growing season), and exploitation rates. In general, we believe that mean lengths of salmon at various ages in most salmon lakes are greater now than when the two previous editions of this report were written (Havey and Warner 1970, and Warner and Havey 1985), especially in lakes dependant upon stocking.

Table 21. Growth of wild landlocked salmon in certain Maine lakes. Samples from spawning run surveys, 1985-2003. Data are arranged hierarchically by length at age IV+.

Water	County	Year(s)	No. fish sampled	Total length at age (inches) I+	II+	III+	IV+	V+	VI+
Rangeley L.	Franklin	1985-2002	789	9.0	13.0	15.7	18.1	20.0	21.3
Square L.	Aroostook	1987,1993-96, 1999-2000	179	8.5	12.0	14.8	16.6	17.3	18.1
Sebec L.	Piscataquis	1989,1992-95, 1997-98	63	*	*	13.5	16.2	18.5	*
Lower Hudson P.	Piscataquis	1997-98	71	7.5	9.8	12.5	15.4	16.1	*
Eagle L.	Aroostook	1985-88, 1993-98	425	8.2	10.9	13.1	15.2	17.2	18.1
Aziscohos L.	Oxford	2000	62	*	10.0	11.9	15.2	15.1	16.1
Long P.	Piscataquis	1997	54	*	10.5	13.5	15.0	16.3	*
Munsungan L.	Piscataquis	1992	51	*	10.6	12.5	15.0	*	*
Chesuncook L.	Piscataquis	1997-98	55	*	*	12.4	14.8	16.6	*
St. Froid L.	Aroostook	1985,1987	37	*	9.3	12.7	14.6	*	*
Arnold P.	Franklin	2003	68	6.8	8.8	12.2	14.3	14.5	17.5
Dodge P.	Franklin	2001	104	6.1	8.7	12.0	14.2	15.8	16.3
Chain of Ponds	Franklin	1998	41	*	9.9	12.2	13.4	14.8	18.8
Mooselookmeguntic L.	Franklin	2001-03	235	*	8.4	11.4	13.2	14.5	15.9
Parmachenee L	Oxford	1999	62	*	8.8	10.7	13.0	16.3	16.1
Beaver Mountain L.	Franklin	2000	85	*	11.0	10.2	13.0	15.9	17.1
Unweighted means±standard errors:				7.9±0.5	10.1±0.4	12.5±0.4	14.8±0.4	16.4±1.0	17.5±1.3

Our extensive studies on salmon growth have revealed that dramatic shifts in growth can be expected in the same lake from one year to the next. Indeed, this phenomenon continues to represent the most salient challenge faced by Maine's salmon managers. Determining and correcting causes of slow growth are important if a given population is to express its potential as a sport fishery resource. We emphasize that a slow growth rate does not endanger the population in question, but it does reduce its value as a sport fishery.

Fluctuating growth rates are usually associated with changes in forage (smelt) populations (Havey 1973b) and, related to this, salmon densities (Havey 1980). Salmon densities are strictly controlled in populations sustained by hatchery stocks, whereas annual recruitment is often highly variable in wild populations. In lakes supported by hatchery fish, salmon are stocked at rates sufficiently low to maintain an appropriate balance of salmon and smelts, so in general rapid growth is maintained. In many wild populations, where little control over annual recruitment can be exerted, growth often remains slow or highly variable from year to year. The effects of these two distinctly different situations are clearly demonstrated in Tables 21, 22, and 23. Weighted mean length, weight, and body condition of wild and hatchery salmon indicate that for most cohorts there are statistically significant differences between the two groups (Table 23). Wild salmon are generally slower growing, weigh less at age, and are less robust. Among lakes sampled since 1985, wild salmon were not recruited to 14 inches (the general legal length limit) until age IV+ or V+, whereas hatchery salmon in most lakes reached legal size by age II+.

Growth differences are also apparent between lakes supported by West Grand-strain and Sebago-strain fish (Tables 24 and 25). Among most of the lakes analyzed, Sebago strain salmon were longer at the same age than West Grand fish. Significant weight and body condition differences were also observed between pooled samples of salmon from those lakes tabulated (Table 26). It is possible that the larger size of Sebago fish is simply a function of stocking location (high exploitation lakes in southern and central Maine) – rapid harvest and a longer growing season may accommodate faster growth and improved weight. The observed differences may also be genetically related. Late nineteenth century reports of Fish and Game Commissioners made note of rather dramatic size differences between these two populations (Stillwell and Stanley 1888). The performance of paired plantings of each strain is currently being tested in three waters located in western, north central, and northern Maine.

A length-weight relationship for Maine landlocked salmon is depicted in Figure 6. The curve was compiled from 37,978 salmon sampled in 137 lakes from 1985 to 2002. The analysis included both wild and hatchery-reared salmon. Most wild salmon were collected from western and northern

Table 22. Growth of hatchery-reared landlocked salmon in certain Maine lakes. Samples from spawning run surveys, 1985-2002. Data are arranged hierarchically by length at age III+.

Water	County	Year(s)	No. fish sampled	Total length at age (inches)					
				I+	II+	III+	IV+	V+	VI+
Wassookeag L.	Penobscot	1988-89,1992, 1997	129	*	19.3	22.3	*	*	*
West L.	Hancock	1996,1998	182	*	18.0	21.3	*	*	*
Thompson L.	Oxford	1997-98	144	*	18.9	21.2	*	*	*
Duck L.	Hancock	1998,2001	244	13.1	17.6	20.7	*	*	*
Tunk L.	Hancock	1987,1990,1992, 1995-98	296	12.1	18.0	20.4	22.3	*	*
Alligator L.	Hancock	1995-98	154	12.4	18.2	20.3	*	*	*
Long L.	Aroostook	1985,1987, 1996-97	265	12.7	16.8	20.3	21.7	22.2	22.9
St. George L.	Waldo	1985-91,1993, 1995,1997	842	13.8	17.8	20.2	20.8	*	*
Sebago L.	Cumberland	1985-98	3,739	14.0	17.8	20.1	21.3	21.9	22.5
Long P.	Kennebec	1989-93,1995-98	627	13.2	17.3	19.5	20.9	*	*
Kingsbury P.	Somerset	1986,1993-98	135	11.5	16.1	19.4	20.7	*	*
Phillips L.	Hancock	1993-94,1996-98	172	13.6	17.8	19.3	*	*	*
Branch L.	Hancock	1993,1996-97	132	12.6	17.3	19.3	19.6	*	*
Roach P. (1st)	Piscataquis	1985-97	593	12.8	17.3	19.1	20.0	*	*
Rangeley L.	Franklin	1985-2002	1,822	12.5	16.1	19.0	20.8	21.9	24.1
Long (Great) P.	Hancock	1994-98	162	*	16.0	18.8	19.4	*	*
Cathance L.	Washington	1993-98,2000	264	*	17.0	18.6	20.3	*	*
West Grand L.	Washington	1985-95,1998	1,365	*	16.3	18.3	19.1	20.0	*
Parker P.	Kennebec	1988-93,1995-98	692	12.4	16.0	18.3	19.0	*	*
Square L.	Aroostook	1999-2000	276	12.1	15.0	17.2	18.3	18.3	21.8
Moosehead L.	Piscataquis	1985-96	758	12.2	15.3	17.0	17.5	*	*
Sebec L.	Piscataquis	1992-95,1997	268	*	14.4	16.4	17.8	*	*
Eagle L.	Aroostook	1985,1987,1995, 1997-98	102	11.1	13.6	16.3	*	*	*
Big Wood L.	Somerset	1985-86,1994	163	10.6	14.0	15.7	17.4	*	*
		Unweighted means±standard errors:		**12.5±0.2**	**16.7+0.3**	**19.1±0.4**	**19.8±0.4**	**20.1±0.8**	**22.8±0.5**

Table 23. Weighted mean size and condition (Fulton's K) at age of wild and hatchery-reared salmon from lakes listed in Tables 21 and 22. Data are from spawning run surveys, 1985-2003. SE denotes standard error of the weighted means. Bolded entries indicate a significant difference (p<0.05) in means between the two groups.

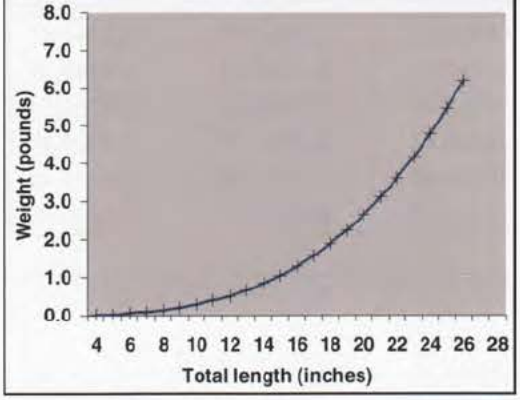
Age	Total length±SE (in)		Weight±SE (lb)		Condition±SE (K)	
	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery
I+	**8.7±0.2**	**12.9±0.1**	**0.23±0.01**	**0.69±0.01**	**0.89±0.02**	**0.85±0.01**
II+	**11.7±0.1**	**17.1±0.02**	**0.52±0.01**	**1.7±0.01**	**0.82±0.01**	**0.91±0.01**
III+	**14.3±0.1**	**19.0±0.03**	**1.0±0.02**	**2.4±0.01**	0.84±0.01	0.92±0.01
IV+	**16.4±0.1**	**20.5±0.1**	**1.5±0.03**	**3.0±0.03**	**0.88±0.01**	**0.93±0.01**
V+	**17.2±0.1**	**21.7±0.1**	**1.9±0.05**	**3.6±0.07**	0.89±0.01	0.92±0.01
VI+	**17.7±0.2**	**22.8±0.3**	2.0±0.10	4.3±0.18	0.89±0.01	0.98±0.02

Table 24. Growth of Sebago strain landlocked salmon in certain Maine lakes. Samples from spawning run surveys, 1985-1998. Data are arranged hierarchically by length at age III+.

Water	County	Year(s)	No. fish sampled	Total length at age (inches) I+	II+	III+	IV+	V+	VI+
Wassookeag L.	Penobscot	1988-89, 1992,1997	129	*	19.3	22.3	*	*	*
Thompson L.	Oxford	1997-98	144	*	18.9	21.2	*	*	*
St. George L.	Waldo	1985-91,1993, 1995,1997	842	13.8	17.8	20.2	20.8	*	*
Sebago L.	Cumberland	1985-98	3,547	14.0	17.8	20.1	21.3	22.0	22.5
Long P.	Kennebec	1989-93, 1995-98	627	13.2	17.3	19.5	20.9	*	*
Kingsbury P.	Somerset	1993-98	65	*	16.0	19.2	20.5	*	*
Rangeley L.	Franklin	1985-1998	900	12.6	16.1	19.0	20.8	22.2	*
Echo (Crotched) P.	Kennebec	1991		12.7	15.9	18.8	*	*	*
Roach P. (1st)	Piscataquis	1986-89, 1991-97	210	13.4	17.1	18.3	*	*	*
Parker P.	Kennebec	1988-93, 1995-98	690	12.4	16.0	18.3	19.1	*	*
Moosehead L.	Piscataquis	1986-89, 1995-96	112	*	15.4	17.7	*	*	*
Sebec L.	Piscataquis	1992-95,1997	138	*	14.5	17.7	*	*	*
Big Wood L.	Somerset	1994	41	*	*	15.4		*	*
Swan L.	Waldo	1993,1995-96	27	*	20.2	*	*	*	*
Tunk L.	Hancock	1987	71	*	17.0	*	*	*	*
	Unweighted means±standard errors:			**13.6±0.4**	**17.3+0.4**	**19.1±0.5**	**20.6±0.3**	**22.1±0.1**	**22.5±0**

Maine; hatchery salmon were from lakes distributed throughout the state. Smaller salmon (those less than 14 inches or younger than age II) were taken by netting or electrofishing. For lengths of 14 to 20 inches, values used to determine the length-weight relationship were largely from angler-caught salmon. The largest fish sampled were from spawning run surveys. The curve represents average values for lake-dwelling populations.

Figure 6. Relationship between length and weight for lake-dwelling Maine landlocked salmon. Includes fish of both wild and hatchery origin collected from 1985 to 2002.



The length-weight relationship is described by the formula: $\log_{10}$ weight in grams = 3.226($\log_{10}$ length in millimeters)-5.648. Fish used to graph the length-weight relationship of salmon over 14.0 inches were mostly from lakes where smelts were reasonably abundant when the samples were taken. Weights may be less for salmon exceeding 13 inches that are feeding primarily on insects. The negative effect of a fishless diet on the length-weight relationship appears to become increasingly pronounced as salmon increase in length.

While knowledge of "average" or "usual" salmon growth is basically important, information on causes of marked departures from these usual rates is vital to fishery managers. Determination of causes of unusually rapid growth in a given lake could reveal a management principle that, when applied, could lead to better growth in many salmon lakes. Conversely, as noted earlier, prompt correction of slowed growth is important if salmon are to express their potential as a renewable, usable fishery resource.

Slow-growth situations are generally undesirable from a recreational standpoint, particularly if the fish are of hatchery origin. If a population is not legally harvestable prior to age V or VI, many salmon will die from natural causes

Table 25. Growth of West Grand strain landlocked salmon in certain Maine lakes. Samples from spawning run surveys, 1985-1998. Data are arranged hierarchically by length at age III+.

Water	County	Year(s)	No. fish sampled	Total length at age (inches) I+	II+	III+	IV+	V+	VI+
West L.	Hancock	1996,1998	172	*	18.0	21.3	*	*	*
Duck L.	Hancock	1998	114	13.3	17.2	21.0	*	*	*
Long L.	Aroostook	1985,1987, 1996-97	208	12.7	16.7	20.9	22.3	22.2	*
Tunk L.	Hancock	1987,1990, 1992,1995-98	225	12.2	18.7	20.4	22.3	*	*
Alligator L.	Hancock	1995-98	154	12.4	18.2	20.3	*	*	*
Roach P. (1st)	Piscataquis	1985-97	330	12.2	17.3	19.6	20.1	*	*
Kingsbury P.	Somerset	1986,1993-98	65	11.5	16.2	19.6	*	*	*
Branch L.	Hancock	1993,1996-97	132	12.6	17.3	19.3	19.6	*	*
Phillips L.	Hancock	1993-94, 1996-98	172	13.6	17.8	19.3	*	*	*
Long (Great) P.	Hancock	1994-98	159	*	16.0	18.8	19.4	*	*
Cathance L.	Washington	1993-98	211	*	17.0	18.6	20.3	*	*
West Grand L.	Washington	1985-95,1998	1,165	*	16.2	18.2	19.0	20.0	*
Rangeley L.	Franklin	1985-89, 1998-97	412	11.9	15.0	17.9	20.5	*	*
Schoodic L.	Washington	1985	27	*	16.1	17.9	*	*	*
Square L.	Aroostook	1987,1993, 1995-96	119	12.2	15.0	17.4	18.0	*	*
Moosehead L.	Piscataquis	1985-96	387	11.9	15.6	17.3	17.3	*	*
Eagle L.	Aroostook	1985,1987, 1995,1997-98	101	11.1	13.6	16.3	*	*	*
Sebec L.	Piscataquis	1993-95	117	*	14.1	16.2	*	*	*
Big Wood L.	Somerset	1985-86,1994	86	10.6	13.0	16.0	17.4	*	*
Togue P.	Aroostook	1997	27	*	14.2	*	*	*	*
Unweighted means±standard errors:				**12.2±0.2**	**16.2+0.4**	**18.8±0.4**	**19.7±0.5**	**21.1±1.1**	*

Table 26. Weighted mean size and condition (Fulton's K) at age of Sebago Lake strain and West Grand Lake strain salmon from lakes listed in Tables 23 and 24. Data are from spawning run surveys, 1985-2002. SE denotes standard error of the weighted means. Bolded entries indicate a significant difference ($p<0.05$) in means between the two groups.

	Total length±SE (in)		Weight±SE (lb)		Condition±SE (K)	
Age	Sebago strain	West Grand strain	Sebago strain	West Grand strain	Sebago strain	West Grand strain
I+	**13.4±0.1**	**12.3±0.1**	**0.77±0.01**	**0.59±0.01**	0.85±0.01	0.84±0.01
II+	**17.5±0.1**	**16.6±0.03**	**1.8±0.01**	**1.6±0.01**	0.91±0.01	0.92±0.01
III+	**19.4±0.04**	**18.7±0.04**	**2.5±0.02**	**2.3±0.01**	**0.90±0.01**	**0.95±0.01**
IV+	**21.0±0.1**	**19.9±0.1**	**3.2±0.04**	**2.8±0.05**	0.93±0.01	0.94±0.01
V+	**22.1±0.1**	**21.1±0.2**	**3.7±0.07**	**3.3±0.14**	0.92±0.01	0.94±0.01

rather than from fishing, and cost per fish creeled is multiplied accordingly. While many anglers enjoy "action" provided by large numbers of small salmon, some prefer to catch fewer, but larger, fish. Populations of rapidly growing individuals are usually sparse in number, which may not provide catch rates that satisfy many anglers. For example, salmon at Parker Pond in Kennebec County grew exceedingly well in the years following their introduction in 1959 and reached large sizes by 1961, but fishing success was low (Warner and Havey 1985, and M. Scott, personal communication).

Populations with average growth, from which moderate numbers of large salmon are taken annually, seem to satisfy most anglers. With recent refinements in fish management techniques, the apparent willingness of modern anglers to embrace them, and our improved understanding of salmon populations, management for particular kinds of salmon fisheries may become more prevalent. For example, in certain lakes emphasis could be on a "quantity" fishery for large numbers of small or moderate-sized salmon. In other lakes, a "size-quality" fishery could be emphasized – one that provides fewer fish but of a larger size. However, considering the infertility of Maine lakes that provide habitat for salmon (Mairs 1966, Davis et al.1978, and MDEP, unpublished data), it is doubtful that fisheries for large numbers of large fish can ever be provided on a sustained basis.

Our data indicate that origin (wild or hatchery) is an important factor to consider in managing salmon sport fisheries, and that the specific strain of hatchery fish should perhaps be considered. The data provide evidence that precise management for some types of fisheries, such as those emphasizing "trophy-size" salmon, can be better achieved with hatchery stocks rather than wild stocks, and that the Sebago strain of salmon may provide at least a marginal advantage in lakes managed for larger fish.

Food habits of adult salmon

Early observations on food habits stressed the importance of smelt in the diet of landlocked salmon. Stillwell and Smith (1879) noted the large size attained by salmon in Sebago Lake and stated, "*Among the chief causes conducive to this unparalleled development, may be attributed the fact that smelts abound in the lake, and they form the chief and favorite food of the Sebago salmon at all seasons of the year.*"

In a subsequent early Commissioners' report, Stillwell and Stanley (1883) further emphasized the reliance of salmon on a smelt diet by saying, "*The landlocked salmon has been found, to our knowledge, indigenous to no waters in Maine unaccompanied by the smelt, both evidently being landlocked fishes. The smelt seems to be their natural food, but what is of far greater importance, its young fill the place to the newborn progeny of the landlocked salmon, of the milk to the young of animals.*" Stillwell and Stanley (1891) later became more strongly convinced of the dependence of newly introduced salmon on smelts. In the Maine Commissioners' Report for 1889-90, they stated, "*To succeed we feel sure the waters where they are to be introduced – must also contain plenty of freshwater smelts or spring spawning minnows for food. The smelt spawns and hatches at the same time in the spring the young salmon are beginning to feed, and is just what they need at that time to sustain them... We have caught the young smelts at Sebago in the spring and put them with the young salmon beginning to feed in the hatching house, and they would be as eager after them as a cat after a mouse, and would pursue them until the last one was eaten.*"

Most of the early introductions of landlocked salmon in Maine were apparently accompanied by introductions of smelt to serve as a forage fish. Kendall (1935) stated, "*As pertains to the lakes and streams of Maine, it has been quite generally stated to be a fact that salmon introduced into new waters where there are no smelt, do not thrive unless smelts are also introduced.*"

Kendall (1935) examined stomachs of salmon from Sebago Lake over a period of years. He states, "*The stomachs of a great majority of the many Sebago Lake salmon that from time to time I have examined in 16 seasons from April to October, between 1898 and 1916, both inclusive, contained smelts when they contained anything at all. The smelts were always the small form and translucent young.*"

The first detailed studies on salmon food habits were made by Dr. G. P. Cooper in his early biological surveys of Maine lakes. Cooper's data for percentage by volume of various food items in salmon stomachs are summarized in Table 27. In three Rangeley Lakes and four other lakes, Cooper

Rainbow smelts are the most important food item in the diet of Maine landlocked salmon.

Table 27. Stomach analysis (volumetric) of landlocked salmon in Maine Lakes, 1939-1965.

Lake	Number of stomachs examined	Number of stomachs with food	Food item and percent by volume: Smelts	Unidentified fish remains	Insects and other invertebrates	Other fish and miscellaneous items
Fish River Lakes	606	543	55	13	14	18
Moosehead Lake	30	25	87.5	*	0.5	12
Six lakes, as follows: Mooselookmeguntic, Rangeley, Sebago, Kezar, Sebec, Moosehead	61	44	68	3	4	25
Seven lakes, as follows: Green, Phillips, Beech Hill, Eagle, Lower Patten	42	24	99	1	*	*
Long Lake (1965) (Aroostook County)	229	226	41	2	19	38
Square Lake (1965)	218	201	66	5	18	11
Richardson Lake (1964)	38	27	17	24	59	0
Richardson Lake (1965)	74	61	54	30	9	7
Mooselookmeguntic Lake (1964)	49	32	26	46	19	9
Mooselookmeguntic Lake (1965)						
14 inches and over	158	131	34	39	17	10
12-13.9 inches	238	215	16	23	60	1
Sebago Lake (1965)[1]						
Under 15 inches	27	27	62	25	13	0
Over 15 inches	21	21	63	25	2	10

1 Percent composition by weight.

(1940) found that smelts made up an average of 68% of the food volume in salmon stomachs. In four lakes in south-central Maine, smelts comprised 75% of the volume of food eaten by salmon (Cooper 1941). In Moosehead Lake, 87% of the food volume in salmon stomachs consisted of smelts (Cooper and Fuller 1945). Cooper and Fuller also found that fishes other than smelts were fed on to a comparatively small extent by salmon in Moosehead. This was attributed to the pelagic distribution of both salmon and smelts. The food of salmon in seven lakes of the coastal section of central Maine was 99% smelts by volume (Fuller and Cooper 1946).

In studies at the Fish River Lakes (1953 to 1964), stomachs of 804 salmon from five lakes were examined, and the numbers of stomachs that contained each food item were tabulated for the 700 stomachs containing food (Table 28). Volumes of the various food items in 543 salmon stomachs are presented in Table 29. Smelts were the most frequent food items found in salmon stomachs; this forage fish was found in 34% of the stomachs examined. Smelts occurred most frequently (51%) in salmon from Portage Lake and least frequently in salmon from Long Lake (16%). Smelts were also the most important food item volumetrically, comprising an average of 55% of the food in 543 stomachs. The volume of smelts in salmon stomachs ranged from 33% of total volume in Long Lake to 77% in St. Froid Lake (Table 29).

The food habits of salmon in Sebago Lake were studied in 1965. Here, 48% of 27 stomachs of salmon less than 15 inches in length contained smelts, and smelts comprised 62% (by weight) of the stomach contents of salmon in that size range. The diet of salmon over 15 inches was similar to the diet of those less than 15 inches in length. Among salmon over 15 inches in length, 52% of the stomachs contained smelts. By weight, 88% of the diet of salmon in this size group was comprised of smelts or unidentified fish remains (Table 27).

In Richardson Lake in 1964, 27 salmon stomachs with food contained 17% smelts by volume. In 1965, 74 salmon stomachs contained 54% smelts by volume. In 1964, 32 salmon stomachs from Mooselookmeguntic Lake with food contained 26% smelts by volume (Table 27). In 1965, salmon stomachs from Mooselookmeguntic were analyzed separately for size groups 12-13.9 inches and over 14 inches. Stomachs of salmon under 14 inches contained only 16% smelts by volume, and those over 14 inches contained 34% smelts by volume (Table 27).

Table 28. Numbers of landlocked salmon stomachs in which various food items occurred, Fish River Lakes, 1953-1964. Percentages of stomachs with food items are in parentheses.

Lake	No. of stomachs examined	No. of stomachs with food	Food item and frequency of occurrence					
			Smelts	Sticklebacks	Minnows	Unidentified fish remains	Insects and other invertebrates	Miscellaneous and unidentified items
Square Lake	404	360	128 (36)	26 (7)	7 (2)	69 (19)	176 (49)	58 (16)
Eagle Lake	86	63	30 (48)	3 (5)	6 (9)	19 (30)	7 (11)	14 (22)
Long Lake	183	166	26 (16)	30 (18)	8 (5)	34 (20)	17 (10)	31 (19)
St. Froid Lake	66	54	21 (39)	3 (6)	1 (2)	19 (35)	13 (24)	17 (32)
Portage Lake	65	57	33 (51)	3 (5)	6 (10)	15 (26)	17 (30)	7 (12)
All lakes	**804**	**700**	**238 (34)**	**65 (9)**	**28 (4)**	**156 (22)**	**230 (33)**	**127 (18)**

Table 29. Percentage by volume of food items found in landlocked salmon stomachs, Fish River Lakes, 1957-1964.

Lake	Years	No. of stomachs examined	No. of stomachs with food	Food item and percent by volume					
				Smelts	Stickle-backs	Minnows	Unidentified fish remains	Insects and other invertebrates	Miscellaneous and unidentified items
Square Lake	1957-64	301	268	53	2	4	9	22	10
Eagle Lake	1957-59	52	41	67	trace	9	19	trace	4
Long Lake	1957-64	169	157	33	14	10	13	24	6
St. Froid Lake	1957-59	51	44	77	trace	trace	18	1	4
Portage Lake	1957-59	33	33	55	trace	15	14	4	12
All lakes		**606**	**543**	**55**	**4**	**6**	**13**	**14**	**8**

Our most recent assessments of salmon food habits are summarized in Tables 30 through 33. These data were collected from field examinations during routine angler and lake surveys, or from specific research projects. Frequency of occurrence data are from 1,775 stomachs collected from 50 lakes located primarily in northern, north central, and western Maine from 1980 to 1999. Stomachs were from salmon ranging in total length from 6.3 to 25 inches sampled during each month except April, November, and December. Volumetric data (Table 31) are from this same dataset but include 843 stomachs collected from only nine lakes; these are mostly winter samples from Moosehead, Sebec, and Big Wood Lakes. From 1980 to 1999, 1,412 of 1,775 salmon stomachs examined contained food (Table 30). For all data combined, smelts occurred in 808 (57%) of the stomachs examined. There was little difference in the occurrence of smelts between the two geographical regions.

Smelts comprised 80% of the volume of food in salmon stomachs collected during the winter months, suggesting they are of particular importance to salmon during that time (Table 31). Sayers et al. (1989), in their study of salmon food habits in Moosehead, Chesuncook, Caribou, and Schoodic Lakes, showed that smelts were the primary winter food of salmon, when available. This study concluded that the availability of smelts during the winter period was a critical factor determining growth of salmon in lakes.

Seasonal variability in the use of smelts by salmon is illustrated in Table 32. Smelts occurred in 81% of salmon stomachs examined during the winter and declined in subsequent months. During the open water season, smelt occurrence was lowest during September and October and highest during the mid-summer months.

Smelt occurrence increased as salmon attained larger sizes (Table 33). Fish items, including smelts, were largely absent from the stomachs of 22 salmon less than 8 inches long. For salmon between 8 and 11.9 inches, smelts occurred in 14% of stomachs. For those between 12 and

Table 30. Occurrence of food items in landlocked salmon stomachs from 50 Maine lakes, 1980-1999. Asterisks denote occurrence is less than 0.5%.

	Location					
	Aroostook, Piscataquis, Penobscot Counties (31 lakes)		Somerset, Franklin, Oxford Counties (19 lakes)		All waters (50 lakes)	
No. stomachs examined:	1,208		567		1,775	
No. (%) with food:	986 (82)		426 (75)		1,412 (80)	
Prey item	Number of stomachs	Percent occurrence	Number of stomachs	Percent occurrence	Number of stomachs	Percent occurrence
Rainbow smelt	552	56	255	60	808	57
Unidentified fish remains	181	18	96	23	278	20
Threespine stickleback	26	3	0	0	26	2
Stickleback species	11	1	0	0	11	0.8
Ninespine stickleback	2	*	0	0	2	*
Unidentified minnow species	20	2	5	1	25	2
White perch	12	1	0	0	12	0.9
Yellow perch	9	0.9	0	0	10	0.7
Lake chub	3	*	2	0.5	5	*
Unidentified sunfish species	2	*	0	0	2	*
Banded killifish	1	*	0	0	1	*
Common shiner	1	*	0	0	1	*
Slimy sculpin	1	*	0	0	1	*
White sucker	1	*	0	0	1	*
Landlocked alewife	0	0	5	1	5	*
Landlocked salmon	0	0	1	*	1	*
Blacknose dace	0	0	2	0.5	2	*
Golden shiner	0	0	2	0.5	2	*
Chain pickerel	0	0	1	*	1	*
Unidentified crayfish species	4	*	1	*	5	*
Insects	283	29	108	25	391	27
Amphipods	1	*	0	0	1	*
Mysis relicta	1	*	0	0	1	*
Unidentified snail species	1	*	0	0	1	*
Earthworm	0	*	3	0.7	3	*
Leech	0	0	2	0.5	2	*
Zooplankton	2	0	1	1	3	*
Miscellaneous items:						
Vegetation	15	2	0	0	15	1
Fish hooks	14	2	1	*	15	1

Table 31. Percentage by volume of food items found in 843 landlocked salmon stomachs from nine Maine lakes, 1990-1999. Samples were primarily obtained during January to March, and May (85%). Asterisks denote occurrence is less than 0.1%.

Prey item	Percent by volume
Rainbow smelt	79.8
Unidentified fish remains	3.4
Unidentified minnow species	1.7
Landlocked alewife	1.0
Threespine stickleback	0.6
Ninespine stickleback	*
White perch	0.6
Landlocked salmon	0.2
Yellow perch	0.2
Lake chub	0.2
White sucker	0.2
Unidentified sunfish species	*
Golden shiner	0.2
Insects	11.6
Zooplankton	*

15.9 inches and between 16 and 19.9 inches, smelts were present in 34% and 46% of stomachs, respectively. Smelt occurrence rose to 72% of the stomachs of salmon exceeding 20 inches. We presume that fish listed as "other fish" were mostly comprised of partially decomposed smelts, so smelt occurrence was probably underestimated.

Data on the size of smelts consumed by salmon in Maine lakes are not extensive. For early studies on Sebago Lake, Kendall (1935) said that the smelts he found in salmon stomachs were always the small form or translucent young. Cooper and Fuller (1945) reported that 88 smelts found in the stomachs of salmon gillnetted from 0 to 30 feet of water in Moosehead Lake averaged 1.4 inches (range: 1.1 to 3.8 inches). Eighty-eight smelts taken from salmon netted in depths of 30 to 60 feet ranged from 0.9 to 3.5 inches and averaged 1.6 inches.

The mean total length of 81 freshly eaten smelts (Table 34) in the stomachs of salmon from five of the Fish River Lakes (1957 to 1964) was 5.4 inches (range: 3.0 to 6.8 inches). Over 75% of the smelts ranged between 5.0 to 6.9 inches. Smelts in four of the five lakes averaged 5.1 to 5.5 inches, but they averaged 6.4 inches in St. Froid. In 1965, however, smelts from salmon stomachs in Long Lake averaged 4.0 inches and those from Square Lake averaged only 2.3 inches. This was attributed to a predominance of young-of-the-year smelts.

In Moosehead Lake, 85% of 1,816 smelts in stomachs of winter-caught salmon ranged between 2.0 and 3.9 inches. The size distribution of smelts in salmon stomachs collected from three nearby lakes, also from the winter period, were similar to the Moosehead samples, and their average size ranged from 2.7 to 3.0 inches. Summer samples from five western Maine lakes were slightly larger, with 67% ranging between 3.0 and 4.9 inches. In all lakes from which data are available, smelts exceeding 6.5 inches in length were rarely observed in salmon stomachs (Table 34).

The size differences of smelts in the studies cited above presumably reflect the availability of certain sizes of smelts rather than selectivity in feeding, at least for smelts less than 6.5 inches. Smelts in Maine lakes are known to be highly variable in abundance in the same lake from year to year, and highly variable in size attained in different lakes (Rupp 1959).

Table 32. Seasonal changes in the occurrence of smelts, other fish, and insect remains in salmon stomachs from 50 Maine lakes, 1980-1999.

Season	No. of stomachs examined	No. (%) with food	Food items and frequency of occurrence: Smelts	Other fish[1]	Insect remains
Winter (January to March)	681	585 (86)	81	30	1
Spring/early summer (May and June)	473	403 (85)	33	21	66
Summer (July and August)	265	177 (67)	37	37	29
Fall (September and October)	176	97 (55)	23	14	67

[1] Includes remains of unidentified fish and fish species other than smelts.

Table 33. The occurrence of smelts, other fish, and insect remains in the stomachs of various size groups of salmon from 50 Maine lakes, 1980-1999.

Length range of salmon	No. of stomachs examined	No. (%) with food	Food items and frequency of occurrence: Smelts	Other fish[1]	Insect remains
Less than 8 inches	22	14 (64)	0	7	86
8 to 11.9 inches	114	72 (63)	14	50	75
12 to 15.9 inches	410	310 (76)	34	25	56
16 to 19.9 inches	280	229 (82)	46	22	45
Over 20 inches	39	32 (82)	72	16	41

[1] Includes remains of unidentified fish and fish species other than smelts.

Table 34. Length frequency distribution of smelts found in salmon stomachs from several Maine lakes.

Water	Years	Season	Number smelts (%) in each inch group: 1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	Mean length (range)
5 Fish River Lakes	1957-64	Summer	0	0	2 (2)	17 (21)	37 (46)	25 (31)	5.4 (3.0-6.8)
5 western Maine lakes	1999-02	Summer	0	16 (31)	23 (44)	12 (23)	1 (2)	0	3.6 (2.4-5.1)
Moosehead Lake	1972-98	Winter	84 (5)	1,129 (62)	423 (23)	171 (9)	8 (0.4)	1 (0.1)	2.9 (1.4-6.1)
Lobster Lake	1989-90	Winter	1 (3)	13 (36)	10 (28)	12 (33)	0	0	3.4 (1.7-4.8)
Sebec Lake	1992-98	Winter	3 (4)	51 (71)	12 (17)	6 (8)	0	0	2.7 (1.8-4.5)
Big Wood Pond	1990-97	Winter	3 (3)	68 (62)	16 (14)	22 (20)	1 (1)	0	3.0 (1.8-5.0)

At Moosehead Lake in 1973, AuClair (1982) measured and aged "intact" smelts taken from salmon stomachs. Mean length of smelts was 3.8 inches, with a range of 2.0 to 5.9 inches. Lengths and ages are presented below:

Age	Number (%)	Total length (inches) ±95% confidence interval
I	7 (13)	2.3±0.1
II	13 (26)	2.8±0.3
III	25 (47)	4.3±0.1
IV	8 (15)	5.2±0.3

AuClair believed that the poor representation of younger (age I and II) smelts in the 1973 sample was the result of low population abundance at that time, possibly caused by heavy predation on young-of-the-year smelts by large numbers of yellow perch and hatchery-reared salmon. For an excellent discussion on smelt variation at Moosehead Lake, the reader is referred to AuClair (1982).

That salmon consumed food other than smelts was first indicated by Kendall (1935) as follows: "*During the summer months salmon frequently contained a number of species of insects in varying quantities, sometimes insects only, at other times smelts also. The insects were obtained from the surface of the lake where they had been blown by the wind. On some days the surface of the lake would be covered locally by a variety of forms upon which the salmon appeared to feed indiscriminately; sometimes some particular insect would predominate, or perhaps it* *would be the only insect present. But the salmon gorged themselves on them. At this time it was impossible to enumerate all the forms that have been found in salmon's stomachs. But I recall various beetles, including June bugs and potato beetles; various winged insects such as flying ants, bumblebees, mayflies, moths, grasshoppers, and various others, including spiders*".

Insects and other invertebrates were the second most important food items found in salmon stomachs in the Fish River Lakes, both numerically and volumetrically (Tables 28 and 29). These forms occurred in 33% of the salmon stomach examined and comprised 14% of the food volume of all stomachs. The percentage by volume of insects and other invertebrates found in salmon stomachs in the Fish River Lakes compares closely with Cooper's findings for other Maine lakes (Table 27). Most insects found in salmon stomachs were terrestrial forms. Salmon fed heavily on adult flying ants during certain periods in May and June. Immature aquatic insects were primarily represented by mayfly nymphs.

In Mooselookmeguntic Lake in 1965, insects and other invertebrates made up 60% of food volume in stomachs of salmon from 12 to 13.9 inches, but only 17% of food volume in stomachs of salmon over 14 inches in length (Table 27). In Richardson Lake in 1964, these forms contributed 59% of salmon food by volume, but in 1965 only 9%. Earthworms, most of which were probably anglers' baits, are included in this group. At Sebago Lake in 1965, insects and other invertebrates contributed 13% of salmon stomach contents (by weight) for fish under 15 inches, but only 2% for fish over 15 inches. Insects were mainly terrestrial forms, including flying ants. In the recent statewide salmon food studies previously mentioned, insects and other invertebrates occurred in 407 (29%) of 1,412 salmon stomachs with food (Table 30). Invertebrates other than insects included crayfish, amphipods, *Mysis relicta* (Moosehead Lake), snails, leeches, earthworms, and zooplankton. Winter and early spring samples were comprised of 12% insects by volume (Table 31).

Fish other than smelts usually contribute relatively little to the diets of salmon. In the Fish River Lakes, threespine sticklebacks occurred more frequently in salmon stomachs (9%) than any fish except smelts (Table 28). The pelagic habits of sticklebacks may make them more available to salmon than other species, such as minnows or suckers. Sticklebacks contributed about 4% to the volume of food eaten by salmon (Table 29). In statewide studies, sticklebacks were found most frequently in stomachs of salmon from lakes in Aroostook, Piscataquis, and Penobscot Counties (Table 30).

Minnows comprise a minor part of salmon diets in Maine lakes studied to date. Kendall (1935) in writing of salmon food habits stated, "*Rarely some other fish such as a perch or cyprinid was found*". In the Fish River Lakes, minnows occurred in only 4% of the 700 salmon stomachs that contained food and were represented primarily by the lake chub (Table 28). Minnows comprised 6% of salmon food by volume (Table 29). In the most recent statewide sample, minnows occurred in 2.5% of 1,412 stomachs with food (Table 30). Other than lake chubs, minnows occasionally observed in salmon stomachs include blacknose dace, common shiner, golden shiner, fallfish, and creek chub.

The scarcity of minnows in salmon stomachs in some Maine lakes does not reflect their abundance, because many salmon lakes also support sizeable minnow populations. Minnows are noticeably less abundant, however, in salmon lakes containing warmwater species such as smallmouth bass and pickerel. The minor role of minnows in salmon diets may reflect their lack of availability due to their distribution in the shallows along shore, and salmon may prefer smelts to minnows where both are present.

Other fish occasionally encountered in salmon stomachs are white perch, yellow perch, white sucker, slimy sculpin, banded killifish, lake whitefish, alewife, chain pickerel, sunfish, and landlocked salmon. Accidentally ingested materials found in salmon stomachs include vegetation, small stones, pieces of wood and bark, and fish hooks.

Of 1,412 salmon stomachs (Table 30) found with food in Maine studies, 278 (20%) contained unidentified fish remains. In the Fish River Lakes, unidentified fish remains made up 13% of the food volume in salmon stomachs between 1957 and 1964; fish remains occurred in 22% of salmon stomachs examined between 1953 and 1964. In Sebago Lake studies, unidentified fish remains comprised 25% by weight of the stomach contents of salmon over 15 inches in length, and occurred in 14% of all salmon stomachs that contained food. Unidentified fish remains made up 23% to 46% by volume of the stomach contents of salmon from Richardson and Mooselookmeguntic Lakes in 1964 and 1965. It is likely that a large part of the fish remains in the studies mentioned above were smelts.

The importance of smelts in the diet of landlocked salmon in Maine lakes has been repeatedly documented by the early Maine Commissioners' Reports, studies of Kendall, Cooper, and by recent, more extensive statewide studies. Smelts are present in nearly all lakes that currently support moderate-to-abundant salmon populations.

The primary disadvantage of the salmon's reliance on smelts as a forage fish is their marked fluctuation in abundance from year to year. Rapid, sharp reductions in salmon growth have resulted from declines in smelt abundance in many Maine waters. Thus, the presence of sufficient numbers of smelts to permit growth of salmon to attractive sizes is vital to successful management of salmon populations in Maine.

The disadvantage of extreme fluctuations in smelt abundance suggests that establishing other forage fishes for salmon might be desirable. Landlocked alewives have been introduced in several Maine lakes in attempts to supplement forage supplied by fluctuating smelt populations. Alewives have become established in several waters, but in Echo Lake (Mount Desert Island) it was found that the alewife's diet of plankton was closely correlated with that of the smelt. Competition between the two species evidently depressed smelt growth below the rate of 10 years before when alewives were first introduced (Lackey 1969). While alewives are utilized by salmon, inadequate information exists to predict confidently their trophic interactions with resident planktivores and piscivores (Kircheis and Stanley 1981). Thorough evaluation should precede further introduction of alewives or other potential forage fish for landlocked salmon (Gately 1978).

At the present time, we strongly recommend against introducing forage other than smelts. Rather, we advocate the careful, thoughtful management of smelt predators, including salmon, as a more appropriate means of sustaining stable smelt forage in salmon lakes.

Smelts are a schooling fish that spawn in the early spring in lake tributaries or on lake shoals (David Howatt, MDIFW)

Competition

Throughout their lives, landlocked salmon compete with other kinds of fishes (interspecific competition) and among themselves (intraspecific competition) for food, living space, and at times for stream spawning and nursery area. Theoretically, any species living with salmon in a lake is a potential competitor with salmon. The intensity of competition will depend on the biological and environmental requirements of the competitor and, of course, the more abundant or widely distributed the competitor is, other things being equal, the greater will be its influence on salmon. Some competitor species co-exist with salmon in virtually every lake in which salmon occur, whereas the distribution of other competitors is relatively limited (Table 35).

Competition among fishes is highly complex, and involves not only the species and abundance of competitors but also water chemistry and physical features of the environment. A certain species may compete severely with salmon in one lake but compete little in another lake. For example, bass in a shallow, marginal salmon lake containing only smelts as a common forage fish might compete seriously with salmon for both space and food. In a deeper lake providing both smelts and crayfish in abundance, competition could be negligible, not only for food but also for space.

Certain species such as the brown trout compete directly with salmon throughout their lives. Other species, such as white suckers, may compete directly with salmon for insects when salmon are juveniles, but only indirectly when salmon become fish-eating adults. The competition is then indirect because the suckers utilize food being used extensively by forage fish of salmon, but not by the adult salmon.

In the following pages we have summarized results of several studies, mostly from Maine, that involved species considered to be potential salmon competitors in both lake and stream environments. Most of these studies concern competition under summer conditions. The same general principles apply to the cool as well as warm seasons, but during the cool seasons, potential competition exists throughout a much larger portion of the lake.

Interspecific competition

Brook trout

In Maine waters, landlocked salmon and brook trout frequently occur together in both lakes (Table 35) and streams. Most Maine lakes containing brook trout and salmon also have smelts present as forage, presenting the potential for food competition. Recent data from Moosehead Lake indicate that brook trout are significant smelt consumers in that lake, particularly during the winter season. Roy (2002) analyzed brook trout stomach contents of angler-caught fish collected from 1970 to 2002. A total of 592 stomachs from winter-caught brook trout contained food. During the period when the minimum length limit was 6 inches, smelts occurred in 33% of trout stomachs (28% of the total volume); when the length limit was increased to12 inches, smelts were found in 26 % of trout stomachs (46% of the total volume). Smelts were far less prevalent in the diet of brook trout during the summer months. Of 222 trout stomachs examined during the summer, 195 contained food, and only 5% of these contained smelts (8% by volume). Insects comprised the most important food item for brook trout during the summer months, both in frequency of occurrence and volumetrically. In lakes such as Moosehead, then, we conclude that brook trout may be intense competitors with salmon for smelts, particularly during the winter months.

Table 35. Potential competitor species occurring in lakes supporting principal salmon fisheries[1].

Species	No. salmon lakes	No. salmon acres	Percent of salmon lakes	Percent of salmon acres
White sucker (*Catastomus commersoni*)	169	479,998	96	99
Brook trout (*Salvelinus fontinalis*)	166	443,761	94	92
Yellow perch (*Perca flavescens*)	130	451,324	74	93
Brown bullhead (*Ameiurus nebulosus*)	122	426,692	69	88
American eel (*Anguilla rostrata*)	97	246,265	55	51
Lake trout (*Salvelinus namaycush*)	94	346,048	53	71
Chain pickerel (*Esox niger*)	82	228,825	47	47
White perch (*Morone americana*)	80	334,770	46	69
Burbot (*Lota lota*)	73	350,961	41	72
Smallmouth bass (*Micropterus dolomieu*)	68	270,454	39	56
Longnose sucker (*Catastomus catastomus*)	58	308,931	33	64
Lake whitefish (*Coregonus clupeaformis*)	38	275,284	22	57
Round whitefish (*Prosopium cylindraceum*)	27	140,414	15	29
Largemouth bass (*Micropterus salmoides*)	25	68,494	14	14
Brown trout (*Salmo trutta*)	21	93,883	12	19
Splake (*Salvelinus namaycush* X *S. fontinalis*)	20	20,687	11	4
Northern pike (*Esox lucius*)	2	10,564	1	2
Muskellunge (*Esox masquinongy*)	2	3,123	1	0.6

[1] A principal fishery denotes a lake where salmon are regularly sought by anglers, and they make up a significant portion of the total catch of all species in that water.

There is a plethora of information in the fisheries literature on interactions between both landlocked and sea-run Atlantic salmon and brook trout in streams. These studies indicate that habitat use patterns of yearling salmon and brook trout are similar, and that brook trout may compete with salmon for stream spawning and nursery areas.

Competition between salmon and brook trout for a given nursery area may result from either a trout population residing in the stream, or from trout produced by spawners that have moved into the stream from a larger stream or a lake. In most salmon nursery areas, brook trout probably compete most intensely with salmon during the spring and fall months when temperatures are cool. During the summer, salmon tolerate and apparently thrive in shallow riffle areas where water temperatures exceed 70°F. Brook trout are sometimes found with salmon at these temperatures, but trout usually seek springs and deeper pools. If water temperatures reach levels critical for salmon as well as brook trout, and salmon also seek cooler areas, competition could become intense.

Bley (1986) studied habitat overlap and possible competition between landlocked salmon and brook trout in several tributaries of the St. John River in northern Maine. In the absence of juvenile salmon, young brook trout were distributed throughout all available habitat types, and there was a seasonal movement of brook trout into habitat previously occupied by successively older cohorts. In the presence of salmon, age 0+ and age II+ brook trout were excluded from habitat occupied by salmon of the same ages (fast riffles and midstream positions).

In another Maine study, Sayers (1990) found that the presence of sea-run Atlantic salmon in brook trout nursery streams appeared to cause brook trout to move to deeper, slower holding positions. This trend was most pronounced when brook trout densities were substantially higher. There were considerable differences in the habitat use patterns of fry of sea-run Atlantic salmon among the three streams into which they were stocked. Inter-stream variation was probably due to differential habitat availability in the streams, but also indicated the potential bias of comparing habitat use patterns of fish from different streams. There was inter-annual variation in the habitat use patterns of brook trout, which in conjunction with differences in densities of brook trout, suggested that intraspecific competition might be at least as important as interspecific competition. There was relatively little inter-annual variation in the habitat use patterns of stocked sea-run Atlantic salmon fry. Patterns of intra-annual variation indicated that sea-run Atlantic salmon move to deeper, faster holding positions with increasing age.

Bley's and Sayers' findings are reinforced by the following review of previously published literature on sea-run Atlantic salmon-brook trout interactions and competition.

The seasonal distributions of brook trout and juvenile sea-run Atlantic salmon were compared below two waterfalls on the Matamek River, on the north shore of the Gulf of St. Lawrence (Gibson 1973). Where cohabiting, both species were found close to rapids in early summer when food was abundant. In mid-summer, when food was scarcer, salmon were still abundant in the rapids, but most trout had moved away from the rapids. Where trout occurred alone, they also moved towards rapids in early summer, and remained abundant in the rapids all summer.

An example of morphological differences contributing to habitat partitioning is the segregation of brook trout and sea-run Atlantic salmon into pools and riffles (Gibson 1973). Sea-run Atlantic salmon are less buoyant than brook trout and have enlarged pectoral fins – adaptations that enable salmon to exploit riffles more efficiently than brook trout. Brook trout compete more successfully with salmon in pools, possibly because they emerge earlier as fry, maintain a size advantage over the more aggressive sea-run Atlantic salmon, and are more buoyant.

Trout are known to seek thermal refuge when water temperature rises to about 68°F (Elson 1942), but the movement of salmon parr into cooler water is not as well documented. Salmon parr have been observed moving into spring seepage of 63°F when the river temperature rose above 72°F (K. Warner, MDIFW, unpublished data). They were grouped in the cool water, oriented towards the source of spring seepage, and showed no territorial behavior. Salmon parr were found feeding in the main river, but not brook trout, although the latter were seen there when the water was cooler. Local springs attract salmon as well as brook trout, but are not as necessary for the survival of salmon because they can endure higher temperatures than brook trout.

In summary, competition between brook trout and salmon in stream nurseries is apparent but may be lessened by habitat segregation, both temporally and spatially. The degree to which salmon production is reduced in the presence of brook trout is variable, depending on specific habitat conditions and trout abundance.

While this discussion is intended to focus on possible deleterious effects of brook trout on salmon, most studies indicate that salmon are generally the stronger competitor. The introduction of salmon into many lakes outside their original range likely has had negative impacts on Maine's native brook trout populations. In streams formerly occupied by only brook trout, yearling trout numbers have almost certainly been reduced, particularly in habitats highly suited to young salmon (i.e. riffles and flats). Where stream spawning and nursery areas support lake populations of brook trout, lake fisheries for this species would be impacted as well. The Rangeley Lakes chain and Moosehead Lake, where historical evidence indicates brook trout populations were more robust prior to the introduction of salmon, are examples of where this may have occurred (Kendall 1918, Cooper 1940, AuClair 1982).

Lake trout

Cooper and Fuller (1945), working at Moosehead Lake on a study of depth distribution of salmonids and other species in relation to food eaten, established that landlocked salmon were present in about the same degree of abundance at all depths from 15 to 60 feet. Lake trout were especially abundant at depths of 45-60 feet, but were present to depths of 90 feet. Stomach contents were studied for 25 salmon stomachs and 136 lake trout stomachs that contained food. The principal food of both species was rainbow smelts. At the 30 to 60-foot depth level, salmon stomachs contained 194 fish, of which 191 were smelts. In the same depth interval, lake trout stomachs contained 173 fish, of which 142 were smelts.

In a study at Branch Lake in Hancock County, Fenderson (1954) examined the stomachs of 63 lake trout ranging in length from 15.5 to 26.8 inches. Fifty-four of the stomachs contained food, all of which were smelts. Intensive depth distribution studies by Fenderson revealed that lake trout were concentrated below the 50-foot level; other salmonids were concentrated in shallower water, but some overlap occurred. He concluded that competition among game fish for smelts was intense during the summer months.

Roy (2002) examined the contents of 5,322 lake trout stomachs collected from Moosehead Lake from 1970 to 2002. Food habit differences were noted between the winter and summer periods, and between lake trout over 18 inches long and those from 14 to 18 inches long. Smelts comprised the highest volume of food in the winter samples of 14 to 18-inch lake trout (85%) and lake trout over 18 inches (79%). Smelts were less prevalent in the summer diet, comprising 40% of the volume of food in fish from 14 to inches long, and 32% of the volume in stomachs of fish exceeding 18 inches. With the exception of insects (primarily large mayfly larvae, flying ants, and small beetles), no identifiable food item other than smelts was a major contributor to the summer diet of Moosehead lake trout.

At nearby Sebec Lake, home of one of Maine's original salmon populations, winter food habits of lake trout were examined from 1990 to 2001 (S. Roy, MDIFW, unpublished data). Smelts occurred in 66% of the 599 lake trout stomachs (63% by volume) that contained food.

A recent study compared size, body condition (robustness), and age structure of salmon in lakes that supported large lake trout populations with lakes where lake trout were absent or not abundant (Boucher 1999). Salmon samples from the two lake types, which totaled nearly 19,000 fish, were from 111 lakes surveyed during the period 1990-1998. Results showed that salmon growth and body condition (Fulton's K) were significantly higher ($p<0.05$) in lakes where lake trout were absent or not abundant. Negative effects on salmon growth and condition were most pronounced on age III to age V fish of both hatchery and wild origin, while body condition of all wild salmon cohorts were significantly higher ($p<0.05$) in the absence of lake trout. There were also significantly higher ($p<0.001$) ratios of older-age salmon (age IV hatchery fish and age V wild fish) in lakes where lake trout were absent or present only in small numbers. The analysis concluded that while there are myriad biological and environmental factors affecting growth, condition, and age structure of salmon in lakes, interspecific competition with lake trout, primarily for forage (e.g. smelts), is a highly significant one.

Since 1982, lake trout in most waters have been managed with an 18-inch minimum length limit. Increased spawning escapement resulting from this higher size limit has produced large numbers of young wild lake trout in many lakes. This has negatively impacted forage populations, typically smelts, and has affected management of other species, often salmon (Johnson 2001, Boucher and Howatt 2002).

Results of the Maine studies cited above clearly indicate that lake trout are severe competitors with salmon for both forage and space, even though there is a tendency for the two species to occupy slightly different depth levels. Presently (2005), lake trout occur in 53% of Maine's salmon waters, comprising 71% of the total surface acreage of lakes supporting salmon (Table 35), so controlling lake trout numbers has become an important goal on many salmon lakes. Increased harvests of lake trout are often encouraged to reduce their impacts on smelts and to maintain growth and condition of both salmon and lake trout managed in the same lakes (Boland 1999, Johnson 2001, and Boucher 2001). In addition, introductions of lake trout to provide an additional game fish in lakes with salmon are now rarely initiated. When new lake trout introductions are considered, they are carefully reviewed by Department biologists to assure impacts to existing fish are minimized.

As lake spawners and dwellers, lake trout in Maine would rarely compete with juvenile salmon for stream nursery or with adult salmon for stream spawning areas.

Burbot (cusk)

At Moosehead Lake, Cooper and Fuller (1945) found burbot and salmonids occupying the same depths and competing for smelts to some extent. However, burbot consumed more non-game fishes than did the salmonids.

At Moosehead Lake from 1969 to 2002, summer gillnet samples of 330 burbot stomachs with food contained 6% smelts by number. In six other waters in the Moosehead Lake region (both winter and summer data), smelts occurred in 16% of 45 burbot stomachs with food (S. Roy, MDIFW, unpublished data). During winter angler surveys conducted at Moosehead Lake, Chamberlain Lake, and Allagash Lake, Obrey (1987) reported smelts in 16% to 50% of burbot stomachs containing food. Burbot should be considered potential competitors with salmon for food, particularly during the winter months.

Burbot are sometimes stream spawners and young burbot are frequently found occupying salmon nursery streams. Their interactions with juvenile salmon and their role as competitors in nursery streams are unknown.

Brown trout

Fenderson (1954), in his Branch Lake study, concluded that brown trout were severe competitors with salmon. Brown trout occupied the same depths in the lake, ate the same food, and utilized the same spawning and nursery areas. Fenderson concluded that in most lakes salmon are not capable of competing successfully with brown trout where the latter species is firmly established.

Brown trout populations sometimes persist after stocking is discontinued because they are able to utilize smaller spawning tributaries more efficiently than salmon. Existing relic brown trout populations are very small, however, and where they remain sympatric with salmon their impacts on salmon management are negligible. Stocked brown trout fisheries are currently being provided only in waters where salmon management has failed due to marginal water quality, chronically low smelt abundance, or heavy competition from other species (Boland 2001). At present, brown trout occur in only 12% of waters managed for salmon (19% of the total salmon acreage) (Table 35).

Lake whitefish

This species lives in deeper, cooler water in summer along with other salmonids. In winter, whitefish and other salmonids cohabit the same areas. Adult lake whitefish are primarily bottom feeders, consuming a wide variety of benthic invertebrates and small fishes. Plankton forms a large part of that diet in some lakes. Aquatic insect larvae, mollusks, and amphipods are primary food in some areas (Scott and Crossman 1973, Basley 2001).

In Maine lakes containing both whitefish and smelts, whitefish may be serious competitors with salmon for food, particularly during the winter season, as indicated in the table below (MDIFW, unpublished data):

Lake	County	Year (season)	Source	No. whitefish stomachs examined	Percent containing smelts
Chamberlain Lake	Piscataquis	1991 (winter)	Angler survey	150	72
Big Eagle Lake	Piscataquis	1987 (winter)	Angler survey	42	57
Churchill Lake	Piscataquis	1987 (winter)	Angler survey	9	67
Clear Lake	Piscataquis	1992 (winter)	Angler survey	18	60
Sebago Lake	Cumberland	1989 (summer)	Gill net	33	17

Splake

This hybrid between lake trout and brook trout is currently raised in Maine hatcheries on a production basis. Splake stockings are employed primarily to provide fisheries in waters formerly stocked with brook trout. Results have been excellent in most waters. In lakes where both splake and brook trout (spring yearlings or fall fingerlings) are simultaneously stocked, splake reach greater mean lengths than brook trout at each age. Splake routinely survive to older ages, providing a higher quality fishery than brook trout in many waters. Other positive attributes of splake are their high catchabilty by anglers and their ability to expand ice-fishing opportunities for coldwater game fish (Obrey 2001).

Splake are also used to supplant or to augment salmon fisheries. Hoffman (2000) studied summer splake food habits in three central Maine waters to determine potential competition with landlocked salmon. Fishes were the dominant food item (63%) in the overall diet of splake sympatric with salmon, with rainbow smelt (94%) the only identifiable fish species. Fishes were the dominant food item (79%) for sympatric splake in summer, again with rainbow smelt the only identifiable fish. There was a high degree of overlap in diet (>79%) for all food categories of sympatric splake and salmon. Splake showed a more diverse diet when salmon were not present.

In summer gill net samples from four western Maine lakes from 1996 to 1999, 42 splake stomachs with food contained 21% smelts by number (D. Boucher, MDIFW, unpublished data). In Big Wood Pond, of 215 splake stomachs with food examined in winter, 90% contained smelts. (S. Roy, MDIF&W, unpublished data).

Hoffman's study and routine management surveys show that splake might be a serious competitor with salmon. However, it is also apparent that splake exhibit flexible food habits, and although they are very likely to feed on smelts when available, they will also feed on yellow perch, crayfish, sunfish, and minnows (Obrey 2001). These facts, and the limited distribution of splake in salmon waters (Table 35), indicate that splake do not significantly limit salmon production in Maine at the present time.

White sucker

The white sucker is probably the most abundant fish reaching large size in Maine salmon lakes. The species occurs in nearly all lakes that support salmon (Table 35). Salmon and suckers, although they spawn at different seasons, often utilize the same streams as spawning areas. Some juvenile suckers, like salmon, appear to spend 1 or 2 years in the stream nursery areas before moving into larger waters. At Barrows Stream, autumn standing stocks of juvenile suckers ranged from 2.4 to 12.0 pounds per acre over a 6-year period (Havey 1974a). Standing stocks of salmon for the corresponding period ranged from 1.0 to 11.3 pounds per acre. Response in both species at Barrows Stream to a given environmental change seemed to be similar, indicating that the two species had similar biological requirements while in the stream environment.

Adult suckers are primarily insect and crustacean feeders and do not normally compete with fish-eating adult salmon. However, when fish as food for salmon become scarce, as has happened in some salmon lakes, competition for insect food may become intense between the two species. Suckers commonly occupy depths frequented by salmon in their lake environment, so they are also potential competitors with adult salmon for space.

Yellow perch

A study of yellow perch food habits in three Maine lakes – Rangeley, Moosehead, and Beddington – revealed that larger yellow perch fed quite extensively on fish when available (Wohnsiedler 1965). Smelts were important items in the fish diet of the larger perch from all three lakes, and incidence in the diet was thought to be related to smelt abundance. In Rangeley Lake, smelts occurred in 92% of the stomachs of yellow perch more than 10 inches long. While yellow perch in general tended to concentrate in the upper lake levels, Wohnsiedler found that large perch in Rangeley Lake occupied the cooler areas of the lake more frequently than smaller perch. Of course, the larger perch would be those most likely to utilize smelts as food.

Of 201 yellow perch containing food, Warner (1974) found that 31% had eaten one or more species of fish. Smelts were the most frequently eaten fish, but other yellow perch, white perch, sunfish, minnows, and sticklebacks were also consumed. Yellow perch began to eat fish at 5.5 inches, and all size groups of perch utilized forage fish in their diets at a higher rate than white perch

Lake depth and water temperatures probably dictate the degree of competition between yellow perch and salmon. Experiments with salmon in marginal and homothermous lakes (MDIFW, unpublished data) have revealed that salmon can withstand the higher water temperatures and low oxygen concentrations often associated with these lakes. However, competition could be at its greatest intensity in such habitats because depth is not sufficiently great to permit concentration of salmon at depth levels they would normally select. In such lakes, salmon appear to retreat to the most suitable areas for them, where yellow perch may or may not be present. For example, a gill net catch in the deepest sections (30 feet) of Boyden Lake in 1961 consisted of 46 adult salmon and 101 yellow perch; most perch were 10 to 14 inches long. While concentrated in the deepest lake areas, salmon were still at a depth commonly frequented by yellow perch. Water temperature at the 30-foot level was 68°F and oxygen concentration was 7.8 ppm.

Yellow perch are very commonly associated with salmon in lakes (Table 35), and they produce much larger numbers of young than do salmon. Habitat conditions are commonly adequate to permit yellow perch to reach sizes over 5-6 inches, at which time they become primarily piscivorous. These facts indicate that yellow perch, as intense competitors with salmon for smelts, severely limit salmon production in many Maine lakes. Yellow perch are not competitors with salmon for spawning areas, but may be competitors for nursery habitat under certain conditions.

White perch

Cooper (1941) examined 1,252 stomachs of white perch from various Maine lakes and found fish in 29% of their stomachs. About 9% of all stomachs with food contained smelt. White perch from 22 Maine lakes (1952 to 1965) known to support both perch and smelts contained fish in 227 of the 441 stomachs containing food. Smelts were present in 83 (19%) of the stomachs examined. In these studies, smelts were found in perch from 12 of the 22 lakes involved.

Of 153 white perch stomachs examined at Echo Lake, Hancock County, in 1952, 84 stomachs contained food. Fifty-six contained fish, and 35 (42%) contained smelts. It was highly probable that most unidentified fish remains in this study were also smelts. Echo Lake white perch became almost exclusively fish eaters at a length approximating 7 inches.

At Sebasticook Lake in Penobscot County, fish were found in the stomachs of 99 white perch of 133 examined containing food, but none of the stomachs contained smelts. Yellow perch were the predominant fish taken as food by white perch in this study. Smelts were present in Sebasticook, a shallow, warm lake, but they may not have been as abundant there as in Echo Lake, which is a cold, deep lake.

Warner (1974) reported occurrence of one or more species of fish in the stomachs of 18% of white perch examined from 12 Maine lakes during spring studies from 1967 to 1970. Smelts, white perch, and yellow perch occurred most frequently. All fish were found in white perch 9 inches or more in length. Reid (1972) also found that smelts were the main forage fish occurring in the stomachs of white perch from Abrams Pond in Eastbrook, Maine.

White perch commonly concentrate in shallower waters, but they are frequently taken at depths occupied by salmon during summer months. For example, in a biological survey of Lower Sysladobsis Lake, Penobscot County, a single net set in depths ranging from 46 to 56 feet took 189 white perch, mostly of large size. At Spednic Lake in Washington County, nets set at 38 to 48 feet took several salmon and numerous white perch.

The foregoing examples of feeding habits and depth distribution of white perch in Maine lakes strongly indicate that this species competes with salmon for food (smelts) and for space. Where environmental conditions favor growth of large numbers of white perch to lengths of 9 inches or more, serious competition with salmon can be expected. In addition, the tremendous egg production of white perch (about 145,000 eggs per pound of female) far exceeds that of salmon and increases its potential as an intense competitor. The wide distribution of white perch in salmon lakes (Table 35) suggests that the presence of this species is among the most significant limiting factors affecting salmon production in Maine.

White perch rarely compete seriously with salmon for spawning and nursery area. While the species is sometimes a stream spawner, the young perch hatch rapidly (AuClair 1960) and drop downstream into the lake.

Chain pickerel

Barr (1962) studied food habits of chain pickerel at Beddington Lake, and found that up to 14% of stomachs of larger pickerel contained smelts. Greatest utilization of smelts by pickerel was during months when the pond was ice-covered. The chief food of adult pickerel during ice-free months was juvenile anadromous alewives.

In a study of 88 pickerel stomachs from Graham Lake in Hancock County, Fuller and Cooper (1946) found smelts in 4 of 24 stomachs that contained food. Of 58 pickerel stomachs examined from six Washington County lakes that also supported smelts, 19 stomachs contained food, and 17 of these contained smelts. In Ingham Pond in Kennebec County, 20 winter-caught pickerel with food, averaging 12.3 inches in length, contained 30% smelts by number (MDIFW, unpublished data). In spring studies of pickerel food in Maine lakes, Warner (1973) found one or more fish species in the stomachs of 218 pickerel (91%) containing food. Smelts occurred in 18% of the stomachs examined. Because they forage on smelts when available, pickerel may be intense competitors of salmon in certain lakes, particularly during the winter months.

Pickerel are lake spawners and are not competitors with salmon for spawning areas. There is some evidence that pickerel may be minor competitors with salmon in stream nurseries. In 3 to 6 years of electrofishing studies at Barrows Stream, juvenile pickerel were present in small numbers in this salmon nursery area (Havey 1974a). Barr (1962), in his study of pickerel at Beddington Lake, found pickerel living as summer residents in the Narraguagus River, a sea-run Atlantic salmon nursery located below the lake.

Smallmouth bass

The distribution of this species, not native to Maine, has increased significantly during the past 20 years, mainly through illegal introductions (Jordan, 2001). Smallmouth bass are widely distributed in Maine's salmon lakes, occurring in 39% of them (56% of the total salmon acreage) (Table 35).

Cooper (1941) examined 66 stomachs of smallmouth bass from ponds of the Kennebec and Androscoggin River drainages, and found crayfish and fish to make up 80% (volume) of the food contents of the 36 bass that contained food. Sixty-one percent of the fish food (volume) was white perch. Cooper made special note of the absence of smelts from bass stomachs in this particular study.

Stomach contents of 101 and 44 smallmouth bass were studied at Long Pond and Echo Lake in Hancock County, respectively, in 1951 and 1952. Eleven of 72 bass (15%) with food at Long Pond and 13 of 44 bass (30%) at Echo Lake had consumed fish. Predominant fish forage at Long Pond was juvenile anadromous alewives, while at Echo Lake fish forage was most likely smelts. Nearly all bass examined in the Long Pond phase of the study were 10 inches or less in total length, and were competing but little with salmon for forage fish.

In a 1954 study conducted at Long and Great Ponds, Kennebec County, fish and crayfish comprised the major part of the diet of smallmouth bass. Crayfish and fish together made up 98% of the total volume of food contained in 45 smallmouth bass from Long Pond, and 93% of the total volume of food contained in 31 bass stomachs from Great Pond was crayfish and fish. Crayfish predominated at Long Pond, while fish predominated at Great Pond. Part of the fish diet consisted of smelts.

Fenderson (1954) examined stomach contents of 31 smallmouth bass at Branch Lake. Summer food of bass less than 10 inches in length consisted mainly of dragonfly nymphs. Larger bass fed almost exclusively on smelts. Six bass, all over 3 pounds in weight, had consumed a total of 53 smelts. Biologists working throughout Maine have found smelts in bass stomachs on numerous occasions, particularly during the winter months. Bass angled from spawning beds have also been observed regurgitating smelts.

Fenderson (1954) took smallmouth bass in gill nets at the 35-50 foot depth level at Branch Lake. During this study, these depths corresponded to the thermocline and top of the hypolimnion. At Love Lake, nearly all smallmouth bass taken by gillnets set to sample salmon were taken in water less than 25 feet deep; summer temperatures were usually above 70° F. No bass were taken in nets set completely in the thermocline or deeper (K. A. Havey, MDIFW, unpublished data).

The foregoing studies indicate that smallmouth bass, with their diet predominantly of fish and their tendency to make occasional forays to the deeper, colder waters of lakes, are competitors with salmon for food and space in some lakes. Smallmouth bass do not compete with salmon for spawning areas, but are frequently found in salmon nursery areas in rivers and streams. Their impacts on salmon in nursery streams have not been studied in Maine.

Largemouth bass

Largemouth bass, also not native to Maine, presently occur in 372 lakes and ponds. In 141 of these waters, largemouths are the only species of bass; they coexist with smallmouth bass in 231 waters (Jordan 2001). Diet of largemouth bass in Long Pond of the Belgrade Lakes was found to be primarily fish and crayfish (R. E. Foye, MDIFW, unpublished data). Largemouth bass are primarily a shallow water species in Maine, but as fish-eaters, they could be competitors with salmon for food.

Smelt

Smelts not only serve as major food fish for salmon, but they may rarely also be competitors. In environments where they grow to a large size and become piscivorous, they are likely in competition with salmon for food. There is little likelihood of competition of smelts and salmon in spawning or nursery areas.

American eel

Eels are most common in lakes in coastal drainages. They are often very abundant in salmon nursery streams and may be serious competitors with juvenile salmon, but this is not well documented. As fish-eaters, they probably compete with adult salmon for food, but little quantitative data are available concerning their depth distribution or feeding habits in Maine lakes.

Northern pike

Northern pike have been present in Maine only since the 1970's as a result of illegal introductions into the Belgrade Chain of Lakes. Pike are now present in at least 17 waters, and they will likely be distributed to additional waters through natural migration or by illegal transport (Brautigam, 2001).

Northern pike are a voracious predator and consume a large variety of fishes as well as other prey. In some waters they are significant predators on smelt and are therefore in direct competition with salmon for this important forage fish. In winter samples from four waters in the Belgrade Lakes, pike stomachs with food contained 12% smelts, and in one water, Ingham Pond, 50% of pike stomachs contained smelts (MDIFW, unpublished data).

A sharp decline in the landlocked salmon fishery in Long Pond, Belgrade, is believed to be a direct result of the illegal introduction of northern pike, both by competition for smelts and predation (J. Lucas, MDIFW, personal communication). Stocking of larger, fall-yearling salmon is currently underway at Long Pond in an effort to mitigate northern pike predation, but this strategy has thus far met with only limited success.

Black crappie

This species was originally introduced to Maine in 1921 in the Presumpscot River drainage in southern Maine. Subsequent illegal introductions have expanded their distribution to at least 64 waters in central and southern Maine (Lucas 2001).

Diet of this species changes with size and age. In Canadian lakes, young crappies feed on plankton, crustaceans, and nocturnal dipterous larvae. The invertebrate diet continues into the third year of life for individuals as large as 6.3 inches. Beyond that size, a variety of small fishes make up an increasing proportion of the diet (Scott and Crossman, 1973). Occurrence of smelts in black crappie stomachs has not been observed, but consumption of smelts could cause a competition problem in some Maine salmon lakes.

Alewife

Landlocked alewives were introduced by the Department several decades ago in a number of southern Maine waters, primarily as food for lake trout, brown trout, and warmwater sport fish. Within the past 5 years, landlocked alewives have been illegally introduced into East Grand and Spednic Lakes, both located in eastern Washington County, and into several lakes in the Belgrade Lakes chain. Although this species serves as food for landlocked salmon and other salmonids, its role as a competitor with smelts, and therefore as a potential indirect competitor with salmon for food, remains unclear.

The only study we are aware of concerning the interactions between landlocked alewives and smelts was conducted in Echo Lake, Hancock County (Gately 1978). Gately determined that there was significant diet overlap between the two species, and that growth rates of older-age smelts were depressed in Echo Lake compared to lakes that did not support landlocked alewives. Gately also found that the diets of juvenile landlocked smelts and juvenile landlocked alewives overlapped only moderately, and that the growth of juvenile smelt in Echo Lake was equal to or exceeded that found in other Maine lakes.

As for sea-run alewives, Kircheis et al. (2002) found that at a stocking rate of six adult alewives per surface acre in Lake George, Somerset County, smelt and alewife fry showed little dietary overlap overall, although both species fed heavily on Copepoda and Cladocera. This was probably because the two species fed on different taxa within those two major prey groups, with alewives typically feeding on the larger zooplankters. Adult alewife and smelt diets did not overlap significantly. Smelt diets appeared to shift after alewives were introduced, and the growth rate of smelt fry improved significantly. Improved growth of smelt fry may have been related to their altered diet, which was mediated by alewife restructuring of the plankton community, or to lower densities of smelt fry. Smelt population size, as measured by trawl catch rates, was lowest during the period when alewives were stocked. It could not be determined what combination of factors caused the reduced density of smelts – high trawl catches in the early years of the study, commercial harvest of adults during a portion of the study, competition with juvenile alewives, or some other factor.

There is presently a moratorium on Department introductions of landlocked alewives into Maine waters. In addition, stocking rates of anadromous alewives by other state agencies involved in alewife restoration are limited to six adult fish per surface acre.

Other species

Blacknose dace, slimy sculpins, creek chubs, fallfish, common shiners, and other minnows frequent salmon stream nursery areas and are considered potential competitors for food and space.

Intraspecific competition

The most intense competitors of salmon are members of their own kind. Several life history requirements including food, space, and spawning and nursery areas are essentially the same for one individual as for another. Superimposition of redds may become an important limiting factor when spawning runs are large and ideal spawning rubble is scarce; succeeding spawners may dislodge eggs already fertilized and buried.

While salmon up to lengths of about 12 inches rely heavily on insects as food, there is little evidence to suggest that competition for insects between young salmon and other species, or among salmon themselves, is a significant factor limiting growth. Indications are that even where serious growth problems occur in adult fish, growth to lengths of 9 to 10 inches is rapid and relatively consistent between waters (Table 36).

Growth of salmon stocked at three density levels at Long Pond, Hancock County, is summarized on the following page (Havey 1980). During the Long Pond study, salmon were the primary fish species that utilized smelts as food. These data provide a good example of effects on growth of intraspecific competition among salmon for food at different levels of competitive intensity. The least dense stocking (1957) was made with fish averaging about 3 inches long and at a time when 3 years had elapsed since any previous stocking. Growth of this group was the most rapid, with total growth the first 2 years at large approaching 14 inches.

Table 36. Back-calculated lengths of wild salmon from several western Maine lakes.

				Calculated length at age (inches)		
Water	County	Years	Sample size	I	II	III
Beaver Mountain Lake	Franklin	1994-2000	112	3.1	5.8	9.2
Mooselookmeguntic Lake	Franklin	1986-2003	320	2.9	4.9	9.6
Dodge Pond	Franklin	2001	109	3.3	6.2	9.7
Richardson Lakes	Oxford	2001	35	3.0	5.3	9.1
Parmachenee Lake	Oxford	1999	64	3.2	5.8	9.9
Aziscohos Lake	Oxford	1993-2002	193	3.3	5.7	10.1
Chain of Ponds	Franklin	1996-2002	43	3.2	6.3	9.5
			Weighted mean ±standard error:	**3.1±0.02**	**5.5±0.04**	**9.7±0.05**

Growth of salmon stocked at three densities at Long Pond, Hancock County.

Stocking year	Number stocked	Age stocked	Size at age II	III	IV	V	VI
1954	3,000	I+	5.4	11.7	16.6	19.5	24.0
1957	1,021	0+	12.5	17.4	*	*	*
1960	6,015	I+	7.4	11.1	13.9	16.3	*

The 1960 stocking, the densest, was made following the 1957 stocking of 1,021 salmon and plantings of 6,000 age I+ fish in 1958 and 6,010 age I+ fish in 1959. Growth was the slowest among this group during the first 2 years the salmon were at large. Salmon of the 1954 stocking, intermediate in density, grew an intermediate amount during their first 2 years. Stocking of 3,000 age I+ salmon in 1952 and 3,005 age I+ salmon in 1953 preceded the 1954 stocking.

Intraspecific food competition from a stocking rate of about seven salmon per acre was sufficiently intense to markedly suppress normal salmon growth in Long Pond. On the other hand, a stocking rate of about one salmon per acre permitted salmon to express an excellent growth rate.

Recent data confirm that intense intraspecific competition for food is a significant contributing factor in most populations where growth is slow (MDIFW, unpublished data). This phenomenon is well illustrated by comparing size and body condition of salmon at age from wild populations with those supported by hatchery stocks (Table 37). In wild populations, annual recruitment is often highly variable – some years large numbers of smolts are produced, some years small numbers are produced, and at times, several large cohorts in succession may be produced. In populations supported by hatchery-reared fish, biologists strictly control annual recruitment by manipulating stocking rates. In this way, intraspecific competition is maintained at levels that foster higher, more stable levels of smelt biomass and, consequently, better salmon size quality. This relationship between recruitment and salmon size has important implications for management. Hatchery-supported populations usually provide fisheries for larger fish than do those comprised of wild salmon because intraspecific competition is closely monitored and adjusted.

Table 37. Size at age of wild and hatchery-reared landlocked salmon in Maine lakes. Samples are from fall trapnet surveys (spawning runs), 1990-2001. Sample sizes are in parentheses.

	Wild origin (41 lakes)		Hatchery origin(45 lakes)	
Age	Length (in)	Weight (lb)	Length (in)	Weight (lb)
I+	8.2 (121)	0.2 (107)	12.7 (721)	0.7 (636)
II+	11.5 (399)	0.5 (397)	17.0 (5,051)	1.7 (5,032)
III+	14.1 (592)	0.9 (590)	18.8 (4,018)	2.3 (4,001)
IV+	16.3 (596)	1.5 (592)	20.1 (774)	2.8 (768)
V+	17.3 (344)	1.8 (342)	21.7 (202)	3.5 (202)
VI+	17.9 (130)	2.0 (129)	22.6 (19)	4.3 (18)

Competition Summary Discussion

Evaluation of the landlocked salmon's ability to live with other species must consider the ability of the salmon not merely to exist, but to thrive in the presence of competitors. As a sport fishing resource, the species is of reduced value either in the capacity of a relic population, or as a species that is abundant but of undesirable size.

Our data show that landlocked salmon can thrive in the presence of a wide assemblage of other species with at least partly overlapping life requirements. Thriving salmon populations commonly co-exist with lake trout, brook trout, white perch, yellow perch, smallmouth bass, suckers, burbot, and others. Our data also show that salmon production would probably be much higher if certain competitors were not present. This is particularly true in the case of lake trout, a primary smelt consumer that has dramatically increased in abundance in many lakes.

From an ecological standpoint, one or more sport fishes whose life requirements overlap slightly with those of salmon could utilize a lake more efficiently than salmon alone. Considering recreation values, a lake that supports a moderate fishery for salmon, as well as fisheries for one or two other desirable game fish, may have more economic value than if the lake supported a more abundant salmon population. However, we strongly advocate utmost caution whenever multiple-species management is contemplated. Minimum risk will be involved only when all species under consideration are well studied, and when numerous successful examples of the type of multiple-species management being considered are available.

Some of the more serious growth problems involving salmon are related to intraspecific competition for food and possibly space. While a population of slow-growing salmon is not necessarily endangered as far as survival is concerned, the slow growth rate often causes dissatisfaction among anglers; thus, that particular population is not fully expressing its potential. Anglers often request increased stocking in such situations, when actually the problem is too many fish. In Maine, the problem has been partially resolved by manipulating size limits to increase harvest of certain cohorts, or by temporary cessation or reduction in stocking.

Standing stocks

The definition of standing stock, as we use it, is the number and weight of all or a portion of the stock of salmon, both sublegal and legal, present in a water at a given time. Standing stock estimates of salmon at Love Lake (Havey 1974b), Schoodic Lake (Havey and Andrews 1973), and Eagle Lake (Havey, unpublished data) are presented in Table 38. Mean standing stock for the three lakes is 1.6 salmon/acre weighing 1.5 pounds/acre. Love and Schoodic Lakes are of the intermediate type; they are less than ideal salmon habitat. Eagle Lake provides excellent water quality and supports a lake trout population.

Most Maine salmon lakes probably support from two to three salmon of age II or older per acre. In general, we believe standing stocks of salmon have increased on many lakes since 1985. This is attributable to improved post-stocking survival of hatchery-reared salmon, and to the voluntary release of legal salmon practiced by an increasing number of Maine salmon anglers (Boucher 2001).

Fishery Specialist Dave Howatt sets a trapnet in Pierce Pond in Somerset County to sample landlocked salmon during the fall spawning run. (Dave Boucher, MDIFW)

Table 38. Standing stocks (±standard error) of landlocked salmon in three Maine lakes.

Lake	County	Surface area (acres)	Year	Numbers/acre	Pounds/acre
Schoodic L.	Washington	389	1964	3.1±0.4	2.3±0.2
Schoodic L.	Washington	389	1965	5.5±0.8	2.6±0.4
Schoodic L.	Washington	389	1966	4.2±1.0	2.8±0.6
Schoodic L.	Washington	389	1967	3.0±0.5	2.4±0.4
Schoodic L.	Washington	389	1968	1.9±0.4	2.2±0.4
Schoodic L.	Washington	389	1969	1.6±0.4	3.0±0.9
			Mean±SE:	**3.2±0.6**	**2.6±0.1**
Love L.	Washington	672	1963	1.0±0.2	1.9±0.3
Love L.	Washington	672	1964	0.3±0.1	0.6±0.2
Love L.	Washington	672	1965	0.3±0.1	0.4±0.1
Love L.	Washington	672	1966	0.2±0.1	0.4±0.1
Love L.	Washington	672	1967	0.9±0.2	0.7±0.2
Love L.	Washington	672	1968	0.6±0.3	0.4±0.2
Love L.	Washington	672	1969	0.4±0.1	0.3±0.2
			Mean±SE:	**0.5±0.1**	**0.7±0.2**
Eagle L.	Hancock	436	1973	1.1	*
Eagle L.	Hancock	436	1974	1.1	*
Eagle L.	Hancock	436	1975	1.0	*
Eagle L.	Hancock	436	1976	2.3	*
Eagle L.	Hancock	436	1977	1.2	*
Eagle L.	Hancock	436	1978	1.9	*
Eagle L.	Hancock	436	1979	2.9	*
Eagle L.	Hancock	436	1980	0.9	*
Eagle L.	Hancock	436	1981	0.8	*
Eagle L.	Hancock	436	1982	1.1	*
			Mean±SE:	**1.4±0.4**	*
			All Waters:	**1.6±0.3**	**1.5±0.3**

Reproduction

Age composition of spawning runs

The age composition of representative spawning runs in Maine lakes is presented in Table 39. These data show the vast majority – usually over 90% – of wild salmon spawning runs is comprised of age groups II to VI. Age I and II precocious males are sampled in small numbers from several waters. Salmon older than age VII generally contribute little to spawning runs, but they were significantly represented in the Fish River Lakes from 1953 to 1955 (Warner 1962), in Mooselookmeguntic Lake in 1939 (Cooper 1940) and from 2001 to 2003, and recently from Beaver Mountain Lake, Dodge Pond, Parmachenee Lake, and Aziscohos Lake (D. Boucher, MDIFW, unpublished data).

Warner (1962) found no male salmon over age VII represented in the spawning runs at the Fish River Lakes (1953 to 1955). Tag return data also indicated that few males survived after age VII (Warner 1959) – the few salmon over age VII in the spawning runs were females. In statewide surveys conducted from 1960 to 2002, male salmon over age VII represented only 0.2% of spawning runs of 41 wild

Table 39. Age composition (percent) of wild landlocked salmon spawning runs in Maine lakes.[1]

Water	County	Year(s)	No. fish sampled	Age groups									
				I+	II+	III+	IV+	V+	VI+	VII+	VIII+	IX+	X+
Fish River Lakes	Aroostook	1953-55	1,424	0	0	14.4	42.1	22.8	13.3	5.5	1.5	0.3	0.1
Eagle L.	Aroostook	1995-97	70	0	1.4	15.7	38.6	20.0	17.1	2.9	2.9	0	0
Square L.	Aroostook	1993-99	75	0	1.3	33.3	42.7	18.7	4.0	0	0	0	0
Lower Hudson P.	Piscataquis	1997-99	38	2.6	2.6	15.8	34.2	31.6	13.2	0	0	0	0
Chesuncook L.	Piscataquis	1997-98	59	0	1.7	23.7	44.1	25.4	5.1	0	0	0	0
Long P.	Piscataquis	1997	26	0	7.7	46.2	30.8	15.4	0	0	0	0	0
Sebec L.	Piscataquis	1989,1992-95, 1997-98	61	0	1.6	16.4	49.2	29.5	3.3	0	0	0	0
Arnold P.	Franklin	2003	68	10.2	7.4	27.9	39.7	13.2	1.5	0	0	0	0
Chain of Ponds	Franklin	1998	41	0	12.2	31.7	19.5	31.7	4.9	0	0	0	0
Beaver Mountain L.	Franklin	2000	51	0	0	3.9	7.8	31.4	21.6	25.5	7.8	2.0	0
Rangeley L.	Franklin	1963-66	336	0	2.4	7.7	35.4	36.7	11.9	6.0[2]			
		1985-2002	474	1.3	23.8	29.3	28.9	12.7	3.2	0.8	0	0	0
Dodge P.	Franklin	2001	46	17.4	2.2	2.2	10.9	30.4	26.1	10.9	0	0	0
Mooselookmeguntic L.	Franklin	1939	61	0	0	0	13.3	51.7	15.0	15.0	5.0	0	0
		1960-66	1,490	0	0	1.6	31.7	44.0	15.7	5.4	1.3	0.3	0
		1971-75	593	0	0.8	8.3	34.2	37.1	15.2	3.2	1.2	0.	0
		2001-2003	266	0	0	1.5	23.7	37.2	21.8	7.1	5.3	3.1	0.4
Parmachenee L.	Oxford	1999	50	2.0	0	6.0	38.0	20.0	18.0	10.0	4.0	2.0	0
Aziscohos L.	Oxford	2000	37	0	0	0	16.2	67.6	5.4	2.7	8.1	0	0
West Grand L.	Washington	1995-2000	400	0	45.5	47	6.5	0.5	0.5	0	0	0	0
Sebago L. (Jordan R)	Cumberland	1995-2000	643	0.5	55.2	38.6	4.8	0.9	0	0	0	0	0

[1] West Grand Lake and Sebago Lake spawning runs were composed of hatchery-reared fish.
[2] Age VII+ and older.

salmon populations. Females over age VII were also rare, representing only 2% of the runs (MDIFW, unpublished data). The shorter life span of males may be associated with earlier maturation and the hardships attendant with extended lingering on the spawning grounds. The oldest Maine salmon on record was age XIII (Warner 1961).

Annual variations in age composition of spawning runs are often observed in lakes supported by natural reproduction. Variable recruitment in wild salmon populations is strongly influenced by environmental or biological factors such as stream flows and temperatures, or by competition from other salmon cohorts residing in the stream nurseries. In populations dependant on stocking, age composition of spawning-age fish is generally more stable. In those lakes, age structure of spawning runs reflects stocking periodicity and the relative survival of individual stocked cohorts. We believe post-stocking survival of salmon is currently much superior to that observed when the two previous editions of this paper were published (discussed in a later section).

Our data indicate that age III, IV, and V fish are the most prevalent contributors to Maine wild salmon runs (Table 39). The contribution of age III salmon, however, varies considerably among lakes or in the same lake annually. Earlier maturation resulting from faster growth is probably one reason more age III salmon mature to spawn in some lakes. Conversely, the preponderance of older-age salmon (age VI and older) in some populations may reflect slower growth, later maturation and, related to this, delayed recruitment to a size harvestable by anglers.

Size composition of spawning runs

Average lengths and weights of wild salmon in several Maine spawning populations are presented in Table 40. Female salmon in the Fish River Lakes (Cross Lake Thoroughfare) runs of 1953 to 1955 were larger than males (Warner 1962). Females were also longer and heavier than males in several other wild spawning populations, probably reflecting the relative abundance of older females. In the hatchery-supported runs at West Grand Lake, females were larger than males, but males were usually larger in the Jordan River run at Sebago Lake, which is also supported by hatchery stocks.

Table 40. Average size of wild landlocked salmon in representative Maine spawning runs. Number of fish sampled is in parentheses.[1]

Water	County	Year	Total length (inches) Males	Total length (inches) Females	Weight (pounds) Males	Weight (pounds) Females
Long L. Thoroughfare	Aroostook	1953	19.9 (207)	20.9 (174)	2.9 (207)	3.9 (174)
		1954	18.9 (162)	21.5 (198)	2.5 (162)	3.8 (198)
		1957	18.7 (174)	20.3 (186)	2.6 (174)	3.4 (186)
Mooselookmeguntic L.	Franklin	1961	16.8 (103)	16.8 (87)		
		1962	15.7 (35)	14.8 (29)		
		1971	13.1 (28)	13.3 (49)		
		1972	13.3 (57)	13.1 (81)		
		2002	13.9 (30)	16.1 (78)	0.8 (30)	1.5 (78)
		2003	14.1 (49)	15.1 (110)	0.9 (46)	1.2 (107)
Rangeley L.	Franklin	1995	17.3 (43)	18.8 (21)	1.7 (43)	2.4 (21)
		1996	15.1 (52)	18.1 (32)	1.2 (52)	2.0 (32)
		2002	14.6 (71)	17.6 (31)	1.1 (71)	2.1 (31)
		2003	16.8 (63)	17.8 (28)	1.7 (62)	2.2 (28)
Dodge P.	Franklin	2001	13.2 (27)	16.2 (20)	1.4 (18)	1.5 (20)
Arnold P.	Franklin	2003	12.8 (29)	15.5 (8)	0.7 (28)	1.2 (8)
Beaver Mountain L.	Franklin	2000	15.4 (21)	18.0 (31)	1.2 (21)	2.0 (31)
Parmachenee L.	Oxford	1999	14.3 (22)	16.6 (25)	0.9 (22)	1.5 (25)
Scraggly L.	Penobscot	1998	14.5 (70)	14.9 (39)	0.9 (62)	1.1 (38)
Long P.	Piscataquis	1997	15.8 (36)	16.5 (22)	1.3 (36)	1.6 (22)
West Grand L.	Washington	1957	18.6 (118)	19.2 (120)	2.2 (118)	2.8 (120)
		1976	14.6 (49)	16.4 (59)	1.0 (48)	1.5 (59)
		1986	17.1 (58)	17.3 (62)	1.7 (58)	1.9 (62)
		2000	17.4 (50)	18.4 (50)	1.8 (50)	2.4 (50)
Sebago L. (Jordan R.)	Cumberland	1957	20.0 (111)	19.1 (119)	2.4 (111)	2.2 (119)
		1976	15.6 (476)	15.1 (626)	1.1 (169)	0.98 (323)
		1986	17.1 (58)	17.3 (62)	1.7 (58)	1.9 (62)
		1999	18.9 (88)	19.1 (106)	2.0 (88)	1.9 (106)

[1] West Grand Lake and Sebago Lake spawning runs were composed of hatchery-reared fish.

Atkins (1879 and 1886) reported the average length and weight for salmon in the early West Grand Lake runs. In 1876, males averaged 15.7 inches and 1.6 pounds and females averaged 15.9 inches and 1.9 pounds. In 1885, males averaged 21.0 inches and 3.6 pounds. Females averaged 19.2 inches and 3.4 pounds.

It is clear from the data presented (Table 40) that size composition as well as age composition of salmon spawning runs (Table 39) vary among lakes and from year to year within lakes. The size composition of these spawning runs is a direct reflection of age composition and growth rate.

Hatchery Manager Norm Philbrick (left) and Fishery Biologist Kendall Warner handle fish for data collection at Cross Lake Thoroughfare in 1955. (MDIFW)

Sex ratio of spawning populations

Male and female salmon on the spawning run at Cross Lake Thoroughfare in the Fish River Lakes from 1953 to 1955 were present in approximately a 1:1 ratio (Warner 1962). The sex ratio for 3 years was 577 males (49%) to 601 females (51%) . The sex ratio of the Cold Stream Pond spawning run in 1951 was 54% males to 46% males. The

Sex	Percent in age group										
	I	II	III	IV	V	VI	VII	VIII	IX	X	All ages
Males	98	98	66	54	53	43	39	15	0	0	56
Females	2	2	34	46	47	57	61	85	100	100	44
Number of fish	43	192	434	992	889	296	108	47	12	1	3,014

sex ratio of the West Grand Lake run from 1875 to 1930 averaged 44% males to 56% females. Similar data for the Sebago Lake run from 1916 to 1930 showed an average sex ratio of 47% males to 53% females. Since most of these data were taken in conjunction with spawn-taking operations, there was undoubtedly some bias in favor of females (Warner 1962).

Warner (1962) found that the sex ratio differed in the upper and lower age groups in the Fish River Lakes. A higher percentage of the age III salmon were males, and females predominated after age VI. This is consistent with recent statewide surveys of over 3,000 wild salmon from 41 populations (see table above).

Age at maturity

The spawning history of wild salmon on spawning runs in the Fish River Lakes was determined by scale examination (Warner 1962). Salmon spawning for the first time (maiden fish) comprised 70.5, 70.9, and 73.1% of the spawning runs in 1953, 1954, and 1955, respectively. Maiden salmon comprised 87% of the West Grand run in 1957 and 84% of the Cold Stream Pond run in 1951 (Warner 1962). Cooper (1940) found that 76% of 349 salmon from western Maine lakes were maiden fish. Maiden fish comprised 67.6% and 70.7% of spawning runs from Mooselookmeguntic Lake in 2002 and 2003, respectively, and from 1998 to 2003, 69.6% of 434 salmon from six western Maine lakes were maiden fish (D. Boucher, MDIFW, unpublished data).

The high percentage of maiden salmon in age groups III, IV, and V indicate that many fish of these ages were spawning for the first time (Table 41). After age V, scale examinations reveal that most salmon have spawned at least once. Analysis by sexes indicates that most salmon that have spawned before age IV are males. According to spawning check interpretation (Warner 1971) and age composition of the run, some females spawn first at age IV, V, or VI. Most males appear to spawn first at ages III, IV and V, although some precocious males spawn at ages I and II (Warner 1962).

Spawning periodicity

The periodicity of salmon spawning in the Fish River Lakes was determined through analysis of tagged fish returning to the spawning grounds from 1954 to 1958 Warner (1962). During these years, 174 different tagged salmon returned to the spawning grounds. Of these repeat spawners, 157 (90%) were returning to spawn for the second time, and only 17 (10%) were returning for a third time since tagging. Of the salmon recaptured during the 5 years, 47 were spawning for the second consecutive year. About one-half of these fish were males that were mostly ages III, IV, and V at recapture. Seven females and two males were returning to spawn for the third consecutive year.

One hundred and five salmon returned to the spawning grounds in the Fish River Lakes in alternate years only. The males in this group were primarily ages V, VI, and VII, and all the females were age VI or older. Four salmon had spawned for two consecutive years, skipped a year, and were ready to spawn for a third time at date of final recapture. Four female salmon had skipped a year between spawnings at ages IV, VI, and VIII. Two females had skipped 2 years and three had skipped 3 years between spawnings. These data indicate that salmon may spawn in consecutive or alternate years. Some fish may spawn in two consecutive years and skip a year before spawning again. A few salmon skip 2 or 3 years between spawnings. Spawning periodicity may be correlated with growing conditions in the lake and the time needed to recover from the rigors of previous spawnings.

Spawning behavior

Detailed observations on spawning behavior of landlocked salmon have not been documented for Maine waters. Spawning behavior, however, is very similar to that of sea-run Atlantic salmon, described by Cutting (1958). He states, "*Ripe females will choose a nesting site at the head of a riffle or the tail of a pool where the water is accelerating. Nesting areas of salmon and trout are frequently referred to as redds. Each nest or redd contains several egg pits. The female digs the egg pit by turning on her side and flapping vigorously with the caudal fin and peduncle. Most of the digging is the result of the water currents created rather than the actual contact of the body. Digging activity is alternated with frequent rest periods. The male spends his time courting the female or driving away smaller or less vigorous males from the area. When the egg pit is finished, the female settles into the depression, the male swims into position beside her, and the eggs and milt are extruded into the pit. Eddy currents in the pit mix the eggs and sperm for effi-*

cient fertilization and hold the eggs in the pit until the female can cover them with gravel. Frequently the male salmon parr (4 to 6 inches in length) mature early and participate in the spawning act. When spawning is completed in the first egg pit the female moves upstream to dig the second pit. As the gravel is displaced it is carried downstream to cover the eggs in the pit below."

Following spawning, spent salmon may remain on the spawning grounds or in pools for several days or even weeks, or they may return directly to the lake. Warner (1962) found that males commonly lingered on the spawning grounds for many weeks after spawning and were in extremely poor physical condition by December. Salmon that spawn in the outlet of Cold Stream Pond usually remain there throughout the winter following spawning and return to the lake in early spring. This type of post-spawning behavior is known to occur in the outlets of several other Maine lakes containing dams and fishways.

Mature male landlocked salmon captured on the fall spawning run at Jim Pond, Franklin County. (David Howatt, MDIFW)

Predation on salmon eggs

Opportunities for egg predation by fishes are limited because salmon eggs are ordinarily buried beneath several inches of gravel. Several workers have noted that while predation on salmonid eggs does occur during spawning, the eggs consumed by other fishes are usually those which were not buried after deposition and would have died anyway (Greeley 1932).

Suckers are often condemned for eating large numbers of salmon eggs. While some unburied eggs are undoubtedly eaten by suckers, there is no evidence that this species is a serious predator on salmon eggs. In the fall of 1953, stomachs of 49 white suckers and one longnose sucker were examined for evidence of egg predation during the peak of spawning activity at Cross Lake Thoroughfare, but no salmon eggs were found (K. Warner, MDIFW, unpublished data).

Several workers have reported predation on salmonid eggs by other salmonids (Greeley 1932; Briggs 1953). Landlocked salmon parr may be the most important predator of salmon eggs during spawning. In the fall of 1953, 9 salmon parr with distended abdomens were examined when it was suspected that they might have eaten salmon eggs. The parr were ages I + and II+ and ranged from 4.2 to 8.6 inches in length. One parr was a ripe male and the remainder were immature. All parr had eaten salmon eggs, and contained from 27 to 57 eggs per fish. Actual predation was not observed, but it was suspected that eggs

Table 41. Representation of maiden salmon on Maine spawning runs. Percentages represent proportions of each age group that were maiden fish.

			Age (annuli)					
Water	Year(s)		III	IV	V	VI	VII	VIII
Cross and Long L. Thoroughfares	1953	Number	35	207	81	4	2	0
		Percent	90.8	91.4	71.0	9.8	9.1	0
	1954	Number	72	127	51	2	0	0
		Percent	96.0	87.0	64.0	3.7	0	0
	1955	Number	93	202	91	22	2	0
		Percent	98.9	95.3	82.0	23.4	4.5	0
Mooselookmeguntic L.	2002	Number	1	15	39	17	1	0
		Percent	100	93.8	88.6	63.0	14.3	0
	2003	Number	3	43	43	16	4	1
		Percent	100	93.5	78.2	51.6	30.8	20.0
6 western Maine lakes	1998-2003	Number	98	63	69	10	1	1
		Percent	93.3	77.8	65.7	22.2	3.9	10.0

eaten by salmon parr were not the unburied ones that are eaten by suckers and other fishes. Rather, they were eggs consumed by the fast-moving parr after deposition and before being covered with gravel.

Potential egg predators include other species associated with salmon on the spawning grounds, such as eels, minnows, burbot, sculpins, and brook trout. In general, however, predation on salmon eggs during spawning is considered a relatively minor source of loss.

Fecundity and egg size

The most complete information on salmon fecundity available to date was compiled for 57 ovaries collected from 15 Maine lakes from 1957 to 1966 (Incerpi and Warner 1969). Salmon ranged in age from III+ to VIII+ and averaged 19.1 inches and 2.9 pounds. These salmon contained an average of 1,779 eggs per female by actual count. The average number of eggs per pound of body weight of the female was 638±146 (range: 328–1,047).

Recent fecundity estimates of salmon from the Jordan River spawning run at Sebago Lake are summarized below (MDIFW, unpublished data). Number of eggs per unit of salmon body weight was calculated using the volume displacement method.

Female salmon ranged in age from II+ to V+, but most (88% to 95%) were ages II+ and III+. They averaged 19.9 inches (range: 15.0-25.9) and 2.3 pounds (range: 1.0 to 5.7). Over the 3 years, these fish contained an average of 1,418 eggs per female and the mean number of eggs per pound was 617.

The only other fecundity estimates available for Maine landlocked salmon were calculated from tabular data presented by Kendall (1935) for 368 salmon from West Grand Lake. Females, captured for spawn-taking purposes, averaged 540 eggs per pound of body weight. The salmon averaged 3.1 pounds in weight and produced an average of 1,670 eggs per female.

Warner (1952) measured the fecundity of nine landlocked salmon from Little Moose Lake in New York. The females, averaging 17.8 inches and 2.8 pounds, produced 1,633 eggs per fish. The average number of eggs per pound of female body weight was 586 (range: 401-688).

Five female landlocked salmon from Oromocto Lake in New Brunswick, Canada, contained an average of 1,307 eggs per female and 503 eggs per pound of body weight (range: 434-598). These fish averaged 19.7 inches and 2.6 pounds (New Brunswick Dept. Natural Resources and Energy, unpublished data).

From 1954 to 1964, the average size of mature landlocked salmon eggs was determined for 55 wild salmon captured for spawn taking from the Cross Lake Thoroughfare in northern Maine. The ripe eggs averaged 0.245 inches in diameter.

Egg sizes of salmon obtained for stripping from the Jordan River (Sebago Lake) and West Grand Lake are reported below (MDIFW, unpublished data). These salmon were largely ages II+ and III+ when stripped. Egg diameter was calculated from an adaptation of the Von Bayer trough technique (Von Bayer 1910).

Fecundity estimates for Sebago Lake landlocked salmon.

Year	Number of fish	Mean no. eggs/fish	Mean weight of fish (pounds)	Mean no. of eggs/pound
1998	64	2,013	3.1	649
1999	110	1,168	1.9	615
2000	26	1,012	1.7	595

Egg diameter of landlocked salmon eggs from Sebago and West Grand Lakes.

	Jordan River Year			West Grand Lake Year	
	1998	1999	2000	1999	2000
No. eggs/liter:	5,173	5,173	5,173	4,563	4,563
Egg diameter (inches):	**0.240**	**0.240**	**0.240**	**0.250**	**0.250**
Mean length (inches) of fish stripped:	21.5	19.1	18.9	18.6	18.4
Mean weight (pounds) of fish stripped:	3.1	1.9	1.7	2.4	2.4

Movements

Landlocked salmon are migratory or emigratory fish during certain well-defined periods of their lives. Salmon move either upstream or downstream from one waterbody to another, either to spawn (primarily adults) or to reach more favorable feeding areas (primarily juveniles), but some movements might be simply random or accidental. Most landlocked salmon movements in Maine are in May, June, July, September, October and November, but some movements probably occur throughout the year.

Movements are probably most often triggered by changing seasonal habitat conditions, physiological factors, or interactions of the two. At times, physiological changes in the fish may initiate a movement, but whether the movement is completed may depend on habitat conditions. For example, for physiological or genetic reasons, adult salmon may congregate at the mouth of a spawning inlet or outlet in season but never enter the inlet or outlet because of unfavorable water attraction. However, as the peak of the normal spawning season approaches, a lesser degree of water attraction would probably be required to initiate movement into the spawning areas.

Knowledge of salmon movements is important for several reasons. Decisions involving necessity of fishways at dams that could prohibit salmon movement should be based upon site-specific knowledge of such movements. Specific knowledge concerning time and duration of runs may form a basis for protection of the species from certain predators, or certain movement patterns could necessitate special protective fishing regulations. Improved water regulation from water storage and hydroelectric dams can often be achieved if specific migration data are available. Finally, the technical aspects of pollution discharge and control should be based, at least in part, on knowledge of migration periods of salmon where the species may be affected by pollution.

Our most intensive migration data for landlocked salmon in Maine is based on work by Warner (1959) in the Fish River Lakes, DeSandre et al. (1977) in the Rangeley Lakes area, Bond and DeRoche (1956) at Cold Stream Pond, Havey (1960) at Long Pond and other locales, DeRoche (1976) at Sebago Lake, and from miscellaneous short-term projects conducted since 1950 on various waters.

Warner (1959), in his studies in the Fish River Lakes (Figure 7), tagged 1,239 landlocked salmon on their spawning runs to Cross and Long Lake thoroughfares during the falls of 1953, 1954, and 1955. Recoveries of tagged fish by anglers were catalogued from 1954 through 1956. Reports of angler recaptures of 231 tagged salmon were recorded to ascertain distances traveled. Warner's distance data are summarized in the table below.

Most salmon were captured within 8 miles from the point of release; the longest migration was 27 miles. Possible upstream migration distance was about 14 miles, while downstream migration distance was virtually unlimited.

Indications were that about 71% of the tagged salmon originated from upstream lakes while 29% originated from downstream lakes. A combined estimate (spawning area catches plus angler catches) of movement following tagging revealed that 66% of the kelts (spent salmon) moved upstream and 34% moved downstream following spawning.

Long-term movement studies in the Rangeley chain of lakes in western Maine (Figure 8) were described by DeSandre et al. (1977). Trapping studies at the Rangeley Dam fishway and screen showed an upstream movement of predominately young fish (age I to III +) during July and August with fewer in the fall. These young fish were probably produced in the Rangeley River between Rangeley and Mooselookmeguntic Lakes, then moved upstream into Rangeley Lake to take up residence there. Indications were that some of these young salmon spent all their juvenile lives in the river, but more commonly dropped downstream into Mooselookmeguntic Lake at ages I, II, or III, lived one to four seasons in that lake, and then moved upstream into Rangeley Lake. This type of migration behavior had not hitherto been recorded for other Maine lakes.

At the outlet of Mooselookmeguntic Lake (Upper Dam fishway), a punctual upstream run of salmon occurred annually from mid-June through mid-July. The run ceased at a temperature of about 70°F. In most years there was also a small run of salmon at this site in September and October. Of 3,481 salmon tagged at Upper Dam, 759 (22%) were known to have been caught. Seventy-eight percent were caught in Mooselookmeguntic Lake and Kennebago River (a major tributary), 20% in the Richardson Lake (downstream from Mooselookmeguntic Lake) or its outlet (the Rapid River), and 2% were taken upstream at Rangeley Lake. Analysis of growth patterns indicated that most of the run had dropped down from Mooselookmeguntic Lake at ages III+ and IV+ as 10 to12-inch fish.

Distance traveled by salmon in the Fish River Lakes.

	Distance traveled (miles)								
	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16+
Number of salmon	42	50	44	52	19	15	2	3	4
Percentage of salmon	18.2	21.6	19.0	22.6	8.2	6.5	0.9	1.3	1.7

Figure 7. Map of the Fish River Lakes Drainage.

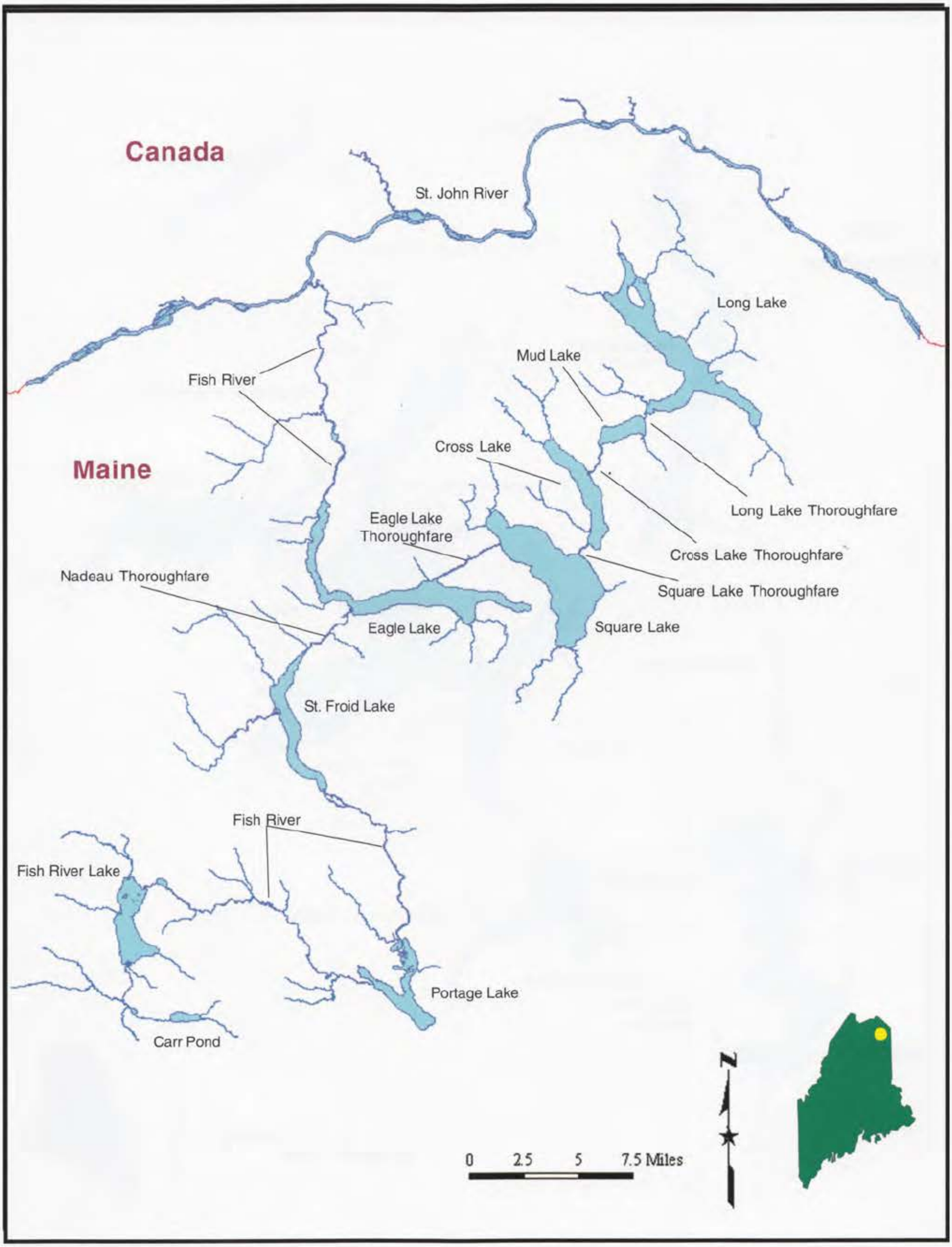
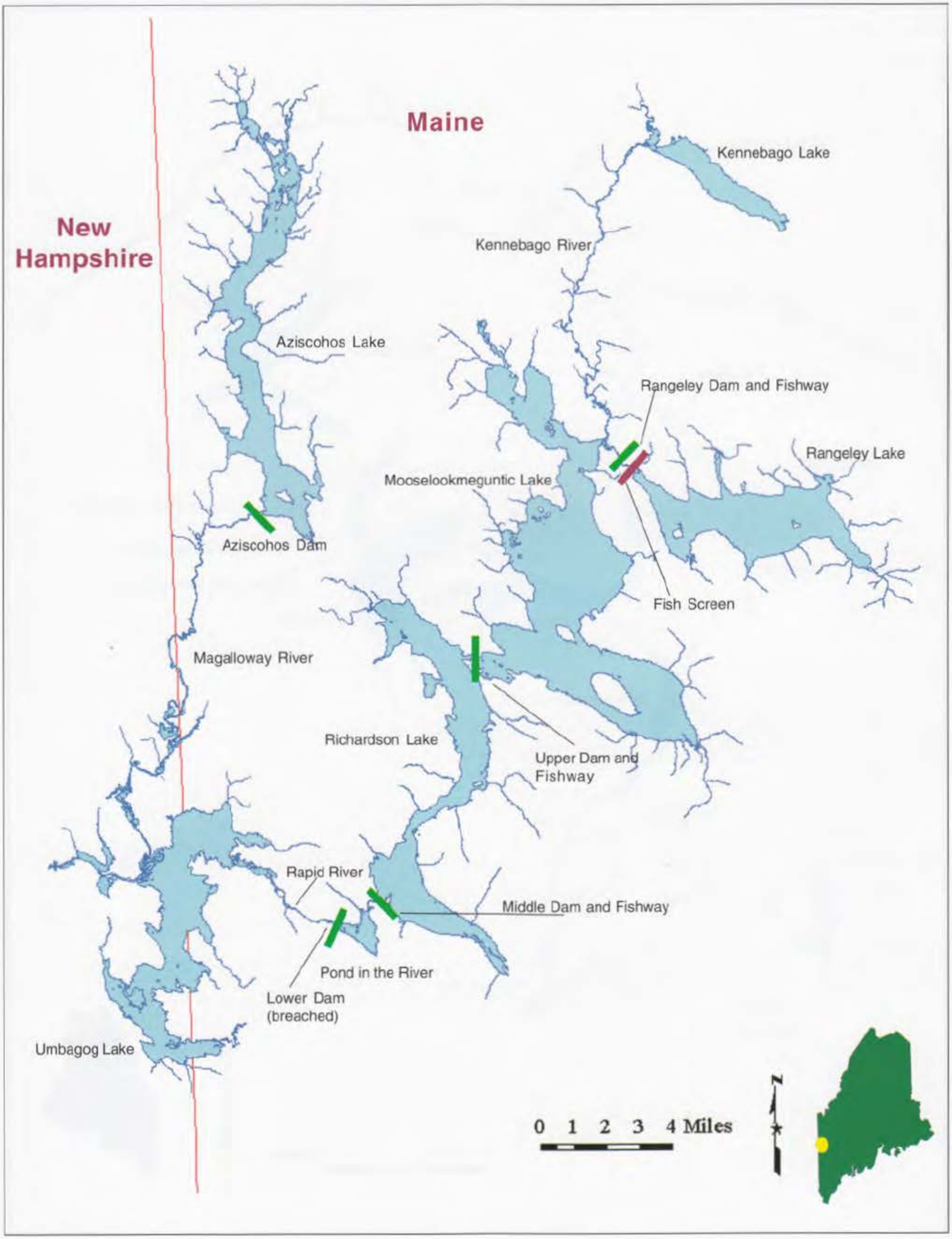


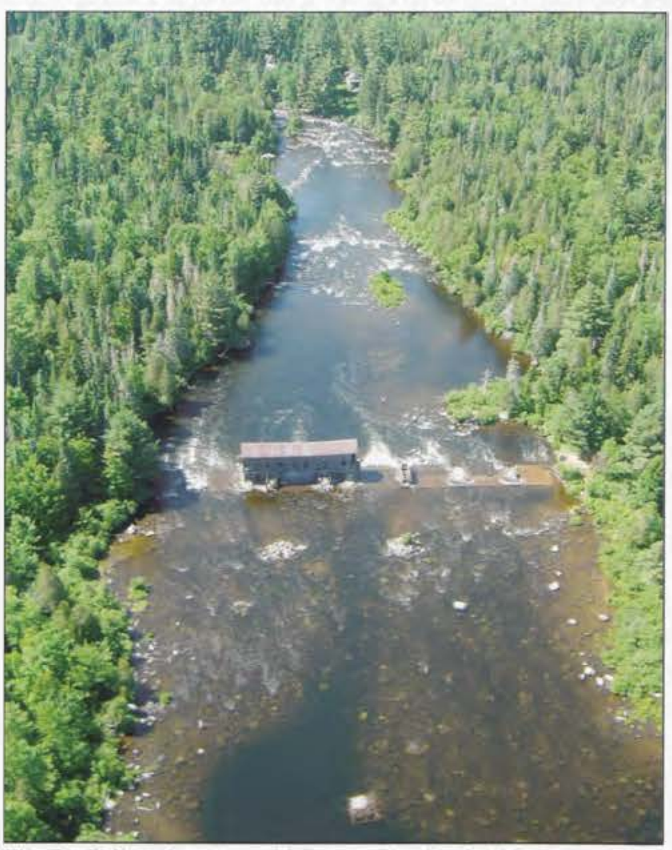
Figure 8. Map of the Rangeley Lakes Drainage.



While most salmon taken at Upper Dam were naturally reared fish, a few were hatchery fish (identified with fin clips). After passing through the fishway trap, these hatchery fish exhibited a behavior different from wild fish. Wild fish were found in the Kennebago River, an inlet to Mooselookmeguntic, much more often than were the hatchery fish, which appeared to frequent Rangeley River (another inlet, and the outlet of Rangeley Lake) to a greater extent.

DeSandre et al. estimated that from 1958-65, between 22 and 66% of the concentration of spawning salmon at Rangeley Lake outlet left the lake. Of these, 32-67% eventually returned to the lake via the fishway in Rangeley dam. Although more than one-half of the outlet spawning run probably left Rangeley Lake, the actual loss to the Rangeley Lake fishery probably did not exceed 2% per year; these fish, however, were large, mature salmon. The preference of hatchery-reared salmon for the Rangeley Lake outlet may have been a homing response to the water in which they were raised in at the Oquossoc hatchery, which used Rangeley Lake as its water source. The greatest percentage of dropdown occurred among the highest concentrations of spawning salmon. The groups that showed the greatest tendency to drop down the Rangeley Lake outlet also showed the greatest tendency to return.

A third trapping site in the Rangeley Chain was Middle Dam at the outlet of Richardson Lake. Here there was a run of salmon in June and July but virtually no fall run. Most fish were age III+ and IV+. Of 517 wild salmon tagged on their upstream migration at Middle Dam, a minimum of 139 (27%) was caught by anglers. Sixty-eight percent were caught in Richardson Lake above the tagging site and 32% in waters below, mostly in the Rapid River, the lake's outlet stream.



The Rapid River in western Maine provides ideal habitat for landlocked salmon. (Ken Wing)

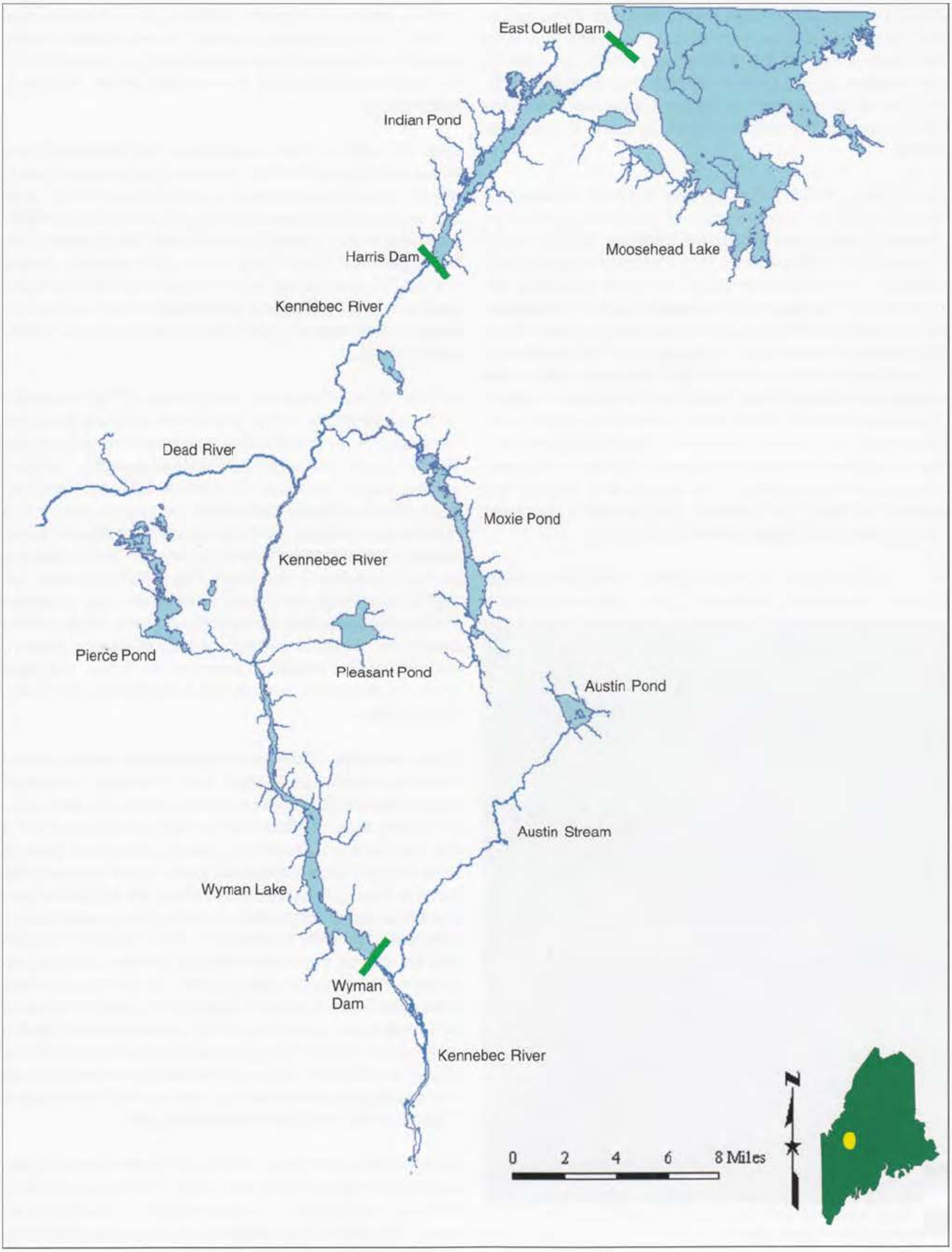
Over 90% of the angler-caught fish in the Rangeley Chain was probably caught within 10 miles of tagging sites. Downstream migration distance was practically unlimited, while fish tagged at the lowermost tagging site could conceivably have moved upstream as much as 25-30 miles. Perhaps the most interesting movement patterns among Rangeley Lake salmon, and the most important for management, was the strong preference of wild salmon to spawn in the inlets and for hatchery-reared salmon to prefer the outlet.

In 1999, Florida Power and Light Energy (FPLE) implanted radio transmitters in 64 landlocked salmon from the Kennebec River (EPRO 2000) between Harris Dam and Wyman Dam, two large hydroelectric projects (Figure 9). This salmon population is considered to be river-resident; that is, virtually their entire life history occurs in a riverine environment. With the exception of Wyman Lake, the large impoundment formed by Wyman Dam, there are no lakes accessible to salmon. The FPLE study was designed to evaluate the effects on behavior (e.g. displacement) of peaking flow operations of Harris Dam, and to determine seasonal patterns of habitat use by salmon. Tagged salmon ranged in age from I+ to VI+, but most (91%) were ages II+ and III+, and the majority (81%) was of wild origin.

There was little upstream or downstream movement of salmon in response to daily flow increases. However, tagged salmon did move up, down, or laterally within specific pools, runs, or riffles that they were occupying prior to the flow changes. Study fish generally remained close to initial tagging sites throughout the summer and early fall months. During these periods, none of the tagged salmon moved to cooler tributaries streams but remained in the Kennebec River. By October 21, 1999, five of 16 tagged salmon moved from their "normal" summer positions to various locations throughout this 19-mile reach of the Kennebec River, and to the Dead River (a major tributary), presumably on spawning runs. By late November 1999, a minimum of 15 of 23 tagged salmon had moved downstream into Wyman Lake and overwintered there. One remaining tagged salmon returned upstream to the Kennebec River from Wyman Lake by late May 2000.

Another telemetry study (FPLE 2004) was recently completed on the Rapid River, the outlet of the Rangeley lakes, which is much smaller (3.2 miles long) than the Kennebec River. This salmon population is also considered river-resi-

Figure 9. Map of the upper Kennebec River Drainage.



dent, except Rapid River salmon do have easy access to Pond in the River and Umbagog Lake. Middle Dam, which is not currently equipped with a fishway, prevents salmon from migrating upstream to the large lakes of the Rangeley chain, but downstream passage is virtually unlimited (Figure 8).

The Rapid River study was intended to provide seasonal habitat use data for adult salmon as part of a broader effort to assess competition with brook trout. A total of 18 salmon was radio tagged during the early summer months of 2003. They ranged in age from III+ to VIII+, but nearly 70% were ages IV+, V+, and VI+.

During the summer months (June to late August), tagged salmon utilized all elements of the Rapid River system, including Pond in the River and Umbagog Lake. Most (75%) tagged salmon remained in the river during June, then migrated to Pond in the River (56%) and Umbagog Lake (33%) in July when river temperatures reached about 72°F. In August, many (57%) salmon remained in Pond in the River, but several had moved back to the Rapid River. Several study fish moved into known spawning areas between late September and early November. There was apparently heavy post-spawning mortality of radio-tagged salmon, so overwintering habitat was not located, but data from three radio-tagged salmon from a smaller study conducted earlier suggested salmon overwinter in Pond in the River, and to a lesser degree in Umbagog Lake.

Florida Power and Light Co. Biologist Bill Hanson prepares to insert a radio transmitter to study salmon movements in the Rapid River. (Dave Boucher, MDIFW)

During a migration study at Cold Stream Pond and Upper Cold Stream, (Bond and DeRoche 1956), it was determined that a segment of the lake population utilized the outlet for spawning, and that up to 71% of the adults returned to the lake after spawning. Most return movement occurred the spring after spawning. Some unusually long movements for landlocked salmon were recorded during the Cold Stream Pond study – two of the salmon captured at the outlet were later taken by anglers about 45 miles downstream, and three were found dead about 35 miles below the tagging site.

Havey (1960), working primarily with hatchery-reared landlocked salmon at Long Pond in Mount Desert, found that over a 6-year trapping period only 46 of 9,271 fall yearling salmon (age I+) stocked in the lake subsequently moved down the outlet, either as juveniles or adults. Only one of these salmon moved out to the ocean. Long Pond is approximately 1.5 miles from the sea.

At Love Lake, only eight of 3,068 salmon stocked in the outlet as fall yearlings (age I+) or spring 2-year olds (age II) were subsequently captured as spawners at the lake (Havey 1974b). Seven of these fish were utilizing the inlet as a spawning area rather than the outlet where they were originally stocked.

Of about 18,000 salmon marked by fin clips and stocked in Love Lake as spring yearlings (age I) between 1960 and 1967, less than 1% was captured as emigrants at a fish trap at the outlet over a 7-year period (Havey 1974b). Since nearly all of the movement was of juveniles captured soon after stocking, these movements probably should be termed wandering rather than true migrations. An even smaller percentage of the newly stocked salmon took up residence in the one major inlet of the lake; these fish were mostly those stocked as spring yearlings. Relatively large numbers of these stocked fish subsequently used the inlet for spawning, and many moved upstream at least as far as Barrows Lake (2.5 miles), which is its source.

At Love Lake, there appeared to be a strong relationship between lake water levels and utilization of the outlet as a spawning area. Heavy rainfall in late summer and early fall of 1967 initiated the first outlet-spawning run of significant size during the 8-year project period. Salmon not only moved through the trap into the outlet stream, but at least three pairs of salmon spawned in the lake above the trap. Donor parents for all stockings at Love Lake have been salmon that utilize an outlet for spawning, yet prior to 1967 only an occasional adult fish emigrated to the outlet to reproduce.

There is good evidence that salmon stocked in Maine lakes have a strong tendency to return to the stocking site when maturing to spawn. In 1968 and 1969, DeSandre et al. (1977) stocked equal numbers of spring yearling (age I) salmon in two locations in Rangeley Lake. The sites were adjacent to the State Park and the Rangeley Lake outlet, located about three miles apart. Salmon were subsequently trapnetted at each stocking site to evaluate relative recoveries. Of the 1968-stocked fish trapped at the outlet site, 72% of the catch was of fish stocked there, and of the 1969-stocked fish trapped at the outlet, 58% were stocked there. Data for the other trapping site showed an even greater tendency for stocked salmon to return to the stocking site.

At Sebago Lake, DeRoche (1976) stocked salmon with different marks at various sites to study movement and tendency to return to the stocking site. In a 12-year period, no adult salmon were taken in the Crooked River that had not been stocked there, and no salmon stocked directly in Sebago Lake were taken in the Crooked River. Sebago Lake salmon were also found to return to areas in the Crooked River where they were stocked or naturally produced.

Returns from netting and angler surveys showed that lake-stocked, hatchery-reared salmon moved about Sebago Lake quite freely and did not remain within the immediate stocking area. Of 512 marked salmon that were recaptured, 91% were captured outside the general area where they were stocked. Returns from Songo Locks showed no Jordan River salmon. Returns from Jordan River, however, were made up of salmon stocked in all locations. Only 10% of all salmon were stocked in the Jordan River, yet 26% of all salmon recaptured in the Jordan River spawning run were salmon that had been stocked there. No Jordan River salmon were captured in the Northwest River, but 24% of the Northwest River catch was made up of naturally produced salmon. This was especially notable because the Northwest River was producing far below its capacity to produce young salmon.

Predation on landlocked salmon

Landlocked salmon in their lake environment are subject to predation by other fish species and piscivorous birds and mammals. Predation is probably most intense during periods when salmon occur in unusual concentrations, making them more vulnerable to predators. Periods of vulnerability include those of spawning concentrations at the mouths of tributaries, feeding concentrations, smolt migrations from tributaries and outlets, and following lake stocking with hatchery-reared fish.

Predation by fishes

Despite their abundance and availability in many Maine lakes, juvenile and adult salmon have rarely been found in stomachs of thousands of potential fish predators examined during our lake studies. Predation, when it occurs, has been mainly from five large predator species: lake trout, burbot, chain pickerel, smallmouth bass, and largemouth bass.

Variable success from early landlocked salmon plantings in Maine lakes containing other predator fishes raised the possibility that predation on newly stocked salmon may have been a limiting factor in survival of some stockings. To evaluate the degree of predation by various fishes on lake-stocked salmon, representative lakes were gillnetted immediately after stocking from 1965 to 1970. Stomachs of chain pickerel were examined after shore-stocking for 42 different salmon plantings; pickerel predation occurred in 27 (64%) of these plantings (Warner 1972). Of 523 pickerel examined, 152 (29%) contained freshly stocked salmon (Table 42). The pickerel that preyed on salmon had eaten an average of 1.9 stocked fish each. The most extreme case was one large pickerel that had devoured 32 newly stocked salmon. There was apparently little selection for size of salmon prey by pickerel. Barr (1962) found significant predation by pickerel on sea-run Atlantic salmon passing through Beddington Lake, Maine. Keith and Barkley (1970) reported heavy predation by pickerel on rainbow trout in Lake Ouachita, Arkansas. Seamans and Newall (1973), however, believed it unlikely that significant losses of newly stocked salmon to pickerel predation occurred in Winnipesaukee Lake, New Hampshire.

Scatter planting of salmon over deep-water areas was suggested by Warner et al. (1968) as a measure to reduce post-stocking predation by pickerel. Pickerel predation was compared for 24 spot plantings from shore and 18 scatter plantings over deep-water areas (Warner 1972). Pickerel predation was recorded for 71% of the spot plantings and 56% of the scatter plantings. Of 289 pickerel examined after spot plantings, 42% contained stocked salmon. Significantly less predation (17%) occurred by 205 pickerel examined from scatter plantings. In New Hampshire, however, Seamans and Newall (1973) found better returns by spot plantings along the shore at carefully chosen stocking sites in close proximity to escape cover.

Warner (1972) evaluated the extent of predation on stocked salmon by several other warmwater fishes, including yellow perch, white perch, smallmouth bass, largemouth bass, American eel, fallfish, and brown bullhead (Table 42). Of 558 yellow perch examined from 26 plantings, 2.5% had eaten stocked salmon. Predation by smallmouth bass had occurred in 13% of 76 fish examined. Only 10 largemouth bass were examined, but 30% had eaten salmon. No predation on stocked salmon was recorded for 383 white perch, 43 fallfish, and 14 brown bullheads examined.

Warner (1972) also examined lake trout, brown trout, brook trout, burbot, and other salmon for evidence of predation on newly stocked salmon. Of 169 lake trout examined from 17 plantings, only 3% had eaten stocked salmon. One of only two brown trout examined contained a newly stocked salmon, and there was no evidence of brook trout predation. Of 68 burbot examined for seven plantings, 8% had preyed on stocked salmon. Of 161 larger salmon examined for evidence of cannibalism, only 4% had eaten other salmon (Table 42).

Based on our data, chain pickerel appear to be the most serious predator on newly stocked salmon in the lakes studied. It is possible that where significant pickerel predation occurs, the survival of a group of stocked salmon

Table 42. Predation by various fishes on newly stocked salmon in Maine lakes, 1965-1970.

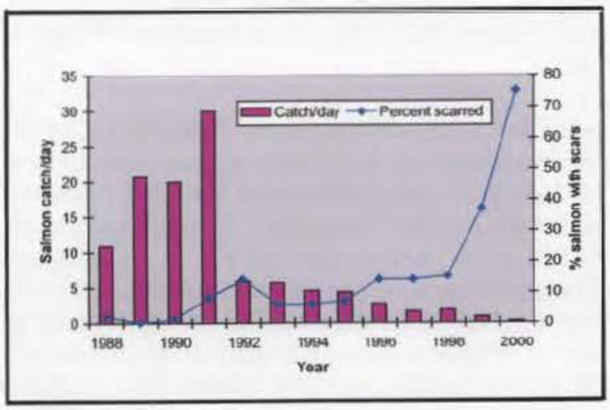
Species	No. plantings examined	Predation recorded		No. predators examined	Predation recorded		No. salmon per stomach[1]
		Number	Percent		Number	Percent	
Chain pickerel	42	27	64.3	523	152	29.1	1.7
Yellow perch	26	6	23.1	558	14	2.5	1.2
White perch	22	0	0	383	0	0	0
Smallmouth bass	12	3	25.0	76	10	13.2	1.3
Largemouth bass	3	1	33.3	10	3	30.0	1.3
American eel	4	0	0	69	0	0	0
Fallfish	9	0	0	43	0	0	0
Brown bullhead	3	0	0	14	0	0	0
Lake trout	17	2	11.8	169	5	3.0	2.4
Salmon	25	6	24.0	161	7	4.3	2.0
Burbot	7	2	28.6	68	5	7.7	2.0
Brook trout	6	0	0	15	0	0	0
Brown trout	2	1	50.0	2	1	50.0	1.0

[1] For those fish containing salmon.

could be seriously reduced. Findings reported by Warner (1972) led to adoption of routine scatter planting of stocked salmon, which was found to significantly reduce pickerel predation. Occasional predation by salmonids and burbot does not presently appear to be a serious factor in reducing survival of stocked salmon.

Northern pike are a relatively new predator in Maine, having been illegally introduced into the Belgrade Lakes during the 1970's. Their range has expanded considerably in recent years through additional illegal introductions, and they presently occur in 16 lakes in central and southern Maine (Brautigam 2001). Pike are known to be voracious predators and they grow to large sizes (Scott and Crossman 1998). While their impacts on Maine salmon have not been studied in detail, there is strong circumstantial evidence suggesting that they are major predators on salmon of all sizes in some lakes. Lucas (MDIFW, unpublished data) showed that increasing incidence of scarring observed on adult salmon was correlated with declining trapnet catches of salmon in Long Pond, Kennebec County (Figure 10). Scars were presumed to be the result of attacks by pike. The proportion of salmon exhibiting scars served as an index of pike abundance in the lake. Spring yearling salmon stockings have been suspended at Long Pond in favor of larger fall-yearlings in an effort to reduce pike predation. This strategy apparently has been unsuccessful, and the Long Pond salmon fishery has continued to decline (J. Lucas, MDIFW, personal communication).

Figure 10. Incidence of scars and trapnet catch rates of salmon on spawning runs at Long Pond, Kennebec County, 1988-2000.



Eels are known predators on sea-run Atlantic salmon in streams (Godfrey 1957 and Elson 1957b), but in four plantings in Maine, 69 eels examined had consumed no stocked landlocked salmon (Table 42). Most of the eels examined, however, were from one lake, and many may have been too small to consume age I stocked salmon. It is almost certain that eels prey on young landlocked salmon during their movements from stream nursery areas into lakes. Young salmon would also be vulnerable to eel predation for at least part of their first year of lake life, before attaining a size at which they would become too large for eels to consume.

Other than newly stocked hatchery-reared fish, salmon in the lake environment are probably most vulnerable to predation by other fishes during migration into the lake from nursery streams. Some predation may also occur in the confined area of fishways during migrations. Barr (1962) found significant predation by pickerel on sea-run Atlantic salmon smolts moving through Beddington Lake on the Narraguagus River. It is likely that considerable predation by pickerel on landlocked salmon occurs where salmon must travel through deadwaters or shallow weedy areas when migrating from stream nursery areas to the lake environment.

Predation by birds

Research on young sea-run Atlantic salmon in New Brunswick streams (Elson 1957b) has shown that both American mergansers and belted kingfishers are significant predators on young salmon. Mergansers were considered the more serious. Both birds are common in Maine and have been reported as predators on Maine landlocked salmon. Predation on landlocked salmon, if significant, probably occurs primarily on young salmon, either in their shallow stream nursery areas, immediately after stocking of hatchery-reared fish, or during movements of wild fish from stream nursery areas.

Seamans and Newall (1973), in New Hampshire, and Maine anglers have reported predation on newly stocked salmon by the common loon. The extent of loon predation on salmon in Maine lakes is not known, but loons are known to have entered trapnets and killed large numbers of trapped salmon.

While the diet of the herring gull is not ordinarily live, healthy fish, several instances of predation on salmon have been noted. Gulls were observed attacking and killing spent adult salmon at the mouth of the Jordan River in Sebago Lake as the fish moved downstream into the lake after spawning. The attacks occurred as the salmon swam over a very shallow sand bar at the mouth of the river. Gull predation on salmon, however, is probably confined to unusual situations where the fish are highly vulnerable or incapacitated. Stomach analyses of 27 gulls from Sebago Lake in the summer of 1967 revealed no predation on salmon.

Predation by mammals

Several species of mammals are piscivorous and are known to be occasional predators on salmon. Potential mammalian predators on Maine salmon include the otter and the mink. Predation by these mammals can be locally serious when salmon occur in unusual concentrations. Otter were observed feeding heavily on adult and parr salmon during the fall spawning run in Jordan River, Sebago Lake, in 1964. During spawning run surveys, otters have occasionally entered trapnets and killed large numbers of adult salmon. Otter have also been known to invade hatchery raceways and kill large numbers of young salmon. While no specific instances of serious mink predation on salmon have been reported, it would most likely occur under the same conditions as otter predation.

In summary, most predation on landlocked salmon by fishes, birds, and mammals occurs during the most vulnerable periods in the salmon's life history, which are primarily during migrations from stream nursery areas and during spawning concentrations. Rapid swimming speed and fast growth during the first year of lake life, resulting in attainment of a size too large for consumption by many predators, minimize predation on salmon during much of its lake life. When hatchery-reared salmon are involved, predation is probably most serious immediately after stocking.

Parasites and diseases of landlocked salmon

Parasites

Most of the research on parasites of landlocked salmon in Maine has been performed by Dr. Marvin C. Meyer of the University of Maine (Meyer 1954; Meyer and Vik 1963), whose studies have served as a main source for the subsequent summary. Additional sources include Hoffman (1999) and Danner (2004). Our purpose here is to list kinds of parasites that have been found in Maine landlocked salmon and comment on their possible effects on salmon populations. The reader is referred to the Meyer, Hoffman, and Danner publications for more detailed information. Data for parasitism on landlocked salmon in Maine fish-cultural stations were furnished by David O. Locke and Peter G. Walker, formerly of the Maine Department of Inland Fisheries and Wildlife, and by Dr. G. Russell Danner, Maine's current fish pathologist.

Parasites known to occur in landlocked salmon are listed in Table 43. The external protozoan parasites occur on young salmon mainly in the hatcheries. They sometimes cause problems with fry, but can usually be controlled by formalin treatments. *Trichophrya piscium* occurs on the gills and is very difficult to control with formalin. *Ichthyophthirius multifilis*, a gill and skin parasite, also occurs in the hatchery, and it could also be a problem on wild fish in warm streams. The trematode (flatworm) *Gyrodactylus salaris* frequently infest salmon in hatcheries. This parasite causes skin and gill irritation and may reduce growth (Danner 2004).

Regarding effects of external parasites, Meyer (1954) states, "*The chief damage caused by adult external parasites, such as fishlice, leeches and monogenetic trematodes, is that they may extract large quantities of blood and sometimes cause mechanical injury to the tissues at the point of attachment, which may result in frayed fins* *and in secondary infestations by fungi and bacteria. Under natural conditions, however, these seldom occur in great numbers and they do comparatively little harm. But when abundant, as is likely to be the case under crowded conditions in hatchery pools, the fish are greatly weakened and may eventually succumb in large numbers."* While mass mortalities of salmon due to external parasitism in the wild have not been reported, the possibility of such an occurrence exists. Rupp and Meyer (1954) reported an unusual mortality of brook trout in Quimby Pond, Maine, resulting from attacks of freshwater leeches.

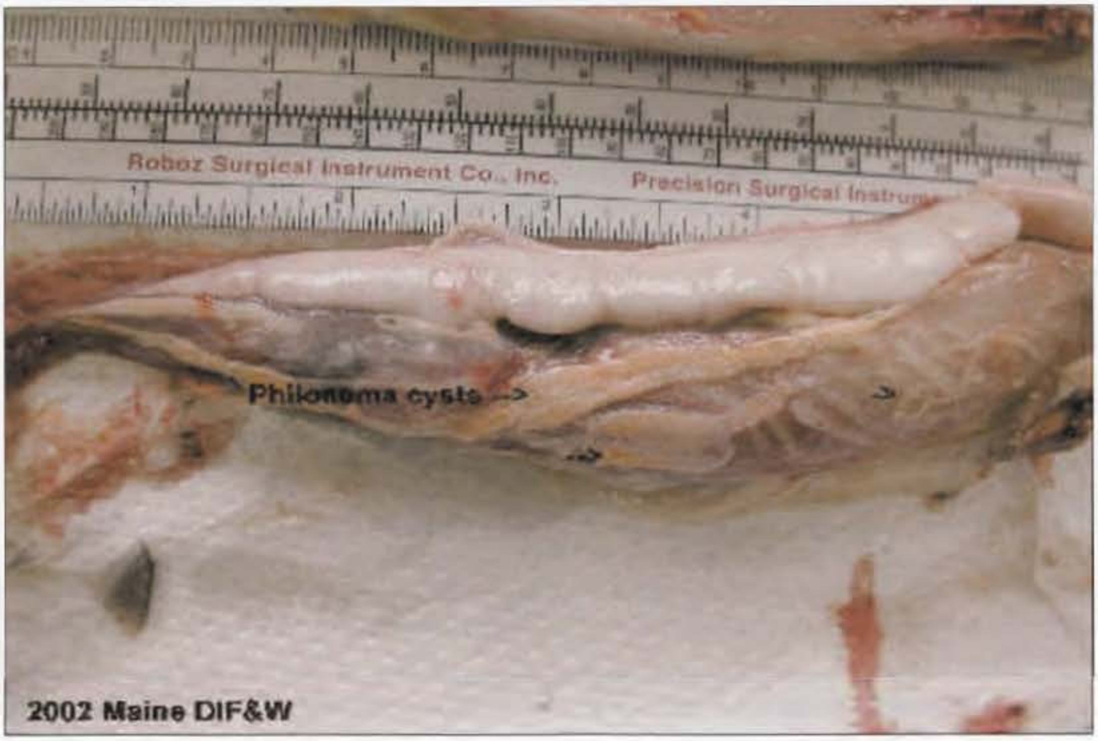
Davis (1967) studied parasitism of newly transformed sea lampreys on salmon at Love Lake in Washington County, and showed that 85% of 564 salmon examined had been attacked by lampreys. Salmon, which ranged in length from 4.5 to 23.5 inches long, were attacked with greater frequency than all other species examined. Some individual salmon were attacked during several successive years and some were attacked multiple times during the same year. Davis concluded that salmon were capable of surviving multiple lamprey attacks, and that lampreys posed no serious threat to salmon or other fish populations in Love Lake.

Heavy infestations of larval and adult stages of the cestode (tapeworm) *Diphyllobothrium sebago* are sometimes a problem in hatcheries, but their role in causing morbidity or mortality in salmon is unclear (Danner 2004). In 1962 and 1963, 11 salmon from Sebago Lake were examined for larval stages of *Diphyllobothrium sebago* in an attempt to compare growth rates of infected and uninfected salmon. Infestation by these larval stages was light. Larvae were found in only five salmon, and four larvae was the highest number found in any one fish.

Probably the most serious parasite on landlocked salmon in Maine is the roundworm *Philonema agubernaculum* (see photo). Danner (2004) states that migrating *Philonema agubernaculum* worms may cause scarring adhesions to

Table 43. Parasites known to occur in Maine landlocked salmon.

Class	Name	Location	Authority
PHYLUM PROTOZOA			
Apicomplexa	*Ichthyoboda necatrix*	Gills	Danner (2004)
Ciliophora	*Trichophyra piscium*	Gills	Locke (pers. comm.)
	Epistylis spp.	External	Locke (pers. comm.)
	Ambiphyra spp.	External	Locke (pers. comm.)
	Icthyophthirius multifilis	Gills, skin	Locke (pers. comm.)
	Chilodonella salvelinus	Gills, skin	Danner (2004)
Sporazoa	*Chloromyxum* spp.	Internal, connective tissue and organs	Locke (pers. comm.)
PHYLUM PLATYHELMINTHES			
Trematoda (flukes)	*Gyrodactylus salar*	Gills, fins	Danner (2004)
	Azygia longa	Esophagus, stomach	DeRoth (1953)
	Azygia sebago	Esophagus, stomach, intestine	Hoffman (1967)
	Crepidostomum farionis	Digestive tract	Meyer (1954)
Cestoda (tapeworms)	*Diphyllobothrium sebago*	Adults migrate through organs	Meyer (1954)
		Larvae in pyloric caeca	Meyer and Vik (1963)
	Eubothrium crassium	Pyloric caeca	DeRoth (1953) and Meyer (1954)
	Eubothrium salvelini	Pyloric caeca, intestine	Meyer (1954)
	Proteocephalus pusillus	Pyloric caeca, esophagus, intestine	Ward (1910) and Meyer (1954)
PHYLUM NEMTHELMINTHES			
Nematoda (roundworms)	*Philonema agubernaculum*	Coelemic cavity	Meyer (1954)
	Camallanus lacustris	Intestine	Meyer (1954)
PHYLUM ACANTHOCEPHALA			
Hookworms	*Leptorhynchoides thecatum*	Intestine	Meyer (1954)
PHYLUM MOLLUSCA			
Molluscs	*Margaritifera margaritifera*	Gills	Danner (2004)
PHYLUM ARTHROPODA			
Crustacea	*Argulus americanus*	Gills, fins	Hoffman (1977)
	Salmonicola edwardsi	Gills, fins	Danner (2004)
PHYLUM ANNELIDA			
Hirudunea (leaches)	*Piscicola milneri*	Skin, fins	Meyer (1954)
PHYLUM CHORDATA			
Agnatha (lampreys)	*Petromyzon marinus*	Body surface	Davis (1967)



The nematode *Philonema agubernaculum* can cause functional sterility in landlocked salmon. (Russ Danner, MDIFW)

develop in the body cavity, destroying internal organs and rendering adult salmon functionally sterile. Adhesions caused by this worm also affect the aesthetic value of dressed fish. Meyer (1954) described the effects of this parasite on salmon as follows: "*This worm ... is found in both the immature and mature stage in the same fish host. In the larger fish worms cause adhesion of the viscera. These adhesions may not only bind the organs together but also attach the mass of viscera to the body wall ... When these adhesions are broken and the organs separated, many worms of both sexes in different stages of development are freed. Apparently this is what happens during stripping, when a mass of worms is often forced out with the eggs or sperm. In such cases the organs are so strongly adhered together that neither normal spawning nor stripping is possible, in which case the host is actually egg-bound. In such cases, pathological changes, particularly of the gonads, are apparent. The wall of the ovary is greatly thickened and firmly attached to the other viscera. The wall loses its normal transparency, becoming nearly opaque. While fully-sized eggs are present, they are abnormally colored, brittle and hard. Also there are membranes of eggs from the preceding season, the egg proper having been reabsorbed in the meantime.*"

Mortalities from external parasite infestation are common in hatchery pools, but these can be controlled in most cases by chemical treatment. The precise effects of most parasites on salmon in the wild, however, have not been measured. In most cases such assessment would require intensive research. Chemical control of parasites under wild conditions is not presently feasible. The best control measure for salmon parasites in the wild is prevention of the spread from home waters of the final and intermediate hosts of parasites known to cause severe harm. A prime example is prevention of the spread of salmon infested with *P. agubernaculum* to waters where the parasite is not present.

Diseases

Diseases affecting landlocked salmon have been a problem under hatchery conditions since the beginning of fish-cultural operations in Maine. In the crowded conditions of hatchery pools, various diseases sometimes reach epizootic proportions, resulting in death of large numbers of salmon. While some diseases have been documented as occurring in wild salmon populations, their effects are usually less severe than under hatchery conditions where stress factors reduce the fish's immune defenses and make infection more likely (Danner 2004).

Fish health investigations and disease monitoring have been routinely carried out in Maine hatcheries since the late 1960's. Most recently, a few wild salmon populations have been screened for several infectious diseases of nationwide concern (Danner 2004). The diseases known to occur in landlocked salmon in Maine are presented in Table 44. For a general account of fish diseases, the reader is referred to Davis (1956) and Hoffman (1999).

Table 44. Diseases known to occur in Maine landlocked salmon.

Disease	Pathogen	Pathology
Bacterial Diseases		
Furunculosis	*Aeromonas salmonicida*	Boils, septicemia
Columnaris Disease	*Flexibacter columnaris*	Necrosis in mouth, body surface, gills
Cold Water (Peduncle) Disease	*Cytophaga psychrophila*	Caudal peduncle, tail
Bacterial Gill Disease	*Aeromonas hydrophyilla*	Kidney/gill necrosis, septicemia
Enteric Redmouth Disease	*Yersinia ruckerii*	Septicemia
Fish tuberculosis	*Mycobacterium marinum*	Mycobacteriosis, granulomas in flesh
Pseudomonad septicemias	*Pseudomonas flourescens*	Septicemia, gill disease
Viral Diseases		
Infectious Pancreatic Necrosis	Aquatic birnavirus	Pancreatic necrosis
Salmon Papillomatosis	Herpes virus	Cloudy, circular masses on body surface
Fungal Diseases		
Fish molds	*Saprolegnia* spp	Skin lesions

Bacterial diseases

Furunculosis is a systemic infection caused by the *Aeromonas salmonicida* bacterium. Boil-like lesions are the most typical clinical sign. This disease is transmitted directly from fish to fish through contaminated water or food; the incidence is usually higher in the presence of pollution or other adverse conditions. The disease is endemic in the Rangeley Lakes drainage in proximity to the former Oquossoc Hatchery, where it was responsible for high mortalities of salmon. Furunculosis occurs most frequently in hatcheries, but wild salmon are known to be latent carriers (Danner 2004). Furunculosis infections in Maine's salmon hatcheries have been successfully overcome by installation of water filter/UV light treatment systems, and through strict biosecurity measures employed in the transfer of fish between hatcheries and natural waters.

Bacterial gill disease is an infection of the gill filaments and lamellae, causing a swelling or "clubbing" which interferes with respiration. This condition often occurs above 70°F when fish are crowded. The presence of mud and silt, and ammonia above a concentration of 0.5 ppm, is often involved.

Myxobacterial infections may also cause difficulties in salmon culture in Maine hatcheries. Handling and crowding usually aggravate the situation. These diseases may become a problem in the wild environment in marginal habitats, because opportunistic Myxobacteria are universally present. Myxobacteria are often secondary invaders after a parasite infestation. Columnaris disease produces necrotic areas on the body of the salmon. Some forms attack mouthparts and eventually erode the tissues, while others produce shallow ulcers on the body surface, which superficially resemble a fungus. Gill tissues are usually involved, and in advanced cases, systemic infections of the organism develop. This continues to be the second-most serious bacterial problem (next to furunculosis) in raising landlocked salmon in Maine hatcheries. Good hatchery management (particularly keeping fish densities low), chemical treatments, and antibiotics (oxytetracycline) have been effective in controlling columnaris. *Flavobacterium columnare* is now thought to be an obligate fish pathogen requiring a living fish carrier as a reservoir. Suckers have been implicated in some areas as serving in this role.

Cold water or peduncle disease is caused by a specific myxobacterial pathogen – *Flavobacterium psychrophilum.* It occurs in the winter and is characterized by the slow erosion of the caudal peduncle followed, in some cases, by the complete loss of the tail. The disease is fatal. However, it seldom occurs in more than a few individuals in a population, although epidemics of this disease have occurred in certain Pacific salmon fry in western hatcheries.

In addition to the above, bacterial kidney disease (*Renibacterium salmonarinum*) and enteric redmouth disease have now been reported from Maine landlocked salmon (Danner 2004).

Pseudomonad septicemias are the result of infection by opportunistic *Pseudomonas* species that are ever-present in the environment. They take advantage of fish that are in poor condition or under chronic stress, and they generally occur at low temperatures.

Vibrio disease is a furunculosis-like disease of salt and brackish water. The organism is widespread along the coast and in brackish estuaries. It has severely hampered cage culture operations in some areas. Commercial vaccines are quite effective in its control. In Maine, *Vibrio* has been recorded in Coho salmon and rainbow trout cage culture.

Recent studies indicate that bacterial fish pathogens are acquiring antibiotic resistance. Studies are underway to determine if antibiotic resistance is acquired from selective pressures imposed by certain environmental conditions (e.g. mercury contamination), or from widespread use of antibiotics in commercial aquaculture facilities (Danner 2004).

Viral diseases

Maine landlocked salmon are known carriers of infectious pancreatic necrosis (IPN). This disease, however, has never been implicated in any mass mortality of salmon in Maine.

Mature salmon in some spawning populations occasionally exhibit "epithelial papillomas" (Carlisle and Robert 1977). This condition is caused by a herpes virus and has been noted in adult spawners at West Grand Lake, the Fish River Lakes, the Rangeley Lakes, and in immature fish in Maine and in Scandinavia. The lesions consist of proliferating epithelial cells and are sometimes quite vascular. They usually slough off by a process that appears similar to tissue graft rejection.

Fungal diseases

Fungi, non-vascular plants, are responsible for a variety of diseases in salmon. These diseases occur most frequently in salmon under hatchery conditions, but they may sometimes be found on wild salmon after handling or other stress. Fungal infections may occur on salmon eggs or on the fish itself. Fungal infections in incubating salmon eggs represent the largest source of mortality in Maine hatcheries of any fish pathogen (Danner 2004). Male salmon often develop fungal skin infections following spawning. These infections are often secondary invaders following injury or parasitism, but the lesions may enlarge and cause death.

LANDLOCKED SALMON SPORT FISHERIES

History of salmon sport fisheries

The acrobatic prowess of landlocked salmon was praised in many early popular accounts, and by the state's first Fish Commissioners. Stillwell and Stanley (1874b) commented, "*As a game fish they have no equal. We have caught many fresh and sea salmon in our day, but nothing that we have ever hooked on to can equal one of these fishes in his electric like leaps and runs ...*" Stillwell and Stanley (1888) wrote, "*the wide popularity of this fish, its splendid game qualities, its excellence as a table fish, have all led to a wide popularity almost amounting to enthusiasm.*"

Dr. W.C. Kendall holds a 16-pound landlocked salmon caught in Sebago Lake on August 1, 1907. (Kendall Warner)

Very few anglers benefited from the early sport fishery, however. Stillwell and Stanley (1883) attempted to arouse more interest in Sebago Lake salmon fishing as follows: "*Were the fish better known, this lake would be more visited than Dominion waters, and with the same outlay of time and less money, with as great success... The habits of the fish have not been carefully studied by local anglers...Sebago Lake is worthy of the persevering study of any good angler, and we think with surety of reward.*"

During this period of early development of the sport fishery, poachers accounted for large numbers of landlocked salmon, as evidenced by the following scornful condemnations by the early Commissioners: "*These fishes of Reed's Pond* {Green Lake}, *have not only been very much thinned out by the merciless slaughter of them on their spawning beds, by the class of drunken roughs who lived by pot-hunting and poaching, but to fully as great an extent by being deprived of access to their natural spawning ground in swift running waters*" (Stillwell and Stanley 1874b); and "*A wretched custom of taking these fish on their spawning beds, seems to have existed since time immemorial. Indeed, no other method appears to have been known or recognized. It is apparently a remnant of barbarism*" (Stillwell and Stanley 1877).

Regarding sizes of salmon taken in early sport fisheries, Stillwell and Stanley (1888) wrote, "*We have two varieties of these interesting fish so far as size is concerned, viz: those of Sebec Lake and those of Grand Lakes, being similar in size, making but a small average of some 2 and ½ pounds, while those of Sebago Lake and those of Reed's Pond, are very much larger, attaining the size of over 27 pounds. These cases do not hold good of these fish, when the progeny of their eggs are planted in their waters.*" Kendall (1935) reported that the largest salmon caught by angling was from Sebago Lake and weighed 22 ½ pounds.

Kendall (1935), citing Charles Atkins, provided some of the earliest records of size of angled salmon from West Grand Lake:

Year	Number of salmon	Average weight (pounds)
1856	634	1.38
1857	452	1.49
1858	575	1.42
1865	379	1.33

Commenting on sizes of angled salmon in Green Lake (Reed's Pond) compared with West Grand Lake, Stillwell and Stanley (1874b) stated, "*They are the same fish, only developed to a greater size by the superior range and purity of the water, and greater supply of feed for both the young fry and the growing fish. The Reed's Pond salmon have in the past, been caught of great size and weight, viz., 22, 15 and 10 pounds.*" It is possible that some of the large fish in the very earliest reports were sea-run Atlantic salmon, because many river systems were unobstructed at that time.

For Sebec Lake salmon, Stillwell and Stanley (1874b) stated, "*They are all similar in size and general appearance to the Schoodic shiner or salmon.*" Kendall (1935) reported that the average sizes of Sebec Lake salmon from 1915 to 1929 ranged from about 2 to about 3 ½ pounds.

Kendall (1935) wrote on Sebago Lake salmon: "*Sebago Lake has long had a reputation for large salmon.*" He stated that in 1833 the average number taken in a day by a party of four was near 25, ranging in weight from 2 to 5 pounds.

Kendall cited the following average weights for angled salmon for several different years:

Year	Number of salmon	Average weight (pounds)
1886	10	11.2
1896	26	6.2
1905	39	8.4
1909	164	5.5
1917	176	3.5

Regarding these average weights, Kendall commented, "*The records suggest some decrease in size in most recent years.*"

Some of the earlier introductions initially produced large salmon within a few years as a result of rapid growth in their new environments. Stanley (1882) observed, "*Our work in planting landlocked salmon has been amply repaid to us this year in the exhibition of most gratifying results at Moosehead, at Enfield [Cold Stream Pond], and at Rangeley. At Enfield, fish...were seen on the spawning bed this year...fully equaling 10 to 12 pounds...Quite a number were seen by the Commissioner on the spawning beds in Rangeley Stream in October, some of them very large and estimated by him and others at not less than 10 or 12 pounds.*" The salmon at Cold Stream Pond were introduced in 1876 and could not have been over age VI. Kendall (1918) reported that many 5 to 10 pound salmon were taken in the Rangeley Lakes about 5 years after introduction. Salmon from 10 to 21½ pounds were reportedly common in the Fish River Lakes 9 years after their introduction (Cummings 1903).

The challenge offered by the salmon as a sport fish has been most fully recognized within the past 100 years. Accessibility to salmon waters gradually improved after 1900, first through improved railroads, and later because of improved automobile transportation and better road networks. Logging operations, using more advanced equipment, increased accessibility to more and more salmon waters, especially after World War II. Access to salmon waters in northwestern and northern Maine improved dramatically after the 1970's as permanent logging roads were built to accommodate large-scale salvage of trees damaged by budworm, and to provide a transportation system to replace river drives.

With these improvements in access, an increasing number of anglers began to take advantage of opportunities for salmon fishing, and salmon soon became one of Maine's most sought-after sport fish. Coincident with improved access and increased fishing effort, lake inventories revealed additional potential salmon waters that could provide fisheries through introductions. Successful introductions were made in many waters, further increasing fishing opportunities and angler use. By 1975, 161 lakes supported viable salmon fisheries (Havey and Warner 1976), and by 1990 there were 209 lakes comprising about 548,000 acres (DeSandre 1991).

While access to the salmon sport fisheries was aided by improved mechanical equipment, expanded transportation networks, and new introductions, certain other conditions tended to reduce opportunity for use. With an increasing human population and generally improved access, fishing camps and summer cottages began to proliferate on the shores of many salmon lakes, often leaving no opportunity for public access by other anglers. Opportunity for use by the general angling public was also restricted by chaining of roads in wild lands by some large landowners, and posting of access roads by small landowners in more populated areas. Recently, public access to salmon lakes has been affected by increased user fees, new fees, and by outright purchase or leasing of access rights to private individuals or groups. Aggressive acquisition programs by the Maine Departments of Conservation and Inland Fisheries and Wildlife have met with some success, but landowner and campowner opposition has frustrated efforts to provide access to some waters. This has resulted in cessation of salmon stocking and reduced salmon fishing opportunities in several waters because of "unequal access" by the public.

Beginning with the early battles against abuse by poachers, fishing regulations became more restrictive as numbers of anglers using the salmon resource increased. Overrestriction sometimes resulted from efforts of anglers and

Lucian Cyr caught this large salmon in Long Lake, St. Agatha on June 13, 1941. The fish weighed 19 pounds, 11 ounces. (Reginald Roderick) legislators who became concerned, and even alarmed, that salmon populations might be over-exploited. Types of regulation restrictions most often imposed were closure to ice fishing, shortening ice or open water seasons, closure of specific areas, restrictions in types of angling gear, reduced bag limits, and increased length limits. As more biological information became available, however, fishing regulations were restructured into specific categories based on the biological characteristics of individual salmon populations. (Fishery regulations will be discussed in detail in a later section.)

Salmon fisheries in some lakes have been reduced or eliminated because salmon management is no longer feasible or desired by the public. Poor fishing, resulting from poor salmon survival or growth, sometimes occurred because of increases in predator or competitor species. Examples are a proliferation of illegal introductions of such species as northern pike, smallmouth bass, largemouth bass, and black crappie. In other waters, salmon stocking programs have been terminated or suspended in favor of other coldwater species due to chronic poor performance of salmon. This notwithstanding, salmon fishing opportunities remain abundant in Maine, with about 175 lakes and 64 river segments providing principal fisheries in 2001 (Boucher 2001).

Nature of the Fishery

Landlocked salmon have been taken in the sport fishery by almost every means of legal angling. Early references to methods of fishing landlocked salmon were by Stillwell and Stanley (1883) who recommended the following: "*Trolling by night should also be tried; casting the fly by night; deep fishing with fine tackle and live bait.*" The same authors (Stillwell and Stanley 1888) later stated, "*The smaller variety of salmon of Sebec and Grand Lake take the fly readily and afford fine sport. While the larger fish of Sebago and Reed's Pond are seldom or rarely taken except by trolling with a minnow or smelt.*"

Kendall (1918) commented, "*This salmon is undoubtedly one of the gamest of game fishes, but times and circumstances modify these qualities in one way or another. Trolling or plug fishing will not afford the sport that fly fishing does. As a rule, the smaller fish are far more active than the very large ones...The fish can be caught by some means throughout the open season. The most productive time, however, is usually when the lake is free from ice up to the first of July or the beginning of the heated season. As in the case of trout, in the early part of the season salmon may be taken almost anywhere in the lakes, but particularly about points and shoals and at mouths of streams, especially when smelt are running...Occasionally one is caught by any of the usual methods during the summer, although still fishing with live bait during July and August is the most likely method to yield fish...In some waters the fish has been caught by trolling and on a fly in later September.*"

Present seasonal patterns for landlocked salmon fishing are similar. Angling methods, however, have changed substantially over the past 20 years. With the advent of sonic fish finders anglers are now able to locate concentrations of salmon and target them with relatively light gear with the aid of downriggers. These advantages increase angler efficiency dramatically. When salmon are in a "feeding frenzy," skilled anglers use these gears to select their catches according to their size preferences.

The open water fishery for salmon begins in early spring as soon as the ice cover leaves the lakes. At this time, lake water temperatures are about equal at all depths, as the water is constantly mixed by the wind action. Immediately after ice-out, the water temperature is about 40°F but warms rapidly to the mid-40's and low 50's under the influence of the spring sunshine. With rising water temperature, salmon range widely throughout the lakes and begin to feed ravenously. Trolling in a boat or canoe powered by an outboard motor has been the most common fishing method in early spring months, which may include April, May and June, depending on weather and climatic location of the lake. Salmon may be taken almost anywhere in a lake at this time, but most trolling is done with the bait or lure on or near the surface, along shores, around rocky points and shoals, near mouths of brooks and streams, and in larger rivers and thoroughfares. Early fishing effort is often concentrated at mouths of brooks and streams used for spawning by smelts. Smelt spawning in these brooks may occur before, during, or after ice-out. Thus, the quality of the salmon fishery enjoyed is often dependent on the degree of coincidence between the time of the smelt run, the time of ice-out, and water temperature.

Baits or lures used for landlocked salmon during the early spring fishery vary considerably. However, the Maine streamer fly remains one of the most popular early spring baits. Many of the most popular streamer flies, such as the Gray Ghost, are designed to imitate a smelt or minnow. These flies are usually trolled on or near the surface with varying lengths of line. Earthworms or smelts are sometimes hooked onto the trolled streamers. Some streamer fishermen employ a pumping action of the rod to emulate a darting fish. Some anglers use a "flasher" or "dodger" ahead of their lures to substitute for manual manipulation.

Metal lures and wobblers continue to be very popular baits for spring salmon fishing. The most effective of these lures either resemble a fish or may have a nondescript appearance but display wildly erratic darting action. Another popular early spring bait is a smelt sewed on a snelled hook to resemble a wounded fish when trolled.

As surface temperatures warm to about 65°F, usually in mid-June, salmon often seek deeper, cooler water, and some fishermen follow suit by using heavier rigging and fishing deeper. Some anglers use the same equipment as for early spring fishing but with more weight attached to reach greater depths. A favorite rig for this season is a string of shiny spinners followed by a leader and a sewn smelt or minnow; some anglers prefer earthworms for bait.

As the season progresses through June, July, and August, water temperatures in most lakes become progressively warmer to greater depths. To be successful, anglers must resort to other methods to reach cool water and catch salmon. At this time, many fishermen troll with a lead-core or wire line with various baits attached. As mentioned previously, an increasing number of anglers are using fish finders and downriggers to enhance their late-summer angling efficiency. Some prefer spinners preceding their natural bait or artificial lure, while others simply use a long leader with their bait or lure following. Still or "plug" fishing by anchoring over favored fishing areas is another widely used method of salmon fishing at this time of year. Fishing in deep, cool water using earthworms, a live minnow or smelt, or a piece of "cut bait" will often produce salmon when other methods fail.

During especially cool and rainy summers, surface water temperatures sometimes remain cool throughout the season. When such conditions occur, salmon may remain near the surface and provide "spring-type" fishing with light trolling gear throughout the summer. Salmon may also provide summer fishing when rainy, cool summers produce an abundant flow of cool water in larger rivers and thoroughfares. Some skilled anglers are successful in taking salmon throughout normal summers by surface trolling in very early morning or late evening.

As air and water temperatures begin to cool in September, salmon return to the surface waters and range widely throughout the lake. Trolling, using methods employed in early spring, often produces good fall fishing. Fast September fishing is often enjoyed by trolling or casting flies near tributaries or outlets where salmon gather in preparation for their fall spawning migrations.

Fly fishing can be one of the most fascinating and productive methods for catching salmon when conditions are right, and is a preferred method for river fishing. Hatches of mayflies or other aquatic insects may occur almost anytime during the open water fishing season, and fishing at such times with a dry fly may yield furious action. In lake outlets where "smelt drift" occurs, streamer flies imitating a wounded smelt are often used with good success.

Spin casting has become a popular and effective method of salmon angling. This method is usually most effective in spring and fall when salmon inhabit riffles and pools of streams, rivers, and thoroughfares, or in lakes at the mouths of spawning streams.

In an early reference to ice fishing for salmon, Stillwell and Stanley (1874b) commented, "*They are not as a general rule fished for in the winter through the ice with much success. We have known of exceptions where quite a number have been taken through the ice, but it is our opinion that they resort to the muddy bottoms of very deep waters, and exist in a semi-hibernating state.*" While salmon may be somewhat less active during the winter, the ability of many anglers to catch salmon through the ice, often in large numbers, indicates that the opinion of early Commissioners was not entirely accurate.

Ice fishing for salmon has gained wide popularity with Maine anglers. Technological advances have made ice fishing far more efficient and comfortable than even 20 years ago. Few anglers now venture forth on snowshoes with a pack basket of tip-ups, ice chisel, a bucket of live bait, and a hand-dragged tote sled. Most present-day anglers are equipped with power ice-augers, snowmobiles or all-terrain vehicles, and portable shelters. Some anglers are even equipped with fish finders and global positioning systems to locate and mark salmon concentrations. "Cities" of ice fishing "shacks", "cabins", or "shanties" are common sights on many salmon waters. Nearly all have some sort of stove to keep warm, and some even have bunk beds, tables, chairs, and radios or televisions.

Live smelts are the most popular bait for ice fishing, and they are very effective for salmon, but minnows or night crawlers are also used. Tip-ups remain the most prevalent gear for salmon ice fishing. Tip-ups used for many years by anglers have even been modified for more efficient angling. A battery-operated "automatic jigger", for example, is now on the market. "Jigging" or "bobbing" a natural bait or artificial lure has become an increasingly popular method of ice fishing. Metal lures such as the lead fish, Swedish pimple, or Vike are popular jigging baits. A small piece of fish or earthworm is often attached to the lure. Cut fish, dead smelts, or earthworms are also pre-

Winter angling for salmon is sometimes conducted from rather elaborate and comfortable "ice shacks". (Dave Boucher, MDIFW) ferred natural baits. Anglers have learned through the years that the best way to catch salmon through the ice is to fish a few inches to several feet below the ice, regardless of the gear or bait selected for use.

Fishing Quality and Effort

Standard measures to evaluate fishing quality, or fishing success, are catch per angler hour and catch per angler trip. Catch per angler hour is defined as the average number of fish caught by anglers for each hour of fishing. Catch per angler trip (or catch per day) is the average number of fish caught during each day or part of a day fished. In practice, both of these estimators are usually reported based on numbers of legal fish caught (those above a certain minimum length or within a defined length range). Fishing success varies considerably among anglers, among seasons of the year, among years on the same lake, and among various lakes. Fishing success estimates are also heavily influenced by the severity of fishing regulations on individual waters – that is, as minimum length limits increase, ratios of legal-size fish in the catch generally decline. Average fishing quality reported here incorporates all of these variations.

Season-long angler surveys are routinely conducted on a large number of Maine salmon waters to obtain estimates of fishing effort and success. The number of waters and sampling frequency has increased quite substantially since 1970, when the original edition of this paper was published. The intent of the following discussion is to characterize recent salmon fishing quality and angler use from a variety of Maine waters, including rivers.

Lake Fisheries

The limited number of anglers who participated in early sport fishing for landlocked salmon apparently enjoyed considerable success, judging from the data in Table 45 taken from the first Commissioner's Report (Foster and Atkins 1868). From 1856 to 1858, anglers fishing 2,367 rod-hours in West Grand Lake caught 1,641 salmon, for an average of about 0.70 salmon per rod-hour. It is notable that these salmon averaged only 1.4 pounds in weight.

Recent examples of fishing success experienced by salmon anglers in Maine waters are presented in Tables 46a and 46b. Salmon populations in these waters are comprised of fish of wild origin (e.g. Mooselookmeguntic Lake, Aziscohos Lake, Chain of Ponds), hatchery stocks (e.g. Long Lake, Wassookeag Lake, Parker Pond), or a combination of each (e.g. Rangeley Lake, Moosehead Lake, Sebago Lake). During the 1988 to 2004 period, open water catches of salmon per hour on these lakes averaged 0.072 and ranged from a low of 0.004 to a high of 0.233, and catches per angler trip averaged 0.32 and ranged from 0.01 to 0.92. Ice fishing catches per hour ranged from 0.002 to 0.378 and averaged 0.051 during the same period. Catches per angler trip for ice anglers ranged from 0.01 to 1.98, averaging 0.31.

These data on average catch rates only rarely approach the early figures quoted above. Relative comforts afforded modern anglers and the propensity of many to spend the entire day or weekend fishing, regardless of whether fish are biting, tends to increase the number of unproductive fishing hours and reduce average catch rates. An increase in the number of novice fishermen unskilled in taking salmon likewise lowers the average catch per hour.

The ability of a few skilled anglers to take a high percentage of the total salmon catch is exemplified by data from Eagle Lake in Bar Harbor (Warner and Havey 1985). Because individual anglers were issued identification numbers, it was possible to determine what percentage of the catch was taken by each angler. For winter and summer fisheries combined, 94% of the anglers caught no fish, 5% caught 1 fish, 1% caught 2 fish, and only 0.3% caught 3 or more salmon. The entire salmon catch was taken by about 6% of the anglers. For summer fisheries only, 8% of the anglers took the entire catch, while in winter 5% of the anglers caught all the salmon.

Fishing effort for salmon in Maine lakes varies considerably among lakes and among seasons of the year. The famous salmon lakes such as Rangeley, Moosehead, Sebago, East and West Grand Lakes, and the Fish River Lakes generally receive the most fishing effort, in terms of numbers of anglers per year, probably because anglers

Table 45. Fishing success for landlocked salmon in West Grand Lake, Maine, 1856-1858. Calculations are from data of Foster and Atkins (1868).

Year	Number of rod hours	Number of salmon	Number of salmon/rod hour	Average weight (pounds)	Pounds/ rod hour
1856	810	634	0.78	1.4	1.08
1857	810	432	0.53	1.5	0.80
1858	720	510	0.71	1.4	1.00
1858	27	65	2.41	1.4	3.48
All years	**2,367**	**1,641**	**0.69**	**1.4**	**0.98**

have been exposed to publicity and popular articles about salmon fishing in these waters. However, many lesser-known lakes provide equally good or better salmon fishing than the "name" waters. Fishing effort on most salmon waters is greatest during May and June, declines during the mid-summer months, and increases again during the late-summer and fall periods.

In Maine, fishing effort, or "fishing pressure", is usually reported as the number of angler trips per surface-acre of water per year. Examples of recent estimates of fishing effort during the open water and ice fishing seasons are shown in Tables 46a and 46b. From 1988 to 2004, number of angler trips per acre per year ranged from 0.16 to 4.67 and averaged 1.28 during the open water season. Ice fishing effort ranged from 0.06 to 5.13 trips per acre per year, averaging about 0.77. Per-unit fishing effort is strongly influenced by lake size, with large lakes such as Moosehead Lake (74,890 acres) and Mooselookmeguntic Lake (16,300 acres) showing lower rates compared to smaller waters such as Pierce Pond (1,650 acres) or St. George Lake (1,095 acres).

Trends in fishing effort and success, based on several hundred creel surveys conducted on Maine salmon lakes, are summarized in Table 47. Statewide fishing effort during the open water season increased steadily during the period from 1970 to about 1990, thereafter declining to pre-1970 levels. As of 2000, open water anglers fished Maine salmon lakes at an average rate of about 0.92 angler trips per acre per year. Ice fishing effort peaked during the years following MDIFW's decision to expand winter fishing opportunities in 1978, and then declined steadily. By 2000, ice fishing effort was about 35% of annual effort on those waters open during both seasons. Early samples (1950-1979), particularly for the winter seasons, were heavily dominated by Moosehead Lake, so statewide effort was probably underestimated during that period.

Declining angler use of Maine's salmon fisheries mirrored statewide trends reflected in declining license sales and numbers of anglers (Boucher 2001). Several factors may have contributed to this decline. Biologists in most regions of the state have observed that the "novelty" of ice fishing has waned in favor of other winter activities such as snowmobiling. Poor ice conditions that prevailed during several recent winters in southern and coastal regions negatively affected winter fishing accessibility in those areas. Recent salmon growth problems on several major salmon lakes, including Moosehead Lake and Sebago Lake, reduced fishing effort because stocking rates, and therefore salmon catch rates, were temporarily reduced to rebuild smelt populations (P. Johnson and J. Boland, MDIFW, personal communication). Angler use of salmon fisheries in central Maine was reduced by the collapse of a major fishery in Long Pond (Belgrade) through predation and food competition with northern pike (J. Lucas, MDIFW, personal communication), and from management changes on several lakes that emphasize other coldwater species. In addition, increasingly popular coastal fisheries for striped bass (*Morone saxatilus*) and bluefish (*Pomatomus saltatrix)* probably attracted many anglers away from inland waters.

Despite recent declines in statewide fishing effort, demand on Maine's salmon lakes remains in excess of that observed during the preceding decades, and high rates of angler use continues to be a major factor determining Maine's salmon management strategies (Boucher 2001).

Salmon are exceedingly vulnerable to skilled ice anglers, and we observed a dramatic shift in the annual distribution of catch and harvest toward the winter season on many individual lakes. High winter harvest rates resulted in reduced fishing quality for open water anglers on many waters (Table 47), prompting the establishment of lower bag limits and shortened winter seasons to distribute the catch more equitably while still allowing anglers to enjoy ice fishing opportunity. In some cases, minimum size limits were increased in an attempt to allocate more of the annual catch to summer anglers, or winter trap limits were imposed to reduce the salmon catch by redirecting fishing effort to other species.

Creel survey data suggested that both open water and ice fishing catch rates improved following the imposition of these more restrictive regulations (Table 47). While some of these improvements can be attributed to the regulations, declining angler effort during both seasons, and the propensity of modern anglers to release a significant portion of their catch of legal salmon also may have played an important role. Salmon anglers currently release about 50% and 20% of legal fish during the open water and winter seasons, respectively (Table 47). Any further changes in general law or special regulations will depend on information gathered through constant monitoring of fishing effort, catch rates, and other parameters of winter salmon fisheries.

River fisheries

Riverine salmon fisheries are usually associated with lake spawning runs, either in outlets or in tributary streams. The specific timing of spawning runs, and therefore the timing of the fishery for them, often depends on flows and water temperatures. Most spawning runs commence in September, but there is wide variation among rivers and within the same river annually. Spawning runs can commence as early as late August during cool, wet years, or they can be delayed until October if river flows are low and temperatures remain elevated. In some cases, September fisheries are enhanced by providing "attraction flows"

Table 46a. Angler use and fishing success for landlocked salmon in Maine lakes, 1988-2004. Data are from clerk creel surveys.

OPEN WATER SEASON						
Lake	County	Year	Number of angler trips	Number of angler trips/ acre/year	Catch of legals/ angler trip	Catch of legals/ angler hour
Long Lake	Aroostook	1988	7,070	1.18	0.62	0.115
Long Lake	Aroostook	1994	20,528	3.42	0.28	0.062
Cross Lake	Aroostook	1988	3,405	1.35	0.09	0.020
Cross Lake	Aroostook	1994	3,166	1.26	0.01	0.004
Cross Lake	Aroostook	1996	2,210	0.88	0.08	0.027
Square Lake	Aroostook	1988	7,973	0.98	0.63	0.088
Square Lake	Aroostook	1994	5,771	0.71	0.59	0.097
Square Lake	Aroostook	1996	6,785	0.83	0.48	0.085
Eagle Lake	Aroostook	1994	6,964	1.25	0.34	0.071
East Grand Lake	Washington	1990	28,617	1.78	0.46	0.089
Chesuncook Lake	Piscataquis	1996	4,164	0.16	0.39	0.070
Moosehead Lake	Piscataquis	1996	18,454	0.25	0.36	0.075
Moosehead Lake	Piscataquis	1997	22,983	0.31	0.19	0.050
Moosehead Lake	Piscataquis	1998	21,837	0.29	0.23	0.065
Moosehead Lake	Piscataquis	1999	26,517	0.35	0.23	0.069
Moosehead Lake	Piscataquis	2000	28,068	0.38	0.25	0.066
Moosehead Lake	Piscataquis	2001	25,035	0.33	0.22	0.060
Moosehead Lake	Piscataquis	2002	18,060	0.24	0.22	0.057
Sebec Lake	Piscataquis	1990	5,017	0.74	0.08	0.021
Sebec Lake	Piscataquis	1997	3,351	0.52	0.13	0.039
Pierce Pond	Somerset	1990	5,327	3.23	0.19	0.028
Pierce Pond	Somerset	1995	3,641	2.21	0.17	0.025
Spring Lake	Somerset	1991	1,117	1.47	0.15	0.030
Rangeley Lake	Franklin	1995	14,242	2.37	0.58	0.140
Rangeley Lake	Franklin	1998	15,486	2.58	0.65	0.156
Rangeley Lake	Franklin	2000	13,472	2.25	0.55	0.120
Rangeley Lake	Franklin	2002	15,588	2.60	0.57	0.122
Rangeley Lake	Franklin	2004	12,688	2.15	0.50	0.117
Mooselookmeguntic Lake	Franklin	1991	12,944	0.79	0.43	0.107
Mooselookmeguntic Lake	Franklin	1995	9,580	0.59	0.92	0.233
Mooselookmeguntic Lake	Franklin	1998	6,081	0.37	0.56	0.141
Mooselookmeguntic Lake	Franklin	2002	6,304	0.39	0.24	0.061
Richardson Lake	Oxford	1991	11,552	1.63	0.29	0.054
Richardson Lake	Oxford	1996	7,090	1.00	0.28	0.053
Richardson Lake	Oxford	1998	2,352	0.33	0.06	0.013
Richardson Lake	Oxford	2002	6,882	0.97	0.24	0.053
Aziscohos Lake	Oxford	1991	4,146	0.62	0.66	0.111
Aziscohos Lake	Oxford	1996	6,477	0.97	0.36	0.141
Aziscohos Lake	Oxford	1999	3,703	0.55	0.22	0.046
Aziscohos Lake	Oxford	2002	4,692	0.71	0.83	0.196
Long Pond	Kennebec	1990	11,666	4.30	0.11	0.032
Long Pond	Kennebec	1993	12,686	4.67	0.09	0.025
Auburn Lake	Androscoggin	1994	3,854	1.71	0.11	0.040
Sebago Lake	Cumberland	1994	39,112	1.36	0.24	0.050
Sebago Lake	Cumberland	1995	38,063	1.32	0.11	0.023
Sebago Lake	Cumberland	1996	33,382	1.16	0.07	0.017
Sebago Lake	Cumberland	1998	32,494	1.13	0.15	0.032
Sebago Lake	Cumberland	2000	26,443	0.92	0.30	0.061
			Means±standard error:	**1.28±0.15**	**0.32±0.03**	**0.072±0.007**

Table 46b. Angler use and fishing success for landlocked salmon in Maine lakes, 1989-2004. Data are from clerk creel surveys.

WINTER SEASON

Lake	County	Year	Number of angler trips	Number of angler trips/acre/year	Catch of legals /angler trip	Catch of legals /angler hour
Long Lake	Aroostook	2000	4,498	0.75	0.74	0.110
Long Lake	Aroostook	2001	6,296	1.05	0.46	0.067
Long Lake	Aroostook	2002	4,141	0.69	0.47	0.065
Long Lake	Aroostook	2003	3,641	0.61	0.78	0.110
Cross Lake	Aroostook	2000	684	0.27	0.03	0.005
Cross Lake	Aroostook	2001	908	0.36	0.40	0.059
Cross Lake	Aroostook	2002	536	0.21	0.06	0.008
Cross Lake	Aroostook	2003	489	0.19	0.26	0.034
Square Lake	Aroostook	2000	1,330	0.16	0.96	0.154
Square Lake	Aroostook	2001	1,280	0.16	0.81	0.120
Square Lake	Aroostook	2002	2,305	0.28	1.10	0.160
Square Lake	Aroostook	2003	1,478	0.25	0.84	0.122
Square Lake	Aroostook	2004	2,793	0.34	0.98	0.161
Eagle Lake	Aroostook	2000	1,267	0.23	0.52	0.078
Eagle Lake	Aroostook	2001	1,538	0.28	0.39	0.056
Eagle Lake	Aroostook	2002	1,637	0.29	0.41	0.062
Eagle Lake	Aroostook	2003	1,535	0.28	0.19	0.030
Carr Pond	Aroostook	2000	536	1.76	0.09	0.012
Portage Lake	Aroostook	1994	434	0.18	1.25	0.227
Portage Lake	Aroostook	2000	314	0.13	0.16	0.030
St. Froid Lake	Aroostook	2000	968	0.40	0.20	0.031
St. Froid Lake	Aroostook	2002	1,563	0.65	0.24	0.036
St. Froid Lake	Aroostook	2003	1,753	0.73	0.17	0.026
Glazier Lake	Aroostook	2004	886	0.79	0.02	0.002
East Grand Lake	Washington	1990	7,275	0.45	0.48	0.085
East Grand Lake	Washington	1991	7,223	0.45	0.53	0.102
West Grand Lake	Washington	1992	4,686	0.16	0.24	0.042
Alligator Lake	Hancock	1999	815	0.70	0.07	0.013
Green Lake	Hancock	1990	4,271	1.14	0.04	0.041
Long (Great) Pond	Hancock	1994	671	0.75	0.24	0.049
Phillips Lake	Hancock	1994	1,462	1.77	0.07	0.010
Tunk Lake	Hancock	1994	2,277	1.13	0.07	0.010
Tunk Lake	Hancock	2000	859	0.43	0.05	0.007
Millimagassett Lake	Penobscot	1993	423	0.30	0.32	0.047
Millimagassett Lake	Penobscot	1998	671	0.48	0.33	0.049
Cold Stream Pond	Penobscot	2000	2,612	0.72	0.12	0.025
Wassookeag Lake	Penobscot	1993	1,450	1.37	0.08	0.019
Wassookeag Lake	Penobscot	2000	1,756	1.65	0.10	0.043
Millinocket Lake	Piscataquis	1993	206	0.08	0.61	0.095
Millinocket Lake	Piscataquis	1998	150	0.06	0.92	0.147
Lobster Lake	Piscataquis	1990	920	0.26	0.18	0.024
Lobster Lake	Piscataquis	1991	1,944	0.56	0.09	0.014
Moosehead Lake	Piscataquis	1998	11,052	0.15	0.06	0.009
Moosehead Lake	Piscataquis	1999	11,182	0.15	0.09	0.012
Moosehead Lake	Piscataquis	2000	11,820	0.16	0.07	0.011
Sebec Lake	Piscataquis	1997	2,615	0.38	0.09	0.012
Sebec Lake	Piscataquis	2000	2,640	0.39	0.13	0.018
Hancock Pond	Somerset	2000	293	0.92	0.18	0.041
Spencer Lake	Somerset	1995	578	0.32	0.22	0.050
Spencer Lake	Somerset	2000	477	0.26	0.49	0.106
Swan Lake	Waldo	1996	1,147	0.84	0.13	0.031
St. George Lake	Waldo	1996	1,803	1.65	0.06	0.013
Parker Pond	Kennebec	1999	597	0.39	0.15	0.032
Parker Pond	Kennebec	2000	470	0.31	0.07	0.015
Chain of Ponds	Franklin	1989	1,074	1.53	0.14	0.041
Chain of Ponds	Franklin	1996	647	0.92	0.08	0.024
Chain of Ponds	Franklin	2002	766	1.09	0.09	0.024
Tricky Pond	Cumberland	1993	1,607	5.13	0.05	0.012
Tricky Pond	Cumberland	1994	1,068	3.41	0.01	0.002
Tricky Pond	Cumberland	1995	1,391	4.44	0.14	0.034
			Means±standard error:	**0.77±0.12**	**0.31±0.04**	**0.051±0.006**

Table 47. Trends in fishing effort and success for landlocked salmon in Maine Lakes, 1950-2000. Data are from clerk creel surveys on principal fishery salmon lakes.

Years	Season	Number of surveys	Mean number of trips/acre	Percent of annual effort	Mean number of legals/ angler trip	Mean number of legals/angler hour	Percent legals released
1950-1959	Open water	10	0.34	*	0.26	0.057	No data
1960-1969	Open water	34	0.39	*	0.29	0.057	No data
1970-1979	Open water	25	0.79	73	0.26	0.056	<1
1980-1985	Open water	22	1.50	65	0.23	0.044	7
1986-1990	Open water	58	1.90	60	0.20	0.044	22
1991-1995	Open water	47	1.26	54	0.30	0.070	35
1996-2000	Open water	41	0.92	65	0.25	0.060	52
1970-1979	Winter	23	0.29	27	0.19	0.034	9
1980-1985	Winter	72	0.82	35	0.14	0.025	7
1986-1990	Winter	103	1.27	40	0.18	0.030	7
1991-1995	Winter	86	1.06	46	0.23	0.038	15
1996-2000	Winter	74	0.50	35	0.35	0.059	22

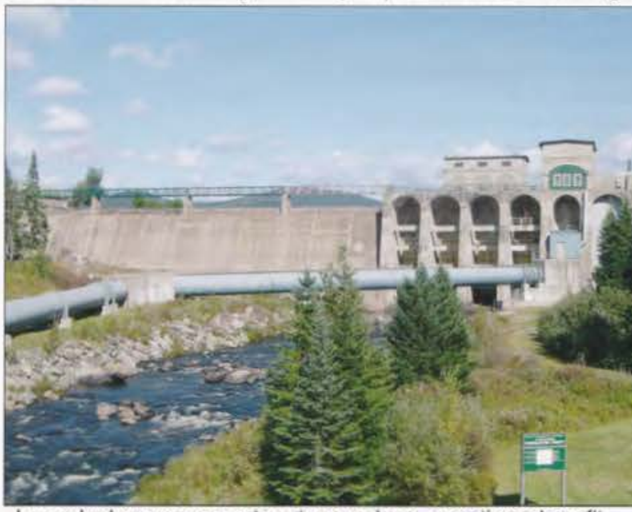
from dams located either upstream or downstream, followed by the release of lower flows to facilitate safe and efficient access for anglers. The Moose River, a major tributary to Moosehead Lake, is an example of where this type of flow management is being used with success (P. Johnson, MDIFW, personal communication).

Salmon that have spawned often linger in rivers through the entire winter before returning to lakes. These fish, termed kelts, provide early-season fisheries in many rivers. Later in the spring, lake salmon commonly enter tributary streams in pursuit of spawning smelts. The timing and quality of these transient fisheries are highly dependent on river flows and smelt abundance.

Several Maine rivers support resident salmon populations that provide season-long fisheries. Fishing quality in these rivers is usually highest during the spring and fall periods, but freshets, either from dam releases or naturally occurring, can draw fish into popular or accessible fishing locations at any time. The most notable fisheries for river-resident salmon occur in the West Branch Penobscot River below Chesuncook Lake, the Kennebec River below Moosehead Lake and Indian Pond, and the Rapid River in western Maine.

Many popular salmon fisheries occur in rivers located below large lake systems that are highly regulated by hydroelectric or water storage dams. Water releases from dams often benefit salmon production because river flows are stabilized, resulting in lower maximum flows and higher summer minimum flows. Natural recruitment may be enhanced below dams if flows are adjusted to maximize nursery or spawning habitat, or if discharges from upstream waters provide cooling temperatures during the critical summer period. Special flow regimes tailored to benefit sport anglers and boaters are sometimes provided in heavily fished rivers.

The importance of dams in maintaining or enhancing riverine salmon populations and the fisheries they support has been most fully recognized during the past few decades. Most dam owners are now required to consider impacts to important fishery resources, and many now monitor fish populations and fisheries as a condition of their operating licenses. This has significantly improved our knowledge of



Large hydropower or water storage dams sometimes benefit salmon and anglers by providing a steady supply of cool water to rivers during the summer months. (Dave Boucher, MDIFW)

Table 48. Angler use and fishing success for landlocked salmon in Maine rivers, 1983-2004. Data are from clerk creel surveys.

River (and reach)	County	Year	Number of angler trips	Number of angler trips/mile/year	Catch of legals/ angler trip	Catch of legals/ angler hour	Percent legals released
W. Branch Penobscot R. (Above Chesuncook L.)	Piscataquis	1983	870	145	0.93	*	75
W. Branch Penobscot R. (Above Chesuncook L.)	Piscataquis	1986	795	133	0.52	*	63
W. Branch Penobscot R. (Ripogenous Dam/Abol Bridge)	Piscataquis	1990	8,781	878	0.42	*	75
W. Branch Penobscot R. (Ripogenous Dam/Abol Bridge)	Piscataquis	1991	9,079	908	0.40	*	76
W. Branch Penobscot R. (Ripogenous Dam/Abol Bridge)	Piscataquis	1992	8,719	872	0.43	*	90
W. Branch Penobscot R. (Ripogenous Dam/Abol Bridge)	Piscataquis	1993	10,230	1,023	0.43	*	81
Kennebec R. (East Outlet)	Piscataquis	1984	*	*	0.50	0.156	37
Kennebec R. (East Outlet)	Piscataquis	1985	*	*	0.83	0.223	55
Kennebec R. (East Outlet)	Piscataquis	1987	*	*	0.56	0.178	72
Moose R.	Somerset	1988	1,331	90	0.87	0.307	88
Moose R.	Somerset	1991	*	*	0.17	0.067	63
Grand Lake S. (September 1 to October 15 only)	Washington	1990	*	*	1.36	0.356	91
Grand Lake S. (September 1 to October 15 only)	Washington	1991	*	*	0.65	0.155	80
Grand Lake S. (September 1 to October 15 only)	Washington	1992	*	*	0.42	0.106	74
Grand Lake S. (September 1 to October 15 only)	Washington	1993	*	*	0.58	0.130	83
Grand Lake S. (September 1 to October 15 only)	Washington	1994	*	*	2.11	0.529	99
Magalloway R. (Below Aziscohos L.)	Oxford	1998	1,579	232	0.08	0.034	86
Magalloway R. (Below Aziscohos L.)	Oxford	1999	1,205	177	0.45	0.188	100
Magalloway R. (Below Aziscohos L.)	Oxford	2002	1,601	235	0.11	0.049	100
Magalloway R. (Below Aziscohos L.)	Oxford	2003	1,819	268	0.14	0.054	91
Magalloway R. (Below Aziscohos L.)	Oxford	2004	1,622	239	0.23	0.072	100
Upper Dam Pool (outlet of Mooselookmeguntic L.)	Oxford	1987	1,881	4,089	0.20	0.098	95
Upper Dam Pool (outlet of Mooselookmeguntic L.)	Oxford	1998	1,836	3,991	0.13	0.043	97
Upper Dam Pool (outlet of Mooselookmeguntic L.)	Oxford	1999	2,618	5,691	0.12	0.046	97
Upper Dam Pool (outlet of Mooselookmeguntic L.)	Oxford	2002	2,265	4,924	0.14	0.051	100
Upper Dam Pool (outlet of Mooselookmeguntic L.)	Oxford	2003	2,809	6,107	0.14	0.049	100
Upper Dam Pool (outlet of Mooselookmeguntic L.)	Oxford	2004	2,092	4,548	0.10	0.033	96
Rapid R.	Oxford	1994	7,830	2,447	0.52	0.131	99
Rapid R.	Oxford	1998	7,035	2,198	1.16	0.321	99
Rapid R.	Oxford	1999	8,728	2,728	0.87	0.160	98
Rapid R.	Oxford	2002	4,926	1,539	0.53	0.154	100
Rapid R.	Oxford	2003	5,435	1,698	0.39	0.114	99
Rapid R.	Oxford	2004	5,101	1,594	0.46	0.134	99
		Means±standard error:		**1,948±432**	**0.51±0.07**	**0.146±0.023**	

the nature and extent of several important riverine salmon fisheries.

A summary of recent estimates of fishing effort and success in some Maine salmon rivers is provided in Table 48. Fishing effort on eight rivers or river reaches surveyed since 1983 ranged from 133 to 6,107 angler trips per mile. Angler use is highly concentrated on several rivers due to the limited number of holding pools accessible to most anglers, and by the seasonal nature of fish availability, which is generally highest during the fall and early spring months. Catch rates, which averaged 0.51 fish per trip and 0.146 fish per hour, were higher than for most lake fisheries, probably because fish are more concentrated and fishing efficiency is greater than for lakes.

Salmon anglers fishing in rivers release a very high portion of their legal catch when compared to lake anglers. Restrictive harvest regulations are imposed on most spawning-run fisheries to minimize hooking-related stress and mortality of gravid fish. For this same reason, fishing is not permitted after September 30 on most salmon rivers. October fishing is permitted on a few rivers where spawning does not occur, or where natural reproduction is not required to sustain the lake population.

The Salmon Catch

Sizes of landlocked salmon taken by anglers in Maine sport fisheries vary considerably among lakes and among years in the same lake. The chief factor influencing size of angled salmon is their growth rate, which varies among lakes depending on habitat quality, the presence or absence of competitors, and smelt abundance. In individual lakes, annual variations in growth rate can be expected because smelt populations fluctuate widely, which in turn may be influenced by the presence of dominant or weak cohorts of salmon or other predator fish such as lake trout. The influence of variable year classes is sometimes most apparent in fisheries maintained by natural reproduction, because environmental conditions for good recruitment may change from year to year. Growth rates of salmon in hatchery-supported fisheries are currently less influenced by differential survival of cohorts. This is because the size and quality, and hence the post-stocking survival, of hatchery salmon have improved quite dramatically since publication of the two earlier editions of this paper. The role of cultured salmon is detailed in another section.

Recent (1990-2004) average sizes of angled salmon in several important lake fisheries are given in Tables 49a and 49b. Size data are separated by season (open water or winter) and by the origin of harvested salmon (hatchery-reared or wild). Average size of harvested salmon in open water fisheries was 17.4 inches and 1.9 pounds. Salmon harvested during ice fisheries averaged 17.0 inches and 1.7 pounds. The statewide annual salmon harvest is currently comprised of about 69% hatchery fish and 31% wild fish. This ratio differs between seasons – the winter harvest is composed primarily of hatchery stocks (78%) and the summer harvest is nearly evenly distributed between hatchery (49%) and wild (51%) fish. This reflects the closure to ice fishing of several large waters that are supported substantially by natural reproduction. Hatchery-reared salmon provide fisheries with a larger average size than wild fish during both seasons.

Estimated total catches and yield to the angler in numbers and pounds per acre per year have been calculated for a large number of salmon lakes (Table 50). These estimates are based on statistical expansion of data from 283 intensive creel surveys conducted on 81 lakes from 1974 to 1999. Mean yield of salmon during the open water seasons was 0.191 fish and 0.344 pounds per acre per year. Yield from winter fisheries averaged 0.112 fish and 0.177 pounds per acre per year. Combining estimates for each season provides a minimum estimate of total annual yield of 0.303 fish and 0.521 pounds per acre. The estimate is minimal because some lakes that were open to fishing during both seasons were only surveyed during one season or the other, and some lakes were closed to winter fishing.

Many of the studied waters support fisheries for other salmonid species, usually lake trout and/or brook trout. Total yield in these lakes, especially those containing lake trout, are ordinarily higher than those supporting only salmon. Lake size and ratios of hatchery salmon in the fishery also appear to be significant factors determining salmon yields (Tables 50 and 51). Highest yields in open water fisheries are in lakes ranging in size from 1,000 to 10,000 surface acres. During the winter season, lakes from 5,000 to 10,000 acres support the highest yields. Lakes supported by high percentages of hatchery stocks clearly provide higher yields to salmon anglers than those where wild fish predominate. DeSandre (1991) suggested that annual yields in excess of 0.300 pounds per acre resulted in the loss of older-age (age V) salmon from fisheries.

The ages at which salmon reach legal length in Maine lakes depend mainly on growth rate and the minimum legal length at which salmon can be taken. The general law length limit for salmon is presently 14 inches, except in certain waters where minimum legal lengths are 12, 16, or 18 inches. With the 14-inch length limit, salmon in most populations become legal at ages ranging from II+ to V+. Where forage is abundant and growth is rapid, it is not uncommon for salmon in stocked fisheries to be recruited by their first winter at large (age II). On average, however, most hatchery-reared salmon attain the 14-inch limit sometime during their second summer at large (age II+). Wild salmon are recruited to 14 inches from 1 to 3 years later than hatchery fish because their growth is slower. Age at recruitment of wild salmon is also dependant on the number of years spent in the stream environment, where growth is much slower than in lakes.

Statewide summaries of age composition of the salmon harvest in populations supported by hatchery stocks or by natural reproduction are given in Table 52. The summer harvest of hatchery-reared salmon is presently dominated by age II+ to IV+ fish. Age structure of hatchery salmon in the winter harvest is heavily dominated by age III fish, but age II and age IV salmon contribute significantly as well. Age IV+ to VI+ salmon provide the bulk of the harvest from wild populations during both seasons. The contribution of age V+ and older salmon is greatest in waters where the growth rate is slow or where harvest rates are low.

Fishery Biologist Francis Brautigam holds a large male landlocked salmon sampled from Auburn Lake, Androscoggin County, in 2004. (Jim Pellerin, MDIFW)

We observed a shift in the statewide salmon harvest to younger cohorts after about 1980 (MDIFW, unpublished data). This was particularly evident in lakes supported by hatchery stocks, but wild fish were also affected. Age IV and older hatchery salmon comprised from 30% to 50% of the harvest from 1970 to 1979, but these cohorts presently contribute only about 20% of anglers' catches. Much of the observed shift toward younger cohorts in the harvest was probably attributable to faster growth rates, earlier recruitment to legal size, and increased rates of higher exploitation, particularly during the winter season. After 1990, the prevalence of older-age hatchery salmon appeared to stabilize, and in the case of wild fish, ratios of age V and older salmon increased. Because salmon growth rates remained relatively stable in most waters during that period, this suggested that declining angler use and harvest rates, discussed previously, provided enhanced escapement to older ages.

Several Maine studies involving recapture of tagged salmon have provided information on the rate of exploitation by anglers of salmon in the sport fisheries. At the Fish River Lakes, Warner (1959) found that in 3 years anglers recaptured a minimum of 28% of 811 salmon tagged on the spawning grounds. At Cold Stream Pond, anglers caught 29% of 105 salmon tagged on the spawning run (Bond and DeRoche 1956). At Schoodic Lake (Havey and Andrews 1973), 34% of 276 salmon (mostly mature) tagged in the fall of 1964 were caught by anglers in the 1965 fishery. The recovery of tagged fish by anglers in 1965 ranged from 22% (age IV) to 41% (age III). At Sebago Lake, only 3.5% of 2,175 salmon tagged on the spawning run from 1960 to 1963 were reported caught by anglers through the 1964 fishing season (DeRoche 1976). This low recovery was attributed to an unusually high mortality rate of adult salmon.

In Rangeley Lake, 428 salmon were tagged on spawning runs at Dodge Pond Stream and Long Pond Stream in 1964-66. A minimum estimate of recovery was 23%, all from Rangeley Lake itself. From 1966-69, 844 salmon were tagged at Rangeley Lake Outlet; a minimum of 18% was eventually recaptured by anglers (DeSandre et al. 1977). For Moosehead Lake, AuClair (1982) estimated a mean rate of exploitation of 33% for wild salmon and 38% for hatchery-reared salmon. Except for Sebago Lake, where pollution by the pesticide DDT was a problem (Anderson and Everhart 1966), these studies indicate a moderately high exploitation of post-spawning adult salmon by anglers. We believe exploitation rates have declined since publication of these studies, because fishing regulations have become stricter and release rates of legal fish have increased. However, recent exploitation studies have not been conducted to verify this.

Fishing Regulations

Current general law fishing regulations for landlocked salmon have changed only slightly since publication of the most recent edition of this paper (Warner and Havey 1985). The daily bag limit on lakes in Washington County was reduced in 1990 from three to two fish in order to conform to the statewide general rule. The rule prohibiting possession of more than 7.5 pounds of salmon in combination with other salmonids was abolished in 1998; this rule was deemed unnecessary because bag limits on all salmonids were progressively reduced to only one or two

Maine landlocked salmon typically range from 16 to 20 inches in length and 1.5 to 3 pounds in weight. (Rick Jordan, MDIFW)

Table 49a. Average sizes of landlocked salmon harvested in Maine sport fisheries, open water seasons, 1990-2004.

Water	County	Origin of fish	Year	Number of salmon	Average length (inches)	Average weight (pounds)
Long Lake	Aroostook	Hatchery	1994	61	16.3	1.6
Square Lake	Aroostook	Hatchery	1990	32	15.9	1.4
Square Lake	Aroostook	Hatchery	1991	41	17.3	1.8
Square Lake	Aroostook	Hatchery	1994	40	16.5	1.7
Square Lake	Aroostook	Hatchery	1998	59	16.5	1.4
East Grand Lake	Washington	Hatchery	1990	276	16.3	1.5
Moosehead Lake	Piscataquis	Hatchery	1994	51	15.7	0.9
Moosehead Lake	Piscataquis	Hatchery	1996	54	15.6	1.1
Moosehead Lake	Piscataquis	Hatchery	1998	47	16.5	1.4
Pierce Pond	Somerset	Hatchery	1999	30	18.5	2.0
Rangeley Lake	Franklin	Hatchery	1998	66	17.1	1.7
Rangeley Lake	Franklin	Hatchery	2000	40	19.5	2.7
Rangeley Lake	Franklin	Hatchery	2002	49	19.2	2.5
Rangeley Lake	Franklin	Hatchery	2004	28	19.4	2.9
Richardson Lake	Oxford	Hatchery	1991	26	16.4	1.4
Richardson Lake	Oxford	Hatchery	1996	32	17.2	1.7
Long Pond	Kennebec	Hatchery	1990	102	17.5	1.7
Long Pond	Kennebec	Hatchery	1993	29	18.3	2.2
Auburn Lake	Androscoggin	Hatchery	1992	104	17.8	2.3
Auburn Lake	Androscoggin	Hatchery	1994	38	17.6	2.2
Auburn Lake	Androscoggin	Hatchery	1999	39	20.2	3.0
Thompson Lake	Oxford	Hatchery	1991	82	18.1	2.5
Thompson Lake	Oxford	Hatchery	1992	99	18.5	2.7
Thompson Lake	Oxford	Hatchery	1995	352	18.4	2.0
Sebago Lake	Cumberland	Hatchery	1990	380	20.6	3.2
Sebago Lake	Cumberland	Hatchery	1991	171	20.6	3.1
Sebago Lake	Cumberland	Hatchery	1992	193	19.8	2.5
Sebago Lake	Cumberland	Hatchery	1994	50	18.8	2.0
Square Lake	Aroostook	Wild	1994	36	16.5	1.5
Square Lake	Aroostook	Wild	1996	26	16.9	1.3
Square Lake	Aroostook	Wild	2003	27	16.7	1.6
East Grand Lake	Washington	Wild	1990	52	16.9	1.7
Moosehead Lake	Piscataquis	Wild	1990	133	16.8	1.4
Moosehead Lake	Piscataquis	Wild	1991	45	16.6	1.4
Moosehead Lake	Piscataquis	Wild	1992	78	16.4	1.3
Moosehead Lake	Piscataquis	Wild	1993	70	16.2	1.2
Mooselookmeguntic Lake	Franklin	Wild	1991	79	16.9	1.7
Mooselookmeguntic Lake	Franklin	Wild	1994	108	17.3	2.0
Mooselookmeguntic Lake	Franklin	Wild	1995	87	16.9	1.7
Mooselookmeguntic Lake	Franklin	Wild	1998	81	17.1	1.6
Mooselookmeguntic Lake	Franklin	Wild	1999	72	18.0	2.0
Mooselookmeguntic Lake	Franklin	Wild	2001	37	17.5	1.8
Mooselookmeguntic Lake	Franklin	Wild	2002	41	17.4	1.9
Mooselookmeguntic Lake	Franklin	Wild	2003	49	17.0	1.6
Mooselookmeguntic Lake	Franklin	Wild	2004	29	15.8	1.3
Aziscohos Lake	Oxford	Wild	1991	40	15.6	1.3
Aziscohos Lake	Oxford	Wild	1993	56	15.5	1.2
Aziscohos Lake	Oxford	Wild	1996	90	16.5	1.6
Aziscohos Lake	Oxford	Wild	1999	52	17.0	1.7
Aziscohos Lake	Oxford	Wild	2002	46	17.2	1.7
Mean of means±standard error for: Hatchery salmon					**17.9±0.3**	**2.0±0.1**
Wild salmon					**16.8±0.1**	**1.6±0.1**
All salmon					**17.4±0.2**	**1.9±0.1**

Table 49b. Average sizes of landlocked salmon harvested in Maine sport fisheries, winter seasons, 1990-2004.

Water	County	Origin of fish	Year	Number of salmon	Average length (inches)	Average weight (pounds)
Long Lake	Aroostook	Hatchery	2001	185	18.0	2.3
Long Lake	Aroostook	Hatchery	2002	68	18.9	2.5
Long Lake	Aroostook	Hatchery	2003	190	17.0	1.9
Long Lake	Aroostook	Hatchery	2004	72	18.2	2.2
Cross Lake	Aroostook	Hatchery	1998	33	16.5	1.4
Square Lake	Aroostook	Hatchery	2001	101	16.6	1.6
Square Lake	Aroostook	Hatchery	2002	112	16.3	1.3
Square Lake	Aroostook	Hatchery	2003	93	16.6	1.6
Square Lake	Aroostook	Hatchery	2004	112	16.7	1.5
Pleasant Pond	Aroostook	Hatchery	1993	36	18.8	2.7
Pleasant Pond	Aroostook	Hatchery	1995	56	19.5	2.7
Millimagassett Lake	Penobscot	Hatchery	1998	37	18.0	1.7
Millimagassett Lake	Penobscot	Hatchery	2003	32	17.0	1.5
East Grand Lake	Washington	Hatchery	1990	700	16.7	1.5
East Grand Lake	Washington	Hatchery	1991	705	16.5	1.5
Cold Stream Pond	Penobscot	Hatchery	1994	38	17.4	1.8
Duck Lake	Hancock	Hatchery	1992	62	19.3	2.5
Duck Lake	Hancock	Hatchery	1997	48	17.9	1.8
West Lake	Hancock	Hatchery	1996	68	18.6	2.3
West Lake	Hancock	Hatchery	2002	50	17.3	1.6
Alligator Lake	Hancock	Hatchery	1992	67	17.4	1.8
Green Lake	Hancock	Hatchery	1990	31	15.8	1.2
Green Lake	Hancock	Hatchery	1991	42	16.7	1.5
Branch Lake	Hancock	Hatchery	1990	73	16.3	1.3
Branch Lake	Hancock	Hatchery	1991	35	17.2	1.5
Swan Lake	Waldo	Hatchery	1994	53	16.3	1.4
Swan Lake	Waldo	Hatchery	1996	61	16.6	1.8
Parker Pond	Kennebec	Hatchery	1991	29	16.6	1.3
Parker Pond	Kennebec	Hatchery	1992	36	16.4	1.3
Parker Pond	Kennebec	Hatchery	2001	26	17.5	1.9
Spencer Lake	Somerset	Hatchery	2000	58	15.2	1.0
Clearwater Pond	Franklin	Hatchery	1990	86	15.7	1.4
Thompson Lake	Oxford	Hatchery	1996	30	19.0	2.6
Square Lake	Aroostook	Wild	1998	32	16.8	1.6
Square Lake	Aroostook	Wild	2002	47	16.8	1.4
Square Lake	Aroostook	Wild	2003	32	17.1	1.6
Square Lake	Aroostook	Wild	2004	50	17.0	1.6
Eagle Lake	Aroostook	Wild	2001	52	15.6	1.1
Eagle Lake	Aroostook	Wild	2002	37	15.4	1.1
St. Froid Lake	Aroostook	Wild	2003	66	15.3	1.0
Moosehead Lake	Piscataquis	Wild	1990	241	16.9	1.4
Moosehead Lake	Piscataquis	Wild	1991	219	16.8	1.4
Big Wood Pond	Somerset	Wild	1991	26	15.8	1.2
Indian Pond	Somerset	Wild	1998	30	16.3	1.4
	Mean of means±standard error:			Hatchery salmon	17.2±0.2	1.8±0.1
				Wild salmon	16.3±0.2	1.4±0.1
				All salmon	17.0±0.2	1.7±0.1

Table 50. Estimated yield of landlocked salmon to anglers in Maine lakes by season and lake surface area, 1974-1999.

Surface area (acres)	Open water fisheries: Number of lakes surveyed	Number of surveys	Yield/acre/year: Number	Pounds	Winter fisheries: Number of lakes surveyed	Number of surveys	Yield/acre/year: Number	Pounds
Less than 1,000	2	2	0.205	0.397	18	53	0.108	0.177
1,000 to 5,000	6	22	0.244	0.446	32	120	0.104	0.157
5,001 to 10,000	7	16	0.247	0.406	9	36	0.163	0.272
Over 10,000	4	23	0.099	0.199	3	11	0.050	0.081
All waters±SE	**19**	**63**	**0.191±0.027**	**0.344±0.051**	**62**	**220**	**0.112±0.008**	**0.177±0.014**

Table 51. Estimated yield of landlocked salmon to anglers in Maine lakes by percentage of hatchery fish in the catch, 1974-1999.

Percent hatchery fish	Open water fisheries: Number of surveys	Yield/acre/year: Number	Pounds	Winter fisheries: Number of surveys	Yield/acre/year: Number	Pounds
Less than 25%	11	0.098	0.154	23	0.035	0.053
25% to 50%	16	0.116	0.218	27	0.068	0.093
51% to 75%	9	0.163	0.264	29	0.107	0.152
Over 75%	27	0.282	0.523	141	0.134	0.218

Table 52. Age group composition of landlocked salmon harvested from Maine lakes, 1990-2002.

Season	Origin of fish	No. lakes surveyed	Numbers and (percentages) of salmon in age group: I-I+	II-II+	III-III+	IV-IV+	V-V+	VI-VI+	VII-VII+	VIII-VIII+	IX-IX+
Open water	Hatchery	23	1	392	723	204	95	14	3	0	0
			(<1)	(27)	(51)	(14)	(7)	(1)	(<1)	(0)	(0)
Open water	Wild	13	0	1	33	178	403	293	130	36	13
			(0)	(<1)	(3)	(16)	(37)	(27)	(12)	(3)	(1)
Winter	Hatchery	51	0	718	4,409	866	236	22	9	1	0
			(0)	(11)	(70)	(14)	(4)	(<1)	(<1)	(<1)	(0)
Winter	Wild	29	0	0	32	211	213	75	10	1	0
			(0)	(0)	(6)	(39)	(39)	(14)	(2)	(<1)	(0)

fish on most waters. River fishing was extended through September 30 in 1988, except that after August 15 fishing was restricted to artificial lures with a one fish bag limit. Catch and release fishing is now permitted until November 30 on many salmon lakes where significant natural reproduction of salmon does not occur.

A summary of current general law rules for salmon fishing is provided in Table 53. The opening date of April 1 in waters naturally free of ice permits limited early-season fishing in southern and central Maine lakes in years of early ice-out. However, in most years the ice cover does not leave southern and central Maine lakes until mid or late April and northern Maine lakes until early or mid-May. Thus, the effective open water fishing season for salmon can be as much as a month shorter in northern than in southern Maine waters. Nevertheless, it is doubtful that the shorter season in northern counties has much effect in reducing total salmon harvest there.

The closing date of September 30 for lakes was presumably chosen to prevent fishing of salmon spawning concentrations. This closing date prevents fishing of salmon when spawning is actually taking place, but salmon reaching spawning condition, and congregating in the vicinity of their spawning grounds, are frequently caught in sizeable numbers from 4 to 6 weeks before actual spawning occurs. Imposition of an artificial lures restriction and a reduced bag limit after August 16 in rivers provides some additional protection to salmon that have made these early migrations to spawning grounds. Natural reproduction does not support the salmon fisheries in most southern, central, or eastern Maine counties, so extension of the fishing season through November 30 on many of these lakes provides additional fishing opportunities without jeopardizing the fishery.

The ice fishing season of January 1 to March 31 was established in 1978 to provide additional winter recreational opportunity. Statewide bag limits were reduced concurrently to promote the fair distribution of the catch between seasons. The total annual salmon harvest increased on some lakes, and the seasonal distribution of the harvest shifted quite dramatically from summer anglers to winter anglers on many others (DeSandre 1986 and 1991, and Boucher 1996). Shortened winter seasons were later imposed on several lakes in an attempt to allocate fishing effort and harvest more equally between the two seasons. This strategy, which was often employed in combination with reduced winter trap limits, was successful on several lakes. On others, the objectives were not met because winter fishing effort remained too high for even modest reductions in winter harvest to occur (e.g. Boucher 1988). Reduced winter seasons are currently in effect on 13 Maine lakes, and their effectiveness is continually evaluated through intensive creel surveys.

The general law limit of 14 inches for salmon was established to permit salmon to approach spawning size and perhaps spawn once before being caught by the angler. This length limit, however, is only partially effective in accomplishing its objective. The scales of salmon caught by anglers in Square Lake in 1954 were examined for evidence of past spawning, recognizable either by spawning checks formed by repaired scale growth (Warner 1971) or marginal or surface resorption as a result of sexual maturity the previous fall. Of 435 salmon from Square Lake, 23% showed evidence of having spawned. Cooper (1940) found that 24% of 349 salmon from western Maine lakes had spawned previously. Of 2,122 salmon examined from five of the Fish River Lakes (1957 to 1959) only 14% showed evidence of previous spawning (Warner and Fenderson 1963).

Table 53. General law fishing regulations for Maine landlocked salmon (2005).

Water type	Season dates		Bag and possession limit	Minimum length (in)	Terminal tackle	Number of lines	
	Open water	Winter				Open water	Winter
Lakes	April 1 to September 30[1]	January 1 to March 31	2	14	Single baited hook and line, artificial flies, lures, or spinners	2	5
Rivers	April 1 to September 30[2]	Closed	2	14	Same as lakes	2	Closed

[1] Lakes in Androscoggin, Cumberland, Kennebec, Knox, Lincoln, Sagadahoc, Waldo, and York Counties are open to catch and release fishing from October 1 to November 30.

[2] Between August 16 and September 30, rivers are restricted to the use of artificial lures and a daily bag limit of one fish.

These facts notwithstanding, it has been our observation that sufficient spawning escapement occurs regularly in Maine's important wild salmon populations.

The 14-inch minimum length limit in conjunction with a daily bag limit of two fish remains the general law rule on Maine salmon lakes (Table 53). Lakes managed under the general law exhibit a wide range of physical, chemical, and biological characteristics. This regulation is applied in a variety of management situations, but is most often used for populations that exhibit moderate growth rates, and where it's desirable to maximize returns of stocked salmon to anglers. The general law is also applied to most wild fisheries to provide at least some escapement to spawning size, or to encourage harvest of abundant cohorts.

Adjustments of minimum size limits often provide an effective means of manipulating salmon population structure to restore satisfactory growth rates and fishing quality. For example, deterioration of the Square Lake salmon fishery from 1954 to 1961 was attributed to a decreased growth rate and deferred entry into the fishery from age III in 1954 to ages IV and V in 1961 (Warner and Fenderson 1963). A large part of the salmon population was invulnerable to harvest, as evidenced by the change in proportion of sublegal fish released by anglers. Total reported catch of both legal and sublegal salmon was about the same in 1954 and 1961, but only 49% were sublegal in 1954, while 89% were sublegal in 1961. A 12-inch length limit was established on Square Lake in 1964 to allow harvest of the same age groups vulnerable with the 14-inch limit in 1954, but not of legal size in 1961 because of a slower growth rate.

To evaluate possible effects of a reduced length limit on the Square lake salmon fishery, Warner and Incerpi (1969) operated creel surveys in 1964-67. The reduction in the length limit on salmon from 14 inches to 12 inches apparently achieved most of the desired results. Fishing success generally improved, and an increased harvest of 12 to 13.9-inch salmon permitted more salmon to be caught at younger ages, when they were most abundant. Growth rate and average size of salmon increased markedly, which was at least partly attributable to an increased harvest of younger salmon. The apparent abundance of smelts, as reflected by their utilization by salmon, may have also been a factor contributing to improved salmon growth. The increased salmon harvest may have favored recovery of the smelt population. The effects of the 12-inch limit on salmon fisheries of other Aroostook County lakes were detailed by Havey and Warner (1970).

Special fishing regulations, such as the 12-inch limit described above, have been implemented on a large number of Maine salmon fisheries. Special regulations are imposed to better reflect the growth and size potential of individual salmon populations, or to address the desires and expectations of certain salmon anglers, such as those seeking "trophy" fisheries. A summary of special length and bag limit rules currently applied to Maine salmon fisheries is provided in Table 54. Biological characteristics often exhibited by salmon populations managed with these special rules, current guidelines for their use and some recent examples of where they have been applied are provided below.

Table 54. Summary of special minimum length and bag limit regulations for Maine salmon lakes, 2004-2005.

Regulation category (minimum size, daily bag limit)	Number of lakes during the:	
	Winter season	Open water season
12 inches, 2 fish	5	7
16 inches, 2 fish	3	2
14 inches, 1 fish	16	22
16 inches 1 fish	6	7
18 inches, 1 fish	1	1
20 inches, 1 fish	1	1
12 inches, 2 fish, only one over 16 inches	0	3
14 inches, 2 fish, only one over 16 inches	1	1
14 inches, 2 fish, only one over 18 inches	3	3
14 inches, 3 fish, only one over 18 inches	1	1
16 to 20-inches protected slot, 1 fish	2	2
Totals (and percent) of all lakes with principal salmon fisheries[1]	**39 (33%)**	**50 (28%)**

[1] Includes only those open to fishing.

- The 12-inch, 2 fish rule, the most liberal regulation applied to salmon, is intended to maximize harvest in waters with wild salmon that are slow-growing and exhibit high rates of annual recruitment. A recent application of this regulation occurred at Eagle Lake (Fish River Chain), where several large cohorts of wild salmon compromised the growth rates and condition of all the lake's smelt predators. This regulation was also imposed on Pond in the River and the Rapid River in western Oxford County to reduce competitive interactions between native brook trout and a large wild salmon population (Boucher 2005).

- One-fish daily bag limits are used in conjunction with the general law length limit, or with higher length limits, to achieve a variety of management objectives. They are directed primarily at salmon populations exhibiting above-average growth potential, but high exploitation rates limit the average size of the catch and numbers of older-age fish. They are also used to reallocate the catch from winter to summer fisheries. The highest minimums are applied to hatchery-supported populations where growth rates are normally very good and can be quickly manipulated with adjustments in stocking rates. High minimum lengths do not appear to be suitable for most waters supported by natural reproduction. For example, imposition of a 16-inch minimum and a 1-fish daily bag limit at Chesuncook Lake was partially responsible for an increase in salmon population size and a dramatic decline in salmon growth rates and body condition (Roy 1999). High minimum lengths for wild salmon are most appropriate where annual recruitment is very low and growth is very good. Lobster Lake in Piscataquis County is an example where a 20-inch length limit, in conjunction with line limits and a short winter season, has maintained fishing quality in a wild salmon population (P. Johnson, MDIFW, personal communication).

- Various "modified slot limits" are currently being evaluated on several salmon waters. These usually include a 2-fish bag limit with either 12 or 14-inch minimums, but harvest of fish over 16 or 18 inches is limited to one fish per day. The 12-inch minimum rule, with one fish over 16 inches permitted, is applied where it's desirable to maximize harvest opportunities, and yet provide added protection to fish that live long enough to achieve an attractive size. These include waters with wild populations exhibiting high recruitment and slow growth, but with demonstrated capacity to provide a few large, older-age fish. Restricting harvest of older-age fish may provide important genetic benefits to wild populations as well.

  The 14-inch minimum rule, with one over 16 or 18 inches, is applied to hatchery or wild populations that exhibit good growth potential and are capable of supporting significant numbers of older age fish. In these lakes, the average size of the catch is limited either by high exploitation rates, by reduced growth resulting from high release rates of younger hatchery cohorts (or dominant year classes in wild fisheries), or by a combination of both factors. This regulation is designed to redirect harvest from older, larger fish to the younger, more abundant cohorts that consume large numbers of smelts. This would have the effect of maintaining adequate growth where angler release rates are high, or where recruitment is variable. Additional benefits, depending on the water, may be improved age and size structure, a better distribution of the catch of salmon over 16 or 18 inches, and re-allocation of larger, winter-harvested fish to the summer fishery.

  Preliminary assessments of these "one-over" slot limits suggest that objectives are being only partially achieved. There was initial improvement in salmon age structure, growth rates were maintained or enhanced, and catch distribution among anglers of larger salmon was improved on some waters. On these same waters and others, growth and the catch of older-age salmon subsequently declined, probably because anglers resisted increasing their harvest of smaller salmon in favor of "holding out" for their single larger fish. Emphasizing harvest of younger cohorts remains an appropriate objective on these waters, so biologists have increased public education efforts in this regard. More liberal harvest rules for smaller salmon are also being considered.

- A protected slot limit of 16 to 20 inches, combined with a 14-inch minimum length and a 1-fish bag limit, is currently being evaluated at Tunk Lake and Alligator Lake, both located in Hancock County. The intent of this regulation is to provide fisheries for "trophy-size" salmon by protecting younger cohorts until they achieve a size of 20 inches and about 3 pounds. Salmon are stocked at low rates in both lakes to maintain adequate growth rates, so catch rates are slow compared to most salmon fisheries. The regulation has fostered a satisfactory fishery for slot-size fish, but numbers of large salmon (over 20 inches) have remained small during most years, perhaps due to high mortality of slot-size fish released during the winter season. Despite the slow fishing for salmon of all sizes, the regulation has been fairly well received by anglers (Brokaw 2000).

  Maximum size limits, whereby all fish above a prescribed length are released, are not currently used in salmon fisheries. This is due primarily to social rather than biological reasons. The opportunity to harvest a very large salmon appeals to many anglers, even if their likelihood of catching one is small. Knowing they cannot keep a large salmon reduces the quality of the fishing experience for these anglers.

  Maximum size limits may provide benefits to wild salmon where brood stocks are threatened, such as in highly exploited populations with low recruitment. Maximum length limits may also be appropriate where recruitment is high or variable. In these cases, emphasizing harvest of smaller fish "thins out" large cohorts and reduces intraspecific food competition. Growth rates are maintained, as is the availability of large fish above the length limit. This same principle could be applied to develop "trophy fisheries" in waters supported by hatchery fish.

Hooking mortality and injuries

Hooking mortality

Open water angling for landlocked salmon is permitted with a single baited hook and line, or with artificial lures or flies with no specified number, type, or size of hooks; two lines are allowed. These regulations appear to be satisfactory, except that concern has been expressed by both fishery biologists and anglers about possible hooking mortality of sublegal salmon caught on worms and multiple-hooked artificial lures (Havey and Warner 1970). This concern gradually led to a proliferation of special gear restrictions on salmon waters.

In 1972, a detailed study was initiated to evaluate hooking mortality of salmon caused by commonly used angling methods under various environmental conditions. The study was designed to assess hooking mortality:

1. In hatcheries in spring and fall (Warner 1976, 1979);
2. In a lake in spring and fall (Warner 1978b); and
3. In a river nursery area in spring (Warner and Johnson 1978).

Salmon were angled to evaluate mortality caused by hooking with four gear types at the Casco and Grand Lake Stream hatcheries in spring, 1976-78 (Table 55).Overall, mortality of fish hooked on all gear was only 5%, and ranged from 2 to 8% during 3 years; only one control fish (0.3%) died.Mortality of hooked fish was significantly greater than that of (seined) controls, strongly indicating that death was caused by hooking. Studies at the Enfield station in fall 1972-74 were done by fishing with the same four gear types as in spring studies. Mortality from hooking injuries (3.3%) was again significantly greater than that (0.3%) of controls.

In spring and fall, 1973-76, we carried out experiments at Big Bennett Pond in Guilford. Experimental anglers caught salmon by trolling with hardware lures (wobblers) and tandem-hook streamer flies (Table 55). During 4 years of spring sampling, 18% of angled salmon died after hooking; only 4% of the control (trapnetted) fish died. In fall, 8% of hooked and 2% of control fish died during the 5-day holding period. Mortalities of both spring and fall-angled fish were significantly greater than those of controls.

The East Outlet of Moosehead Lake was the study site for angling experiments in a river nursery area in spring, 1975-77. This part of the study was designed to compare salmon mortalities caused by hooking with worms and flies, two of the most popular and controversial gears. Of 177 fish caught on both flies and worms, 22% died after hooking. All control fish caught in the fishway trap at East Outlet survived.

Mortalities of salmon caught on all gears in spring studies in a lake (18%) and in hatcheries (5.1%) were significantly greater than hooking mortalities in the fall (lake: 8%, hatchery: 3.3%). Lower mortalities in the fall may be associated with better physical condition of fish, and with generally

Table 55. Mortality of landlocked salmon caught on various gears and released in Maine hooking studies, 1972-1978.

Location (season)	Hardware lure (Treble-hook)		Hardware lure (Single-hook)		Flies (Treble-hook)		Flies (Single-hook)		Worms (Single-hook)		Controls[1]	
	Number caught	Percent mortality	Number caught	Percent mortality	Number caught	Percent mortality	Number caught	Percent mortality	Number caught	Percent mortality	Number caught	Percent mortality
Hatchery (spring)	302	6.0	300	4.6	*	*	319	4.1	300	5.7	300	0.1
									56[2]	57.0	300	0
									50[3]	90.0		
Hatchery (fall)	300	0.3	300	2.7	*	*	300	4.6	300	5.7	300	0.3
Lake (spring)	55	9.9	42	20.0	23	35.0	29	17.0	*	*	122	4.0
Lake (fall)	61	7.0	53	9.0	16	13.0	23	4.0	*	*	122	4.0
River (spring)	*	*	*	*	*	*	77	4.0	100	35.0	74	0

[1] Un-hooked fish caught by trapping or netting.
[2] Intentionally deep-hooked; hook left in.
[3] Intentionally deep-hooked; hook removed.

decreasing water temperatures and decreasing metabolic rate and physical activity.

Hardware lures commonly used by Maine salmon anglers while trolling or spin casting, especially in spring and fall, were used as test gears in lake and hatchery experiments. Wobblers were equipped with either single or treble hooks to permit comparison of hooking mortality. Treble hooks are often condemned by anglers who believe that they cause more hooking mortality than single hooks. In spring hatchery studies, we found no significant difference in salmon mortality caused by treble-hook (6.0%) and single-hook hardware (4.6%). In fall hatchery studies, treble-hook wobblers caused significantly less mortality (0.3%) than did single hook wobblers (2.7%). In lake studies (combined spring and fall samples), trolled treble-hook hardware caused no significantly greater mortality (8%) than did single-hook lures (15%).

We evaluated salmon hooking mortality caused by trolled tandem-hook Maine streamer flies (single or treble rear hook) during our lake studies (Table 55). No significant difference was found between mortalities caused by all hardware lures and all streamer flies (single and treble hook types grouped). All trolled treble-hook gears combined (lures and flies) did not cause a significantly higher mortality than did all single-hook gears, either in spring or in fall. The results of these studies strongly indicate that special regulations prohibiting use of cast or trolled treble-hook lures serve no useful purpose.

Regulations restricting angling methods to "fly fishing only" have become widely established on many of Maine's salmon and trout waters. Reasons most often cited by those favoring this restriction include: limiting spread of competing bait fishes; higher sporting quality of fly fishing; reduction in fishing pressure by prohibiting fishing by anglers who prefer other methods; and lower hooking mortality of released fish. Part of our study was designed to test the validity of the last reason, which assumes that fly fishing causes less hooking mortality than other methods, especially worm fishing.

In our studies, salmon mortality caused by hooking with flies and worms was measured in hatcheries in the spring and fall and in a river in spring. Hooking mortality of fly-caught and worm-caught salmon in hatcheries was nearly identical in spring and fall:

		Percent mortality	
Study location	Season	Flies	Worms
Hatchery	Spring	4.1	5.7
Hatchery	Fall	4.6	5.7
River	Spring	4.0	35.0

Using more typical angling techniques in spring river studies, however, 35% of worm-hooked salmon and only 4% of fly-hooked fish died after being hooked and released.

Higher mortality of worm-hooked salmon in the wild was clearly the result of different angling techniques used, and possibly differences in fish size. Salmon caught from hatchery raceways were smaller and usually visible to anglers. Consequently, they were usually hooked superficially in the jaws or mouth soon after accepting the bait. Angling techniques used in the river were more typically variable. Some anglers set the hook almost immediately upon receiving a strike, while others allowed the fish to ingest the bait more deeply, resulting in hook penetration of the throat, heart or other vital areas. This resulted in greater mortality.

Several studies on salmonids in other states have shown that fish hooked in certain anatomical areas (e.g. heart, gills, liver, throat) are much more likely to die from injuries caused by hooking than those hooked superficially. We recorded anatomical hooking sites for all salmon caught in lake and river studies and for salmon that died in hatchery studies to evaluate effects on hooking location.

In lake studies using hardware lures and tandem-hook streamer flies, 61% of the salmon were hooked in the jaws, 16% in the mouth, 6% in the gills, and 6% in the eyes. None was hooked in the throat or stomach. Mortality of gill-hooked fish (63%) was significantly greater that that of fish hooked in the mouth area. Mortality of jaw-hooked fish was significantly less than that of fish hooked in the mouth. The proportion and subsequent mortality of fish hooked in each anatomical location differed little among four gear types, two hook types, (single and treble), or two lure types (flies and hardware). There was no indication that any particular gear, hook, or lure type was more likely to hook fish in vital anatomical locations.

In river studies, nearly all of the fly-caught salmon were hooked either in the jaws or mouth, resulting in low mortality (4%). Of the worm-caught fish, about 37% were hooked in the throat, and 4% in the gills, which resulted in a mortality of 35%. About 83% of the gill-hooked fish and 72% of those hooked in the throat died. This contrasts with the results of hatchery studies where most fish were hooked in the jaws or mouth.

One study was carried out in the hatchery to evaluate mortality of salmon that were deeply hooked (stomach or throat) with worm-baited hooks. A total of 106 salmon was purposely allowed to swallow baits and then hooked. The hook was removed (long-nose pliers) from 50 fish, and the leader was cut at the mouth of 56 other salmon. Of all deeply hooked salmon, 73% died, but 90% of the salmon from which the hook was removed died within 24 hours. Of those released after the leader was cut, 57% died. These findings indicate that for each 100 fish caught by deep hooking, 33 could be saved by leaving the hook in place and cutting the leader at the mouth of released fish.

The observation has often been made that fish bleeding from hooking injuries are more likely to die than those that do not bleed. For salmon hooked in lake studies, significantly more bleeding fish died (35%) than did non-bleeding fish (10%). Fish bleeding after hooking also died at a significantly higher rate (86%) than did non-bleeders (15%) in river studies. Anglers who are in the habit of releasing legal-size salmon during periods of "hot" fishing might do well to keep legal-size bleeding salmon to add to their creels.

Mortalities of salmon hooked on trolled streamer flies and wobblers, as measured in spring and fall lake studies, are quite likely typical of such mortalities occurring in Maine. Hooking mortality of salmon caught on cast wobblers and flies in spring and fall hatchery studies is also believed to be representative of mortality occurring in the wild using these gears. This is because most fish caught on these gears under both hatchery and wild conditions are hooked superficially in the jaws or mouth. The same is true for cast flies in river studies.

Mortality measured for hooking with worms in hatchery studies, however, was probably an under-estimate of that experienced under wild conditions. Superficial hooking experienced in the hatchery is not the general rule in the wild, as indicated by results of river studies. Because of more typically variable angling techniques and possibly larger fish size, more river-caught salmon were deeply hooked, causing greater mortality.

We can only speculate on hooking mortality suffered by salmon during winter and summer because no studies have been conducted during these seasons. Deep-trolled wobblers in summer can be expected to cause at least as much, and possibly more mortality of released salmon than the same gears fished in spring. Summer mortality may be greater because of temperature stress caused by bringing fish into the warm surface layers from the deeper, cooler water, thereby increasing their vulnerability to predation. Salmon caught on deep-trolled worms or sewed fish baits could suffer even higher mortality if baits are deeply ingested and fish are hooked in the throat or stomach.

The most common winter fishing methods for salmon are tip-ups (or traps), using a live minnow or smelt as bait, and "jigging" with hardware lures. Mortality of short salmon caught on live fish and released depends on hooking location. Unless the leader is cut at the mouth of a deeply hooked released fish, it will probably die. Most jigged short salmon are hooked in the jaws or mouth and therefore stand a better chance of survival after release. Colder water temperatures in winter may favor survival of released salmon. However, we stress that winter-released salmon should not be exposed to the air and handling times should be minimized to the greatest extent possible.

The following generalizations relating to these hooking studies remain pertinent today:

- Hardware lures, trolled or cast, and trolled streamer flies equipped with treble hooks are no more likely to kill released salmon than are those gears equipped with single hooks. Therefore, regulations restricting hook types used on salmon fishing gears are generally unnecessary.

- Survival of salmon hooked and released in fall is greater than that of fish caught in spring because of their better physical condition and decreasing water temperatures in fall.

- Salmon hooked using variable worm-fishing techniques and then released suffered significantly greater mortality than fish caught by fly-casting and released. Closure of heavily fished salmon nursery streams to worm fishing may be justified in cases where juvenile fish production is important to the lake or river fisheries involved.

- Most salmon worm-hooked deeply in the throat or stomach died if the hook was removed. If the hook was left in place and the leader cut, mortality was reduced by about 30%. This would indicate that a substantial number of short salmon might survive to be caught as legal-size fish if worm anglers cut the leader rather than removed the hook.

- Salmon that bled as a result of hooking injuries died at a significantly higher rate than those that did not bleed.

- Mortality of salmon hooked and released by anglers is influenced by many factors including: season, water temperature, type of environment, anatomical hooking site, variable angling techniques, and feeding behavior of the fish. Our studies were conducted over a multi-year period to evaluate *average* hooking mortality under various environmental conditions, including year-to-year variations that occur during typical fishing experiences for landlocked salmon.

Hooking injuries

As noted previously, Maine salmon anglers currently release a large portion of their catch of legal-size salmon (Figure 11). We believe this reflects a response by anglers to more restrictive harvest regulations, as well as an overall change in angler attitudes toward fishery resources. In our view, the willingness of modern anglers to practice this form of "catch and release" fishing is a positive development, because catch rates for all anglers are often higher, escapement to older cohorts may be improved, and anglers' overall satisfaction with the fishery is thereby enhanced. Yet we acknowledge that salmon repeatedly caught and released are subjected to a variety of stresses associated with exhaustive exercise during the landing process, handling, and air exposure during hook removal and photographing.

The sublethal effects of repeated handling on the physiological response by salmon are unknown. Nor do we understand the potential to affect reproductive and feeding behavior, or resistance to parasites, diseases, and fungal infection. We have, however, observed high incidences of hooking-related injuries coincident with increasing release rates of legal salmon, and we have documented that salmon with hooking scars exhibit reduced growth rates when compared to those without obvious injuries (MDIFW, unpublished data). For the purpose of this discussion, hooking injuries are defined as obvious tissue damage to external areas such as the maxillaries, the mandible, the tongue, or the eyes (see photos).

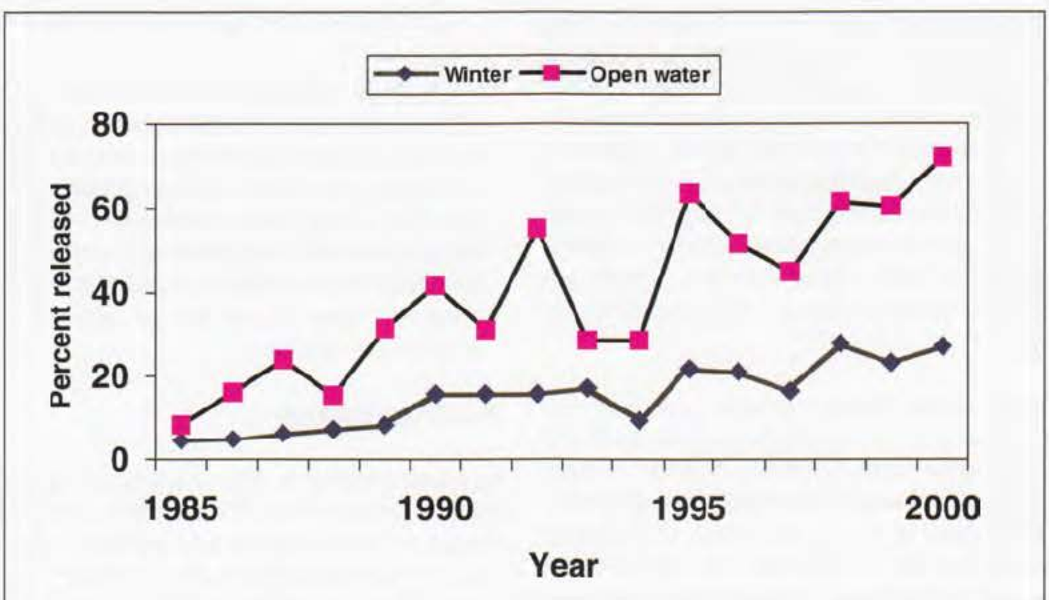
Of 3,026 salmon recently sampled from 27 lakes, 21% exhibited obvious signs of hooking injury. Among the individual lakes, rates of hooking injury ranged from 6% to 39%. Some of the highest incidences of injury occurred in lakes where release rates of legal salmon are known to be very high (e.g. the Rangeley Lakes chain). Injury rates of hatchery salmon (22%) and wild salmon (18%) were similar.

Injuries to both hatchery and wild salmon generally increased with age and the time they were subject to fishing. The peak rates among cohorts occurred at older ages for wild salmon than for hatchery fish. This was attributed to their slower growth, later recruitment to legal size, and delayed vulnerability to fishing gear.

Hatchery-reared salmon exhibiting hooking scars were significantly ($p<0.05$) shorter and weighed less at age than those without scars (Table 56). Suppressed growth and lower body weight were apparent for all hatchery cohorts analyzed (ages II+ to V+). Age V+ and age VI+ wild salmon with injuries were significantly shorter at age than those not injured ($p<0.05$). Age VI+ wild salmon with scars weighed significantly less ($p<0.05$) than uninjured fish.

These data suggest that high release rates practiced by many anglers may place constraints on the maximum growth potential of salmon that are caught and released several times. This has important management implications if release rates continue to rise, or if additional waters are selected for trophy-fish management. While we welcome and support the evolving angler ethic of catch and release fishing, we note that the sublethal effects of hooking injuries need further study to identify ways to reduce the severity of injuries, such as terminal tackle restrictions or angler education programs.

Figure 11. Angler release rates of legal-size landlocked salmon in Maine lakes, 1985-2000. Data from clerk creel surveys.



Landlocked salmon showing no evidence of hooking injury. (Rick Jordan, MDIFW)

Landlocked salmon with a severe hooking injury to the chin. (Rick Jordan, MDIFW)

Landlocked salmon with a torn maxillary from being previously hooked and released (Rick Jordan, MDIFW)

Table 56. Comparative sizes of Maine landlocked salmon with and without hooking scars. Data from spawning run surveys conducted on 27 lakes, 1995-2002. Numbers of fish sampled are in parentheses. Paired values marked with asterisks denote a significant difference (p<0.05).

Origin of fish	Hooking scars present?		Age				
			II+	III+	IV+	V+	VI+
Hatchery	Yes	T. length (in)	16.6 (151)*	18.8 (180)*	19.5 (51)*	20.5 (12)*	-
	No	T. length (in)	17.1 (656)*	19.5 (461)*	20.6 (142)*	22.4 (56)*	-
Hatchery	Yes	Weight (lb)	1.5 (151)*	2.3 (180)*	2.6 (51)*	2.9 (12)*	-
	No	Weight (lb)	1.7 (656)*	2.7 (461)*	3.1 (141)*	4.0 (56)*	-
Wild	Yes	T. length (in)	-	14.2 (28)	15.1 (42)	14.9 (45)*	16.2 (33)*
	No	T. length (in)	-	13.4 (144)	15.9 (111)	16.3 (149)*	17.2 (78)*
Wild	Yes	Weight (lb)	-	1.0 (28)	1.2 (42)	1.1 (45)*	1.4 (33)
	No	Weight (lb)	-	0.8 (144)	1.5 (111)	1.6 (149)*	1.8 (77)

THE ROLE OF HATCHERY-REARED SALMON

History of Maine landlocked salmon hatcheries

The first recorded attempts at formal fish culture in Maine were made using landlocked salmon. In 1867, Nathan Foster and Charles Atkins, Maine's first Commissioners of Fisheries, collected about 2,500 eggs from salmon taken in a tributary to Long Lake in Harrison. These eggs were incubated in a spring at Manchester in Kennebec County. This project failed, but the following year Atkins took eggs at Grand Lake Stream. A portion of these eggs were sent to Massachusetts, 800 were placed in a tributary to Cathance Lake in Washington County, and the remainder were taken to Manchester where about 3,000 salmon were hatched. Eight hundred of these fry were kept at a private hatchery in Alna where they reached a length of about 5 inches after 9 months (Locke 1969).

Around 1873, the U.S. Fishery Commission established the Sebec Landlocked Salmon Breeding Works near Sebec Lake in Piscataquis County. This facility operated for two or three years before being abandoned for unknown reasons. Also in 1873, Maine Commissioners took their first eggs from Sebago Lake, and then in 1875 constructed a small hatching house at Songo Locks. Charles Atkins, now employed by the U.S. Fishery Commission, resumed his egg-taking operations at Grand Lake Stream in 1875. By 1885, Maine Commissioners had constructed a weir at the mouth of the Crooked River at Sebago Lake and improvised a hatching house at Ede's Falls, where a small hatchery was erected in 1892 (Locke 1969).

From the mid 1950's and through the 1960's, landlocked salmon egg-taking operations were conducted primarily at West Grand Lake (Grand Lake Stream), Panther Run (Jordan River on Sebago Lake), and Cross Lake Thoroughfare in Aroostook County. Salmon eggs were also taken periodically at Cold Stream Pond and Rangeley Lake outlets. During this period, eggs taken from Grand Lake stream were hatched and raised at the Caribou Hatchery. Eggs from Cross Lake Thoroughfare were initially hatched at the Caribou Hatchery and raised at both the Caribou and Birch River Stations, both later closed, and subsequently at the Enfield station. Eggs from Sebago were hatched at the Raymond Hatchery on Panther Run, which was later abandoned in favor of a newer facility in Casco. Cold Stream Pond eggs were hatched and raised at the Enfield station, which was later relocated farther down the outlet stream. Rangeley Lake eggs were hatched and reared at the former Oquossoc Station (later sold).

Eggs for Maine's salmon stocking program are currently obtained exclusively from feral fish captured on spawning runs at West Grand Lake (Grand Lake Stream) and Sebago Lake (Jordan River). These two brood sources are preferred over the others because their fish are of outstanding quality, and the spawning runs occur in close proximity to two major rearing facilities.

A minimum of 100 males and 100 female salmon are stripped at each site in order to maintain high genetic diversity. Eggs are incubated and fish are raised to stocking age at the Grand Lake Stream, Casco, and Enfield Hatcheries. Some fry are transferred from these hatcheries to the Ela Rearing Station in Embden where they are held until planting. All these facilities are fed by lakes with exceptionally high water quality. The three hatcheries are equipped with filtration and ultra-violet light treatment systems to improve water quality and reduce the prevalence of bacterial and viral infections.

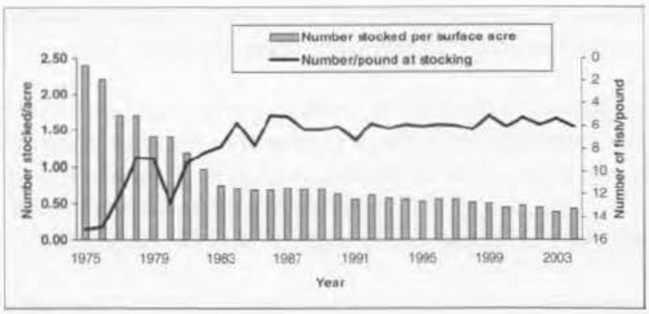
There have been considerable improvements in fish health and rearing conditions in Maine salmon hatcheries. These include reduced rearing densities, improved sanitation procedures, protection from light exposure, the construction of water treatment facilities, and improved nutrition and feeding regimes. A fish pathologist and microbiologist utilize a fully equipped diagnostic laboratory to continuously monitor fish quality at all stations, and they supervise treatment procedures when necessary. In addition, salmon utilized as brood stock are screened annually for a variety of pathogens prior to their eggs being transferred to the hatchery. As a result, the size and quality of Maine salmon raised in the hatchery environment have improved considerably

"Fish Camp" on Cross Lake Thoroughfare, where landlocked salmon eggs were once taken for statewide distribution. Photo taken in November, 1902. (Kendall Warner)

(Figure 12). Additional upgrades to Maine's salmon hatcheries were well underway in 2005.

Hatchery-reared salmon continue to contribute significantly to the landlocked salmon fishery in Maine. Of 176 lakes that provide principal salmon fisheries in the state, 127 (72%) totaling 372,951 acres (77%) are judged by Regional Biologists to require stocking to maintain satisfactory fisheries. Indeed, numerous lakes would provide virtually no salmon fishery if they were not stocked. Hatchery-reared salmon comprise approximately 69% of the estimated legal-size catch in those Maine lakes that provide principal salmon fisheries (Boucher 2001).

Figure 12. Trends in stocking rate (number/surface acre) and size (number/pound) of spring yearling salmon stocked in Maine lakes, 1975-2004.



Salmon stocking policies

Since 1960, salmon stocking in Maine lakes has been guided by written stocking policies. These policies are based primarily upon results of continuous monitoring of salmon fisheries within the state, and are revised and refined periodically. Since the printing of the last edition of this bulletin (Warner and Havey 1985), these policies have been revised three times, most recently in 2001. Primary changes from previous policies involve stocking frequency and density.

Wild salmon are given first priority where fisheries can be maintained through natural reproduction. Salmon are stocked only in waters capable of growing them, but where spawning and nursery habitat is either absent or limited. They may be stocked in waters having other coldwater fish species – the most common associations are with brook trout and lake trout. In any case, abundant quantities of smelts must be present to provide forage and sustain salmon growth.

All salmon stocking falls into one of three categories: maintenance stocking; introductory stocking; or experimental stocking. Maintenance stocking is routine, continuous stocking intended to supplement or substitute for natural reproduction. It is carried out where habitat is suitable for older juvenile and adult salmon, where spawning and nursery habitat is limited, and where fishing pressure is sufficiently high to ensure a reasonable return to anglers. Maintenance stocking is done primarily on an annual basis, but biennial or triennial plantings are made in several smaller lakes where forage is limited by the presence of other salmonids, principally lake trout.

Introductory stockings are made to establish new populations, which are to be later maintained by either natural reproduction or occasional maintenance stockings. Introductions are usually made with a series of annual stockings of spring yearlings (age I). Introductory stockings are rarely undertaken today because the great majority of suitable salmon habitat has already been identified.

Experimental stockings are made in either classical or marginal salmon habitats to obtain information on growth, survival, fishing quality, or effects of certain regulations. Experimental stockings are not required to be either at policy rates or at policy frequencies, but rather are established by the investigator in keeping with the design and goals of the experiment.

The number stocked is determined primarily by the ability of individual waters to grow salmon. Levels of angler use, harvest rates, relative contributions from natural recruitment, and whether the lake is open to ice fishing are also taken into consideration. Numbers of salmon stocked in Maine have been declining steadily over the past two decades (Figure 12), reflecting the realization by management biologists that overstocking, even to a minor extent, can result in depressed smelt abundance, followed by slow salmon growth and reduced fishing quality.

The improved quality of our hatchery fish in itself requires that fewer fish be stocked. Most recently, high release rates practiced by modern anglers and reduced fishing effort have resulted in stockpiling of young salmon in many waters. This has forced biologists to adjust stocking rates further downward to maintain the appropriate balance between salmon and smelts. Havey (1980) discussed the quantitative relationship between stocking rate and growth and yield of hatchery-reared salmon in Maine lakes.

In lakes, the stocking rate is expressed as the number of salmon per surface acre stocked and does not exceed 1.5 fish per acre; most waters receive between 0.4 and 0.7 salmon per acre. Densities are kept lowest where brook trout or lake trout are stocked or are present naturally in significant numbers, or where management emphasizes slow catch rates for larger salmon. Currently (2000-2004), about 113,000 spring yearling (age I) salmon are stocked annually in Maine lakes at an average rate of about 0.43 fish per acre. These fish average about 7 inches long and 3 ounces in size at stocking.

The large size of spring yearling salmon now available for stocking (Figure 12) has nearly eliminated the necessity of using older, more costly fall yearling (age I+) fish for maintenance stocking, even when predation and/or competition from other species is quite intense. Most salmon (83%) presently stocked in lakes are planted as spring yearlings. Other cohorts are occasionally stocked to meet the needs of specific management programs. For example, large fall yearling salmon are now routinely stocked in some lakes to provide immediate winter fishing opportunities in heavily fished lakes, primarily in southern Maine. These new stocking programs have not yet been fully evaluated, but preliminary data suggest that those lakes' spring yearling-based salmon fisheries have not been compromised. Large fall yearlings are also being stocked with increasing frequency to create new, short-term stream fishing opportunities where demand for riverine salmon fishing is high and suitable habitat is limited. Spring yearling or adult salmon are used for this same purpose in some waters. The demand for riverine salmon fishing is increasing in Maine, particularly for those occurring during the fall months (Boucher 2001). We anticipate that more of these types of stockings will be initiated during the next several years, if current or projected hatchery capacity proves capable of supporting it.

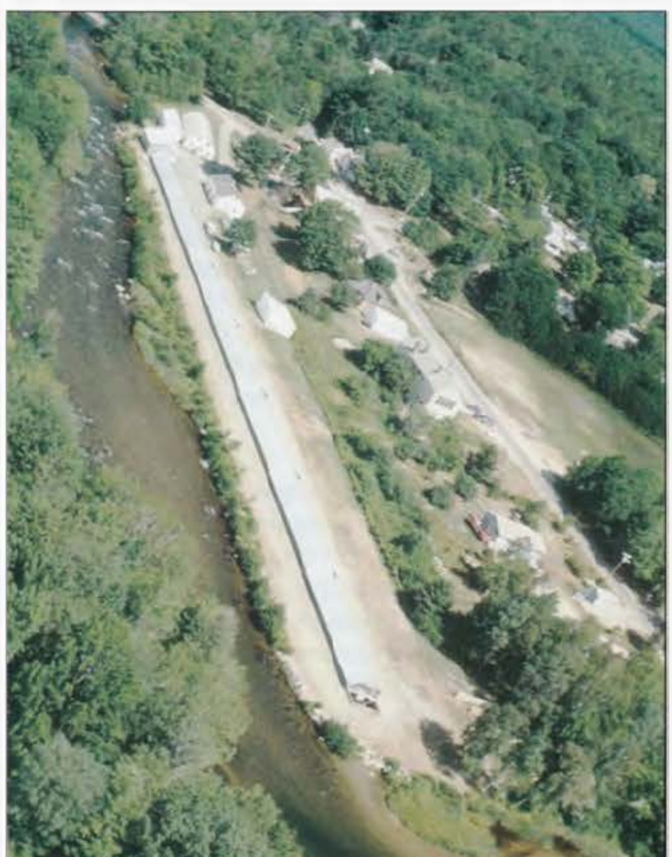
Recoveries of hatchery-reared salmon

Numerous studies conducted in Maine have shown that spring yearling salmon give the best return to anglers. Havey (1973a) could demonstrate no difference (p>0.05) between recoveries of salmon stocked as spring and fall yearlings at Schoodic Lake in Washington County between 1963 and 1966. Fish involved were captured by angling (987 salmon) and trapnetting (1,018 salmon). At Schoodic Lake there was a significant difference between recoveries of fall fingerlings (age 0+) and fall yearlings (p<0.05), but not between fall fingerlings and spring yearlings, possibly because of the smaller size of the spring yearlings commonly stocked in the early to mid-1960's.

Warner and Havey (1985) reported the results of intensive studies designed to compare the performance of salmon planted in four lakes as fall fingerlings, spring yearlings, and fall yearlings. The Schoodic Lake study cited above was included in this analysis. There was a significant difference (p<0.05) between total recoveries of fall fingerlings (5.9%) and fall yearlings (21.1%), but no significant difference (p>0.05) was found between the percentage recoveries of spring yearlings (22.6%) and fall yearlings (21.1%). The overall results of this assessment are tabulated in Table 57.

Havey (1974b), working with spring and fall yearling salmon at Love Lake, Washington County, obtained trap net recoveries of 76 spring yearlings and 525 fall yearlings respectively, from 4,544 spring yearlings and 4,573 fall yearlings planted between 1965-71 (30,073 net hours). Only one of the spring yearling plantings (1967) produced a reasonable recovery (60 fish). This cohort averaged 5.4 inches in total length when stocked. The 1965 and 1966 cohorts of spring yearlings averaged 4.2 inches and 3.9 inches in length, respectively, when stocked. Fall yearlings were somewhat larger. The average length of the three fall yearling cohorts stocked was 6.4±0.5 inches. Within the six cohorts of salmon planted from 1965-67, there was a high positive correlation (0.94, p<0.05) between size at planting and subsequent net catches; i.e. the larger the planting sizes (inches), the greater was the return of salmon in subsequent years. No data for angled fish were available from the Love Lake project. A planting of age II salmon in May 1962 (9.8 inches average length) yielded a high subsequent recovery in trap nets (15%). Havey concluded that spring-planted salmon at lakes similar to Love Lake may be expected to exhibit satisfactory survival if they are of large size. Love Lake has marginal water quality and heavy competition from several warmwater species.

DeRoche (1976) determined that spring yearlings and fall yearlings planted in equal numbers at Sebago Lake occurred at about the same frequency in lake angler catches (1.03:1:00, respectively), and in spawning runs in the Jordan River, a tributary of Sebago (0.99:1.00, respectively).



An aerial view of a modern salmon hatchery located on Grand Lake Stream, Washington County. (MDIFW)

Table 57. Total recoveries of landlocked salmon planted in four Maine lakes[1], 1957-1975 (adapted from Warner and Havey 1985).

	Totals for each cohort in all waters:			
Cohort (age)	Number planted	Mean size (inches)[2]	Total number recovered	Percentage recovered (95% CI)[3]
Fall fingerling (0+)	9,436	3.7±0.3	722	5.9 (1.7-11.4)
Spring yearling (I)	358,270	5.5±0.2	68,770	22.6 (15.8-30.1)
Fall yearling (I+)	35,389	6.2±0.3	2,376	21.1 (8.9-33.4)

[1] Lakes included Long Pond (Mt. Desert), Eagle Lake (Bar Harbor), Schoodic Lake (T18 MD), and Moosehead Lake.
[2] Unweighted mean size at planting.
[3] Percentages and confidence intervals (CI) computed from arc sine-transformed data (Zar 1971).

DeSandre et al. (1977) stated: "*all things considered, there seems to be no advantage to stocking fall yearling salmon in Rangeley Lake* {Franklin County, Maine}. *Despite their larger size they did not demonstrate any higher return than spring yearlings which can be stocked at a lower cost.*" Fall yearling salmon planted in Rangeley Lake during the period 1957-74 returned to the outlet as spawners at the rate of 1.1-2.7% of those planted. Spring yearlings returned at a rate of 0.9-4.9% of those planted.

The most recent study comparing returns of fall fingerling and spring yearling salmon was completed at West Lake in Hancock County (Smith 1992). The impetus for this project arose from the dramatic improvements in size and quality of hatchery-reared fish. The study was designed to determine if fall fingerling salmon, which by the mid-1980's exceeded the size of spring yearlings stocked in earlier decades, could be used in lieu of spring yearlings, with greater economy.

West Lake, with a surface area of 1,344 acres and mean depth of 29 feet, is typical of many Maine salmon lakes. Water quality is highly suited to salmon, there is moderate competition from warmwater fishes, natural reproduction of salmon is negligible, and ice fishing is permitted.

Experimental stocking rates for spring yearling and fall fingerling salmon were established on the basis of pounds rather than numbers of fish, because historic data showed a total of 200 pounds of stocked salmon allowed for stable growth rates and provided acceptable fisheries. One half of the total weight was allocated to each cohort, translating to 500 spring yearlings and 1000 fall fingerlings annually. Returns to anglers and the performance of each cohort were evaluated with intensive creel surveys (both seasons) and fall trapnetting.

From 1985 to 1989, spring yearling salmon were recovered at a significantly higher rate (1.7:1.0) than fall fingerlings, and there was no significant difference in the growth rate of the two groups throughout the study period. The study concluded that spring yearlings were the most economical fish to plant, considering the comparative costs of rearing each cohort ($1.21/fall fingerling and $2.41/spring yearling in 1990), and the relative recoveries of each (1.7:1.0). Costs could perhaps be equalized if larger numbers of fall fingerlings were raised, which reduces the cost of each fish reared.

Numbers and pounds of salmon stocked as spring yearlings and subsequently recovered in several Maine lakes are presented in Table 58. The reported values are minimal, because most harvest estimates were obtained during the ice fishing season only, and in most cases individual cohorts were not tracked through their entire lifespan. Nevertheless, they clearly indicate that spring yearling salmon provided excellent returns to anglers on many lakes. On a statewide basis, anglers recovered about 280% by weight of nearly 90,000 pounds of spring yearlings stocked from 1996 to 1999 (Boucher 2001).

Table 58. Angler recovery of salmon stocked as spring yearlings in Maine lakes.

Water	County	Year stocked	Number stocked	Pounds stocked	Season recovered	Year class(es) recovered	Number (%) recovered	Pounds (%) recovered
Long Lake	Aroostook	1994	6,200	1,425	Winter	III, IV	993 (16)	1,720 (121)
Long Lake	Aroostook	1995	7,000	1,101	Winter	II, III	2,576 (37)	3,361 (305)
Long Lake	Aroostook	1996	4,000	520	Winter	III	1,218 (31)	2,014 (387)
Long Lake	Aroostook	1997	4,400	958	Winter	III	805 (18)	1,456 (152)
Long Lake	Aroostook	1998	4,525	680	Winter	III	1,014 (22)	2,457 (361)
Cross Lake	Aroostook	1996	800	93	Winter	III	107 (13)	131 (141)
Square Lake	Aroostook	1994	4,000	971	Winter, Summer	III, IV	1,697 (42)	2,104 (217)
Square Lake	Aroostook	1995	4,100	733	Winter	III, IV	800 (20)	1,157 (158)
Square Lake	Aroostook	1996	2,700	500	Winter	III	885 (33)	1,055 (211)
Square Lake	Aroostook	1997	3,000	725	Winter	III	1,128 (38)	1,287 (178)
Square Lake	Aroostook	1998	3,000	405	Winter	III	532 (18)	603 (149)
Eagle Lake	Aroostook	1994	750	144	Winter	III, IV, V	159 (21)	437 (303)
Carr Pond	Aroostook	1996	300	37	Winter	V	32 (11)	80 (216)
Squapan Lake	Aroostook	1993	1,000	169	Winter	IV	300 (30)	394 (233)
Squapan Lake	Aroostook	1994	500	85	Winter	III	200 (40)	178 (209)
Drews Lake	Aroostook	1998	250	34	Winter	III	118 (47)	130 (382)
Millimagassett Lake	Penobscot	1996	500	63	Winter	III	64 (13)	89 (141)
Alligator Lake	Hancock	1997	150	23	Winter	III	24 (16)	25 (110)
Clearwater Lake	Franklin	1997	400	87	Winter	II	104 (26)	103 (118)
Rangeley Lake	Franklin	1988	3,500	686	Summer	III+	455 (13)	956 (139)
Rangeley Lake	Franklin	1993	4,000	1,481	Summer	III+	960 (24)	2,319 (157)
Rangeley Lake	Franklin	1995	3,132	454	Summer	IV+	312 (10)	618 (136)
Rangeley Lake	Franklin	1996	3,000	534	Summer	III+	1,009 (34)	1,443 (270)
Richardson Lake	Oxford	1992	3,500	1,207	Summer	V+	61 (2)	120 (10)
Richardson Lake	Oxford	1993	3,500	1,296	Summer	IV+	184 (5)	406 (31)
Richardson Lake	Oxford	1994	1,800	400	Summer	III+	409 (23)	640 (160)
Embden Lake	Somerset	1996	800	143	Winter	III	67 (8)	186 (130)
Totals:			**70,807**	**14,954**			**16,213 (23)**	**25,469 (170)**

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APPENDICES

Appendix 1. Population status of landlocked salmon in Maine lakes (2001)[1].

Water	Township	Principal fishery	Relic population
Androscoggin County			
Androscoggin Lake	Leeds		x
Auburn Lake	Auburn	x	
Aroostook County			
Beau Lake	T19 R11 WELS	x	
Bradbury (Barker) Lake	New Limerick		x
Carr Pond	T13 R8 WELS	x	
Chandler Lake	T9 R9 WELS	x	
Clayton Lake	T12 R8 WELS	x	
Cochran Lake	New Limerick		x
Cross Lake	T17 R5 WELS	x	
Deering Lake	Orient	x	
Drews (Meduxnekeag) Lake	Linneus		x
Eagle Lake	Eagle Lake	x	
East Grand Lake	Weston	x	
Fish River Lake	T14 R8 WELS	x	
Glazier Lake	T18 R10 WELS	x	
Green Pond	New Limerick		x
Long Lake	T17 R4 WELS	x	
Machias Lake (Big)	T12 R8 WELS		x
Machias Lake (Little)	Nashville PLT	x	
Madawaska Lake	T16 R4 WELS	x	
Mattawamkeag Lake	Island Falls	x	
Molunkus Lake	T1 R5 WELS		x
Mud Lake	T17 R4 WELS	x	
North Pond	Orient		x
Pleasant Pond	T4 R3 WELS	x	
Portage Lake	Portage Lake	x	
Pratt Lake	T11 R9 WELS		x
Rockabema Lake	Moro PLT	x	
Round Mountain Pond	T11 R8 WELS		x
Round Pond	T14 R8 WELS	x	
Rowe Lake	T11 R8	x	
St. Froid Lake	Winterville PLT	x	
Sly Brook Lake (1st)	New Canada		x
Sly Brook Lake (2nd)	New Canada		x
Sly Brook Lake (3rd)	New Canada	x	
Soldier Pond	Wallagrass	x	
Spaulding Lake	Oakfield		x
Squapan Lake	Squapan TWP	x	
Square Lake	T16 R5 WELS	x	
Togue Pond	T15 R9 WELS	x	
Umcolcus Lake	T7 R5 WELS	x	
Wallagrass Lakes (1st & 2nd)	St. John PLT	x	
Cumberland County			
Crescent Lake	Raymond	x	
Crystal (Anonymous) Pond	Harrison	x	
Dundee Pond	Windham		x

[1] Where salmon are routinely targeted by anglers and comprise a significant portion of the total catch of all species.

Appendix 1 (cont'd).

Water	Township	Principal fishery	Relic population
Gorham Pond (North)	Windham		x
Long Lake	Bridgeton	x	
Panther Pond	Raymond	x	
Parker Pond	Casco		x
Peabody Pond	Sebago	x	
Sebago Lake	Sebago	x	
Trickey Pond	Naples	x	
Franklin County			
Arnold Pond	Coburn Gore	x	
Beaver Mountain Lake	Sandy River PLT	x	
Chain of Ponds	Chain of Ponds TWP	x	
Clearwater Lake	Industry	x	
Dodge Pond	Rangeley	x	
Gull Pond	Dallas PLT	x	
Haley Pond	Dallas PLT		x
Horseshoe Pond	Coburn Gore		x
Jim Pond	Jim Pond TWP	x	
Johns Pond	Davis TWP		x
Kennebago Lake (Big)	Davis TWP	x	
Kennebago Lake (Little)	Stetsontown TWP	x	
Loon Lake	Dallas PLT	x	
Mooselookmeguntic Lake	Rangeley	x	
Parker Pond	Jay		x
Porter Lake	Strong	x	
Rangeley Lake	Rangeley	x	
Round Pond	Rangeley		x
Tea Pond	Jim Pond TWP	x	
Varnum Pond	Wilton	x	
Webb (Weld) Lake	Weld		x
Wilson Pond	Wilton	x	
Hancock County			
Alamoosook Lake	Orland		x
Alligator Lake	T34 MD	x	
Beach Hill Pond	Otis	x	
Branch Lake	Ellsworth	x	
Branch Pond (Lower Middle)	Aurora		x
Branch Pond (Upper Middle)	Aurora	x	
Donnell Pond	T9 SD	x	
Duck Lake	T4 ND	x	
Eagle Lake	Bar Harbor	x	
Echo Lake	Mount Desert	x	
Graham Lake	Mariaville		x
Great Pond	Great Pond		x
Green Lake	Dedham	x	
Heart Pond	Orland		x
Jacob Buck Pond	Bucksport		x
Jordan Pond	Mount Desert	x	
Lead Mountain Pond (Upper)	T28 MD		x
Long Pond	T10 SD		x
Long Pond	Bucksport		x

Appendix 1 (cont'd).

Water	Township	Principal fishery	Relic population
Long (Great) Pond	Mount Desert	x	
Molasses Pond	Eastbrook	x	
Mountainy Pond	Dedham		x
Nicatous Lake	T40 MD		x
Patten Pond (Lower)	Surry	x	
Phillips (Lucerne) Lake	Dedham	x	
Pistol Pond (Lower)	T3 ND		x
Rocky Pond	Otis		x
Somes Pond	Mount Desert		x
Spring Lake	T3 ND	x	
Spring River Lake	T10 SD		x
Springy Pond (Lower)	Otis		x
Toddy Pond	Surry		x
Tunk Lake	T10 SD	x	
West Lake	T3 ND	x	
Kennebec County			
Cobbosseecontee Lake	Winthrop		x
Echo Lake (Crotched Pond)	Fayette		x
Flying Pond	Vienna		x
Great Pond	Belgrade		x
Ingham Pond	Mount Vernon		x
Long Pond	Windsor		x
Long Pond	Belgrade	x	
Messalonskee Lake	Belgrade		x
Minnehonk Lake	Mount Vernon		x
Narrows Pond (Lower)	Winthrop		x
Narrows Pond (Upper)	Winthrop	x	
Parker Pond	Fayette	x	
Pocasset Lake	Wayne		x
Taylor (Mill) Pond	Mount Vernon		x
Knox County			
Alford Lake	Hope		x
Lermond Pond	Hope		x
Megunticook Lake	Camden		x
Lincoln County			
Damariscotta Lake	Jefferson		x
James Pond	Somerville		x
Oxford County			
Aziscohos Lake	Lincoln PLT	x	
B Pond	Upton	x	
Bear Pond	Waterford	x	
Bryant Pond	Woodstock	x	
Colcord Pond	Porter	x	
Ellis Pond (Little)	Byron	x	
Howard Pond	Hanover	x	
Keewaydin Lake	Stoneham	x	
Kezar Lake	Lovell	x	

Appendix 1 (cont'd).

Water	Township	Principal fishery	Relic population
Moose Pond	Denmark	x	
Papoose Pond	Waterford		x
Parmachenee Lake	Lynchtown TWP	x	
Pennesseewassee Lake	Norway	x	
Pleasant Lake	Otisfield	x	
Pond in the River	Township C	x	
Richardson Lake	Richardsontown TWP	x	
Richardson Pond (West)	Adamstown TWP		x
South and Round Ponds	Greenwood	x	
Sturtevant Pond	Magalloway PLT		x
Thompson Lake	Oxford	x	
Umbagog Lake	Magalloway PLT	x	
Penobscot County			
Brewer Lake	Orrington	x	
Bottle Pond	Lakeville PLT		x
Cedar Lake	T3 R9 NWP		x
Cold Stream Pond	Enfield	x	
Cold Stream Pond (Upper)	Lincoln	x	
Endless Lake	T3 R9 NWP		x
Grand Lake Seboeis	T7 R7 WELS		x
Hay Lake	T6 R8 WELS		x
Jo-Mary Lake (Middle)	T4 Indian Purchase		x
Junior Lake	T5 R1 NBPP	x	
Lombard Lake	Lakeville PLT		x
Matagamon Lake	T6 R8 WELS		x
Millimagasssett Lake	T7 R8 WELS	x	
Millinocket Lake	T1 R8 WELS	x	
Pemadumcook Chain Lakes	T4 Indian Purchase	x	
Pleasant and Mud Lakes	T6 R6 WELS		x
Saponac Pond	Grand Falls TWP		x
Scraggley Lake	T5 R1 NBPP		x
Scraggly Lake	T7 R8 WELS	x	
Shin Pond (Lower)	T5 R7 WELS		x
Shin Pond (Upper)	Mt. Chase	x	
Snowshoe Lake	T7 R7 WELS		x
Sysladobsis Lake	Lakeville PLT	x	
Wassookeag Lake	Dexter	x	
Piscataquis County			
Beaver Pond (Little)	T7 R9 WELS		x
Benson Pond (Big)	Willimantic		x
Buttermilk Pond (1st)	Bowerbank		x
Caucomgomoc Lake	T6 R14 WELS	x	
Chandler Pond	T8 R10 WELS	x	
Chase Lake	T9 R10 WELS	x	
Chesuncook Lake	T3 R12 WELS	x	
Davis Pond (1st)	Guilford	x	
Davis Pond (2nd)	Guilford	x	
Debsconeag Lake (1st)	T2 R10 WELS	x	
Deer Pond	T3 R13 WELS		x

Appendix 1 (cont'd).

Water	Township	Principal fishery	Relic population
Duck Pond	T4 R11 WELS		x
Elbow Pond (Upper)	T10 R10 WELS	x	
Harrington Lake	T3 R11 WELS	x	
Hebron Lake	Monson		x
Houston Pond	T7 R9 NWP	x	
Hudson Pond (Lower)	T10 R10 WELS	x	
Island (Chase) Pond	T10 R10 WELS	x	
Jo-Mary Lake (Lower)	T1 R10 WELS	x	
Jo-Mary Lake (Upper)	TA R10 WELS	x	
Lobster Lake	Lobster TWP	x	
Lobster Lake (Little)	Lobster TWP		x
Long Pond	T7 R9 NWP	x	
Loon Lake	T6 R15 WELS		x
Millinocket Lake	T7 R9 WELS	x	
Monson Pond	Monson		x
Moosehead Lake	Greenville	x	
Mooseleuk Lake	T10 R9 WELS		x
Munsungan Lake	T8 R10 WELS	x	
Nahmakanta Lake	T1 R11 WELS	x	
Onawa Lake	Elliotsville	x	
Passamagamet Lake	T1 R9 WELS		x
Prong Pond	Greenville		x
Ragged Lake	T2 R13 WELS		x
Roach Pond (1st)	Frenchtown TWP	x	
Roach Pond (2nd)	T1 R12 WELS	x	
Roach Pond (3rd)	Shawtown TWP	x	
Roach Pond (4th)	Shawtown TWP		x
Sebec Lake	Willimantic	x	
Seboeis Lake	T4 R9 NWP	x	
Schoodic Lake	Lake View PLT		x
Spectacle Ponds	Monson	x	
Togue Pond (Lower)	T2 R9 WELS		x
Togue Pond (Upper)	T2 R9 WELS		x
Trout Pond	Bowdoin College Grant West		x
Wilson Pond (Lower)	Greenville	x	
Wilson Pond (Upper)	Bowdoin College Grant West	x	
Sagadahoc County			
Nequasset Lake	Woolwich		x
Somerset County			
Attean Pond	Attean TWP	x	
Austin Pond	Bald Mountain TWP T2 R3	x	
Austin Pond (Little)	Bald Mountain TWP T2 R3	x	
Baker Lake	T7 R17 WELS		x
Baker Pond	T5 R6 BKP WKR		x
Baker Pond	Caratunk	x	
Brassua Lake	Rockwood Strip-East	x	
Center Pond	Soldiertown TWP		x
Dimmick Pond (Little)	Caratunk		x
Duncan Pond	Prentiss TWP	x	

Appendix 1 (cont'd).

Water	Township	Principal fishery	Relic population
Embden Pond	Embden	x	
Flagstaff Lake	Flagstaff TWP		x
Grass Pond	Pierce Pond TWP		x
Hancock Pond	Embden	x	
Heald Pond	Moose River	x	
Holeb Pond	Holeb TWP	x	
Indian Pond	Indian Stream TWP	x	
Kingsbury Pond	Mayfield TWP	x	
Long Pond	Taunton and Raynham		x
Long Pond	Long Pond TWP		x
Mayfield Pond	Mayfield TWP	x	
Moose Pond	Hartland		x
Mosquito Pond	The Forks PLT		x
Moxie Pond	East Moxie TWP	x	
Parlin Pond	Parlin Pond TWP		x
Pickerel Pond	Pierce Pond TWP		x
Pierce Pond	Pierce Pond TWP	x	
Rowe Pond	Pleasant Ridge PLT	x	
St. John Pond (4th)	T5 R17 WELS		x
St. John Pond (5th)	T5 R17 WELS		x
Seboomook Lake	Seboomook TWP		x
Spectacle Pond	King and Bartlett TWP		x
Spencer Lake	Hobbstown TWP	x	
Spring Lake	T3 R4 BKP WKR	x	
Wentworth Pond	Solon		x
Wood Pond (Big)	Attean TWP	x	
Wood Pond (Little Big)	Dennistown PLT	x	
Wyman Lake	Carrying Place TWP	x	
<u>Waldo County</u>			
Norton Pond	Lincolnville		x
St. George Lake	Liberty	x	
Sheepscot Pond	Palermo	x	
Swan Lake	Swanville	x	
Unity Pond	Unity		x
<u>Washington County</u>			
Beddington Lake	Beddington		x
Big Lake	Grand Lake Stream PLT	x	
Bog Lake	Northfield	x	
Boyden Lake	Perry	x	
Cathance Lake	No. 14 PLT	x	
Farrow Lake	Topsfield		x
Gardner Lake	East Machias	x	
Grand Falls Flowage	Indian TWP		x
Hadley Lake	East Machias		x
Keene's Lake	Calais		x
Lambert Lake	Lambert Lake TWP	x	
Lewy Lake	Indian TWP		x
Long Lake and the Basin	Indian TWP		x
Love Lake	T19 ED BPP	x	

APPENDICES

Appendix 1 (cont'd).

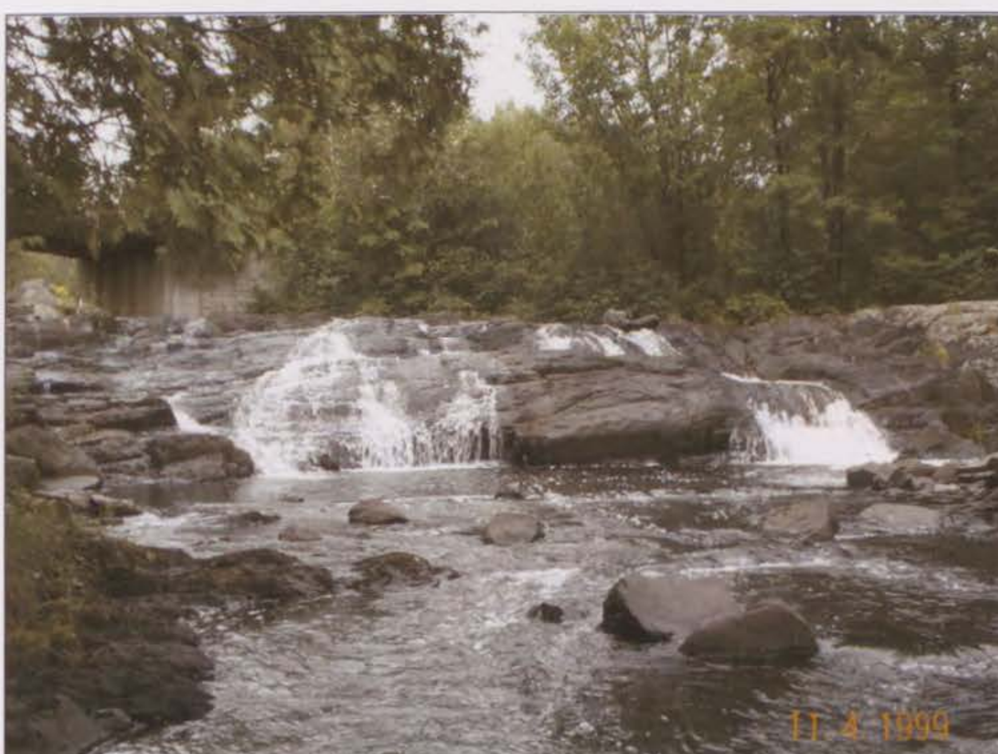
Water	Township	Principal fishery	Relic population
Meddybemps Lake	Meddybemps		x
Mopang Lake	Devereaux TWP	x	
Mopang Lake (1st)	Devereaux TWP		x
Mopang Lake (2nd)	Devereaux TWP		x
Musquash Lake (East)	Topsfield	x	
Musquash Lake (West)	T6 R1 NBPP	x	
Nashs Lake	Calais	x	
Oxbrook Lake (Lower)	T6 R1 NBPP		x
Oxbrook Lake (Upper)	T6 R1 NBPP		x
Pleasant Lake	Alexander	x	
Pleasant Lake	T7 R2 NBPP	x	
Pleasant River Lake	Beddington		x
Pocumcus Lake	T6 ND BPP	x	
Rocky Lake	T18 ED BPP		x
Round Lake	T19 ED BPP		x
Schoodic Lake	Cherryfield	x	
Second Lake	T18 ED BPP		x
Second Lake	Marion TWP		x
Spednic Lake	Vanceboro	x	
Spruce Mountain Lake	Beddington		x
Sysladobsis Lake (Lower)	T5 ND BPP	x	
West Grand Lake	T5 ND BPP	x	
Woodland Flowage	Baileyille		x
<u>York County</u>			
Mousam Lake	Acton	x	
Ossipee Lake (Little)	Waterboro	x	

Appendix 2. List of common and scientific names[2] of freshwater fishes cited in "Maine Landlocked Salmon: Life History, Ecology, and Management".

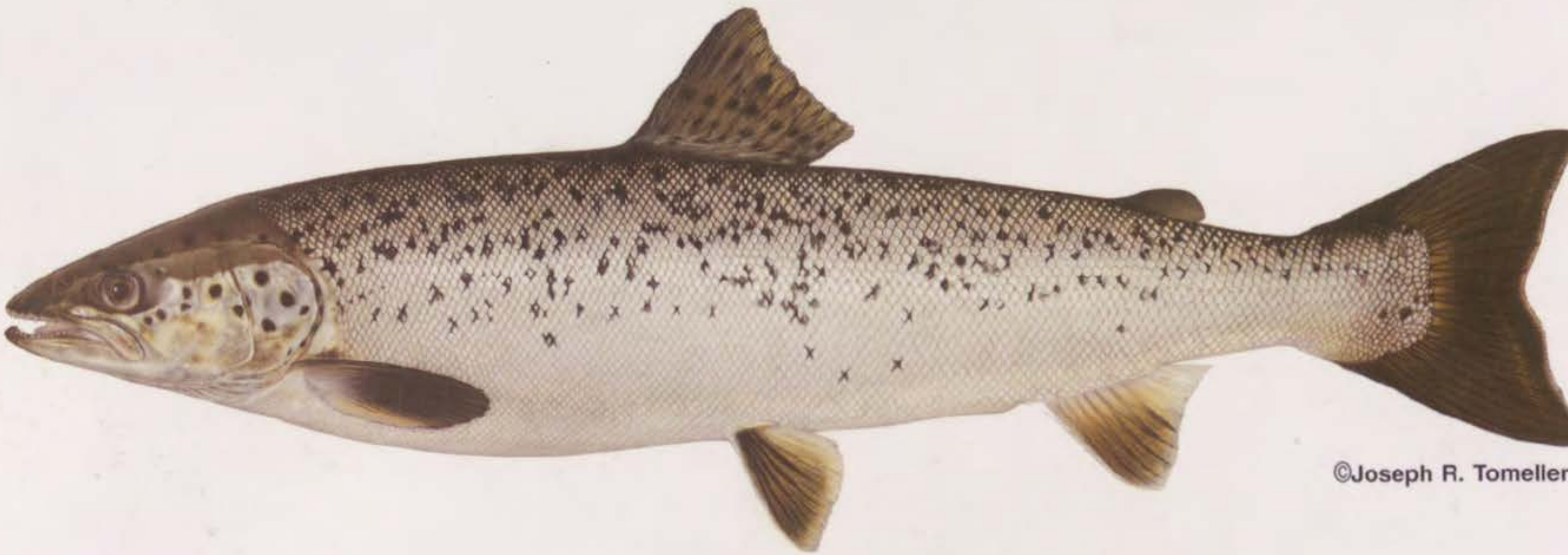
Common Name	Scientific Name
Landlocked Atlantic salmon	*Salmo salar*
Brown trout	*Salmo trutta*
Brook trout	*Salvelinus fontinalis*
Lake trout	*Salvelinus namaycush*
Splake	*Salvelinus namaycush X S. fontinalis*
Burbot (cusk)	*Lota lota*
Lake whitefish	*Coregonus clupeaformis*
Round whitefish	*Prosopium cylindraceum*
Rainbow smelt	*Osmerus mordax*
Alewife	*Alosa psuedoharengus*
Smallmouth bass	*Micropterus dolomieu*
Largemouth bass	*Micropterus salmoides*
Pumpkinseed sunfish	*Lepomis gibbosus*
Redbreast sunfish	*Lepomis auritus*
Black crappie	*Pomoxis nigromaculatus*
White perch	*Morone americana*
Yellow perch	*Perca flavescens*
Chain pickerel	*Esox niger*
Northern pike	*Esox lucius*
Muskellunge	*Esox masquinongy*
Brown bullhead	*Ameiurus nebulosus*
Blacknose dace	*Rhinichthys atratulus*
Northern redbelly dace	*Phoxinus eos*
Finescale dace	*Phoxinus neogaeus*
Golden shiner	*Notemigonus crysoleucas*
Common shiner	*Luxilus cornutus*
Pearl dace	*Semotilus margarita*
Fallfish	*Semotilus corporalis*
Creek chub	*Semotilus atromaculatus*
Lake chub	*Couesius plumbeus*
American eel	*Anguilla rostrata*
White sucker	*Catastomus commersoni*
Longnose sucker	*Catastomus catastomus*
Slimy sculpin	*Cottus cognatus*
Banded killifish	*Fundulus diaphanus*
Threespine stickleback	*Gasterostreus aculeatus*
Ninespine stickleback	*Pungitius pungitius*

[2] Scientific names are from Robins et al. (1991).

Landlocked salmon attempting to jump Cowyard Falls on Ship Pond Stream, inlet to Sebec Lake, 1890. (Photo provided by Kendall Warner)



Cowyard Falls in 1999, 109 years later. (Tim Obrey, MDIFW)



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SPORT FISH RESTORATION