Association between emigration and age structure in populations of brook trout (*Salvelinus fontinalis*) in Adirondack lakes

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Abstract: Patterns of emigration by brook trout (*Salvelinus fontinalis*) from five Adirondack lakes indicated a synchronized, repetitive response to seasonal stimuli over a 13-year period. Emigration occurred in the spring and fall with virtually no movement in the winter and summer. Spring emigration coincided with peak runoff from snowmelt and consisted of small numbers of mostly yearlings (94.8% of emigrants). Large-scale fall emigration from four lakes (32.7–68.8% potential losses from populations), by mostly mature fish (94.6% of emigrants), coincided with the spawning season for brook trout. Fall emigrants were likely searching for spawning sites, which were limited or unavailable within the lakes. In a larger set of 14 lakes, the greatest proportion of older (age 3) brook trout occurred in lakes with no outlets, which prevented emigration. In drainage lakes with outlets present, the proportions of older fish in lakes with later maturing strains (age 2–3) were greater than in those with earlier maturing strains (age 1–2). Later age at maturity would have delayed fall emigration from these lakes. Fall emigration appears to be a major factor that causes the virtual absence of older brook trout in many Adirondack lakes and must be assessed in future population dynamic studies.

Résumé : À l'aide des profils d'émigration de l'omble de fontaine (*Salvelinus fontinalis*) de cinq lacs des Adirondacks, on a mis en évidence une réponse synchronisée et répétitive aux stimuli saisonniers sur une période de 13 ans. La migration survenait au printemps et à l'automne, presque aucun déplacement n'étant observé en hiver et en été. La migration du printemps coïncidait avec le ruissellement maximum dû à la fonte des neiges et regroupait de petits nombres de poissons, surtout des jeunes d'un an (94,8% des émigrants). Les grands mouvements d'émigration partant de quatre lacs (perte possible de 32,7–8,8% des populations), regroupant surtout des poissons adultes (94,6% des émigrants), coïncidaient avec la saison de la fraye de l'omble de fontaine. Les émigrants recherchaient probablement des sites de fraye, qui sont rares ou absents dans certains lacs. Dans un ensemble plus vaste de 14 lacs, la plus forte proportion des poissons plus âgés (de 3 ans ou plus) se trouvait dans des lacs sans exutoires, ce qui empêchait toute migration. Dans les lacs reliés à un réseau par des exutoires, les proportions de poissons plus âgés dans les lacs comportant des souches à maturation tardive (âgés de 2 à 3 ans) étaient supérieures à celles des lacs ayant des souches à maturation précoce (âgés de 1 à 2 ans). La maturité à un âge plus avancé aurait retardé la migration d'automne de ces lacs. La migration d'automne semble être l'un des principaux facteurs expliquant l'absence quasi-totale d'ombles de fontaine plus âgés dans de nombreux lacs des Adirondacks; ce facteur doit faire l'objet d'une évaluation dans les futures études des caractéristiques dynamiques des populations.
[Traduit par la Rédaction]

Introduction

Few brook trout (*Salvelinus fontinalis*) exceed age 4 in Adirondack lakes. Brook trout populations are comprised primarily of age-0 to age-2 fish, while age-3 fish are uncommon and age-4 and older fish are rarely observed (Flick and Webster 1976; Keller 1979). Many lakes are remote, receive light angling pressure, but still lack significant numbers of age-3 and older brook trout. Thus, mortality resulting from angling does not explain the absence of older brook trout in these Adirondack lakes. In contrast, some lightly exploited waters in Canada support wild brook trout populations with age-6 to age-9 fish present. These populations typically exist in large lakes or complex riverine–lake habitats such as those occurring in the Nipigon (Scott and Crossman 1973) and James Bay (Flick 1977) drainages. The last known populations of older, larger brook trout in the Adirondack region existed in similar riverine–lake systems that included Cranberry Lake and the Bog River (Greeley and Bishop 1932).

The historic range of brook trout in the Adirondacks has been significantly reduced with most present-day populations restricted to small (<80 ha) headwater lakes. The range reduction occurred because of changes in the Adirondack ecology including introductions of non-native fish species, range expansion of native fish species, excessive angling mortality, destruction of natural spawning areas by logging and beaver activity, construction of dams, and habitat degradation owing to acid deposition (Pfeiffer 1979; Schofield 1993). Critical habitat and forage types essential to the maintenance of self-sustaining populations of older, larger brook trout may be lacking in many of these smaller, isolated lakes. To mitigate the loss of natural brook trout populations, a fall fingerling stocking program has been implemented to maintain or supplement 90% of the existing brook trout populations in Adirondack lakes (Pfeiffer 1979).

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Table 1. Physical characteristics, location, and stocking history of the study waters.

	Drainage area (ha)	Lake area (ha)	Coordinates	Lake class	Lake type	Stocked strains of brook trout
1 Black Pond	75.9	10.1	44°27′N,74°25′W	Seepage	2	1,2,10
2 Canachagala Lake	351.1	81.0	43°36′N,75°54′W	Drainage	3	2
3 Chambers Lake	244.7	10.4	43°36′N,75°56′W	Drainage	1	2,5,6,7,8,10
4 Deer Lake	217.0	13.2	43°22′N,75°46′W	Drainage	1	2,5,6,7,8,10
5 Fourth Bisby Lake	312.0	24.3	43°23′N,75°58′W	Drainage	1	2,5,6,7,8,10
6 Goose Lake	134.5	5.3	43°23′N,74°43′W	Drainage	1	2,5,6,7,8,9,10
7 Green Lake	5.1	10.3	43°39′N,75°55′W	Seepage	2	2,6
8 Lower Sylvan Pond	48.7	6.5	43°37′N,75°56′W	Drainage	1	4,5,6,7,8,9,10
9 Mountain Pond	64.2	3.4	43°42′N,75°52′W	Drainage	1	2,4,5,6,7,8,10
10 Otter Lake	540.0	9.6	43°23′N,74°44′W	Drainage	1	2,4,5,6,7,8,10
11 Rock Lake	393.6	78.9	43°57′N,74°52′W	Drainage	1	1,2,3,4,5,6,10,11,12,13
12 Upper Sylvan Pond	31.0	4.9	43°37′N,75°56′W	Drainage	4	None
13 Wheeler Pond	7.5	2.6	43°41′N,75°03′W	Drainage	3	2
14 Wilmurt Lake	272.9	39.0	43°26′N,74°43′W	Drainage	4	None

Note: Refer to Table 2 for definition of lake type and Table 3 for stocked strains of brook trout.

Development of brook trout stocking programs has included investigations into the performance of various strains. These studies concluded that stocked wild strains and interstrain crosses outperformed (better survival and yield) domestic strains of brook trout in lakes in New York (Greene 1952; Flick and Webster 1964, 1976; Keller and Plosila 1981; Webster and Flick 1981), Ontario (Fraser 1981, 1989), and Quebec (Lachance and Magnan 1990*a*). Few brook trout in these studies survived beyond age 3.

Emigration associated with the fall spawning season could contribute to the short life-spans of brook trout observed in Adirondack lakes. Evidence of brook trout emigration from lakes is scarce; however, some studies have documented the occurrence of large-scale movements. For example, fall emigration (21.0–67.2% potential losses) by adult brook trout from Woods Lake, New York, occurred in 5 of 7 years studied (Schofield and Keleher 1995). Similarly, large-scale fall emigration (40.0–90.0% potential losses) by adult brook trout occurred over a 4-year period from East Fish Lake and Fuller Pond, Michigan (Alexander et al. 1990).

The purpose of this study was to evaluate emigration and its possible effect on brook trout populations in several Adirondack lakes. The objectives were to determine (*i*) if brook trout emigrated from the lakes, (*ii*) if emigration was strain and (or) age dependent, and (*iii*) if emigration affected the age structure of brook trout populations in the lakes.

Materials and methods

Study sites

Brook trout populations were studied in 14 lakes located on private lands in the Adirondack Mountain region of New York state (Table 1) that represented the general physical characteristics of Adirondack region brook trout lakes. Twelve lakes were drainage lakes with outlets present and two were seepage lakes with no outlets (Table 2). Watershed surface areas greatly exceeded lake surface areas (range 6–56×), which produced rapid flushing of the lakes and "flashy" outlet flows following major events such as heavy rainfall or snowmelt.

Brook trout populations in the lakes originated from stocking, natural reproduction, or a combination of both. Twelve lakes were managed by a fall fingerling stocking program that had included wild strains, interstrain crosses, and domestic strains of brook trout (Table 3). All stocked fish were fin clipped to allow for identification of strain and year-class. Stocking rates ranged from 50 to 125 fall fingerlings/ha. Black Pond, Chambers Lake, Fourth Bisby Lake, Goose Lake, Green Lake, Lower Sylvan Pond, Mountain Pond, Otter Lake, and Rock Lake were stocked with a mix of several strains. The majority of stocked fish in these lakes were Temiscamie × Domestic hybrids, with the exception of Black Pond, which had been stocked primarily with pure strain Assinica and Temiscamie fish. The pure strain Assinica and Temiscamie fish originated from northern Quebec and had been maintained in Adirondack lakes since their introduction in the 1960s (Van Offelen et al. 1993). Canachagala Lake and Wheeler Pond were stocked exclusively with pure strain Temiscamie fish since 1980. Natural reproduction occurred in most of the stocked lakes but was not sufficient to support self-sustaining populations. Brook trout populations in Upper Sylvan Pond and Wilmurt Lake were supported entirely by natural reproduction.

Table 2. Classification of study waters by outlet status, stocking status, and brook trout strains present.

Type	Lake class	Outlet	Stocked	Strains	Number of study waters
1	Drainage	Present	Yes	Mixed	8
2	Seepage	Absent	Yes	Mixed	2
3	Drainage	Present	Yes	Temiscamie	2
4	Drainage	Present	No	Natural	2

Note: Refer to Tables 1and 3 for specific study waters and stocked strains corresponding to lake types.

Emigration assessment

Brook trout emigration was monitored with outlet fish traps on five lakes for 1 year (Table 4). Inclement weather and remote locations necessitated cessation of trap operations during the winter months on Lower Sylvan Pond and Rock Lake. The fish trap on Lower Sylvan Pond outlet was a two-way design that allowed for the capture of upstream and downstream migrants. The fish traps on Rock Lake, Wilmurt Lake, Upper Sylvan Pond, and Mountain Pond outlets were inclined screen traps installed on barrier or low-head dams, captured only downstream emigrants, and prevented upstream movement.

Fish captured in the outlet traps were examined for fin clips, tags, sex, and maturity. Temporary lower caudal fin clips were applied to all first-time captures and all fish were then returned to the lakes. All

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Table 3. Brook trout strains stocked in the study waters from 1978 to 1991.

Strain	Origin	Maturity (age-class)	Longevity (age-class)	Source
1 Assinica	Assinica Lake, Broadback River system, Que.	2–4	7	Webster and Flick 1981
2 Temiscamie	Temiscamie River, tributary to Lake Albanel, Que.	1–3	5–6	Webster and Flick 1981
3 Horn	Horn Lake, SW Adirondacks, N.Y.	3	4	Keller 1979
4 Domestic (Cortland or New York)	Domestic strains, N.Y. state hatchery system	0–1	2	Webster and Flick 1981
5 Assinica × Domestic (F1)	First generation hybrid	1–2	3–4	File data
6 Temiscamie × Domestic (F1)	First generation hybrid	1–2	3–4	File data
7 Assinica × Domestic (F2)	Second generation hybrid	1–2	3–4	File data
8 Temiscamie × Domestic (F2)	Second generation hybrid	1–2	3–4	File data
9 Assinica × Domestic (challenged)	First generation hybrid, acid challenged Domestic	1–2	3–4	File data
10 Temiscamie × Domestic (challenged)	First generation hybrid, acid challenged Domestic	1–2	3–4	File data
11 Temiscamie × Domestic (acclimated)	First generation hybrid, acid acclimated	1–2	3–4	File data
12 Little Tupper	Little Tupper Lake, N Adirondacks, N.Y.	2–3	5	Keller 1979
13 Little Tupper (acclimated)	Little Tupper Lake, acid acclimated	2–3	5	Keller 1979

Table 4. Periods of fish trap operation and strains present in five study waters.

	Fish trap active	Brook trout strains present
Lower Sylvan Pond	1 Oct. 1979 – 20 Dec. 1979	Temiscamie × Domestic
	14 Apr. 1980 – 30 Sept. 1980	
Rock Lake	1 Oct. 1989 – 15 Nov. 1989	Little Tupper
	21 Apr. 1990 – 30 Sept. 1990	
Upper Sylvan Pond	7 Oct. 1991 – 30 Sept. 1992	Natural
Wilmurt Lake	1 Jan. 1992 – 12 Nov. 1992	Natural
Mountain Pond	21 Sept. 1992 – 30 Sept. 1993	Temiscamie × Domestic

subsequent recaptures were examined for fin clips, tags, and maturity and returned to the lakes; however, those fish were not considered again in the absolute count of emigrants. The outlet trap data for each site were analyzed to determine the timing, absolute number, sex, and maturity of captured emigrants.

Brook trout populations in the lakes were sampled in the spring and fall with Oneida-style trap nets and individual fish were marked before they emigrated from the lakes. Fish captured were examined for fin clips, tags, sex, and maturity. Jaw tags were applied to some fish greater than 203 mm in length and all fish were given a temporary upper caudal fin clip. The proportion of fish emigrating (percent emigration) from a lake in the spring and fall was calculated as follows:

$$\text{Percent emigration} = \frac{\text{Number of marked fish recaptured in outlet trap}}{\text{Number of marked fish released from trap nets}} \times 100$$

Percent emigration was determined for all lakes in the fall; however, percent emigration could not be determined in the spring for Rock Lake, Wilmurt Lake, and Mountain Pond because emigration occurred prior to trap-net sampling.

χ^2 contigency analysis ($P > 0.05$) was used to compare differences in the occurrence of marked mature and immature brook trout in fall trap-net and outlet-trap samples from Lower Sylvan Pond.

Population age structure

Age structures in the 12 stocked populations of brook trout were determined using fall trap-net samples of known-age, fin-clipped fish, and in the two unstocked populations they were determined by reading scales. Trap-net surveys had been conducted in these waters for several years and data collected from 1978 through 1992 were analyzed for this study.

Age structures of the stocked populations of brook trout were derived using a standardized percentage of each age-class captured in fall trap-net samples. Catch per unit effort (CPUE) of each age-class from each fall sample was calculated by standardizing the trap-net catch as follows:

$$\text{CPUE}_{\text{age–class}} = \frac{\text{Trap–net catch}_{\text{age–class}}}{\text{Thousands stocked}_{\text{age–class}} \times \text{trap–net nights}} \times 100$$

The calculated $\text{CPUE}_{\text{age-class}}$ values for each age-class were pooled and summed to derive a cumulative $\text{CPUE}_{\text{age-class}}$ for all age-classes from each trap-net sample from 1978 to 1992. Percent catch of each age-class in the stocked lakes, for each trap-net sample, was calculated as follows:

$$\text{Percent catch} = \frac{\text{CPUE}_{\text{age–class}} \text{ of each age–class}}{\text{Cumulative CPUE}_{\text{age–class}} \text{ for all age–classes}} \times 100$$

Age structures in the unstocked lakes were determined by using absolute numbers from the fall trap-net samples. Variability in year-class recruitment was unknown and could not be accounted for by standardizing the data. Thus, percent catch of each age-class in the unstocked lakes was calculated as

$$\text{Percent catch} = \frac{\text{Trap–net catch for each age–class}}{\text{Cumulative trap–net catch for all age–classes}} \times 100$$

Population age structures were developed for four lake types on the basis of outlet status (i.e., present or absent), stocking status (i.e., stocked or unstocked), and strain (Table 2).

Angling effort and catch assessment

Mean annual angling effort (angler trips per hectare) and catch (number creeled per 100 stocked) for each stocked lake were determined for 1978–1992. Data for this analysis were derived from voluntary angler catch and stocking records. Simple linear regression was used to test the hypothesis that no relationship occurred between

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Table 5. Summary of observed spring (March–June) and fall (September–December) emigration by brook trout from five study waters.

	Season	Year	Marks released from trap nets (M)	Marks recaptured in outlet trap (R)	Percent emigration ($R \cdot M^{-1} \cdot 100$)	Total emigrants (N)
Lower Sylvan Pond	Fall	1979	267	105	39.3	190
	Spring	1980	283	0	0.0	11
Rock Lake	Fall	1989	137	51	37.2	454
	Spring	1990	—	—	—	186
Upper Sylvan Pond	Fall	1991	219	1	0.5	4
	Spring	1992	89	0	0.0	0
Wilmurt Lake	Fall	1992	168	55	32.7	258
	Spring	1993	—	—	—	19
Mountain Pond	Fall	1992	64	44	68.8	68
	Spring	1993	—	—	—	14

the creeled catch and the percentage of age-3 and older fish in the eight type 1 lakes ($P > 0.05$).

Results

Spring emigration

Spring emigration occurred immediately after ice-out from late April through early June and coincided with peak runoff from snowmelt and rainfall. Emigrants were primarily yearlings and a small number of age-2 fish. The observed spring emigration from these lakes was minimal (Table 5). The emigrants from Lower Sylvan Pond were all age-1 fish, as were most from Rock Lake (98.4%), Mountain Pond (92.8%), and Wilmurt Lake (57.8%). The age-1 emigrants from Rock Lake originated from a fall fingerling plant of 9200 fish that was 4.5 times greater than normal stocking densities. No spring emigration occurred from Upper Sylvan Pond.

Fall emigration

The timing and magnitude of the fall emigration differed between lakes; however, peak emigration generally occurred from late September through mid-November and coincided with the spawning period for brook trout. The majority of fall emigrants were mature fish (94.6%, primarily age 1 and 2) with a small number of immature fish. Percent emigration varied from 0.5 to 69.3% potential losses of the lake populations (Table 5).

Fall emigration from the lakes by mature fish was significantly greater than by immature fish. Disproportionate numbers of mature and immature fish were sampled in trap nets compared with outlet traps in all of the lakes with the exception of Mountain Pond in which no immature fish were sampled (Table 6). The combined trap-net catches (lake populations) from all waters included 822 (79.5%) mature and 212 (20.5%) immature fish. The combined outlet-trap catches (emigrants) from all waters included 548 (94.6%) mature and 31 (5.3%) immature fish. In Lower Sylvan Pond, significantly more mature fish were caught in the outlet-trap than the trap-net catch (χ^2; $P > 0.05$).

Percent emigration varied between stocked (type 1) and unstocked (type 4) drainage lakes. The greatest percentage of emigration occurred from stocked drainage lakes (type 1 lakes) that lacked suitable spawning sites within the lakes and tributaries. The lowest percentage of emigration occurred from unstocked drainage lakes (type 4 lakes) with abundant natural reproduction and suitable spawning sites within the lakes and tributaries. Percent emigration increased with increasing watershed area in both type 1 and type 4 lakes.

Table 6. Observed maturity of brook trout captured in lakes (i.e., trap-net samples) and emigrating (i.e., fish trap samples) in the fall.

	Maturity	Trap-net sample (N)	Fish trap sample (N)
Lower Sylvan Pond	Mature	230	185
	Immature	36	5
Rock Lake	Mature	76	59[a]
	Immature	63	0
Wilmurt Lake	Mature	299	232
	Immature	47	26
Upper Sylvan Pond	Mature	153	4
	Immature	66	0
Mountain Pond	Mature	64	68
	Immature	0	0
Combined sample	Mature	822 (79.5%)	548 (94.6%)
	Immature	212 (20.5%)	31 (5.3%)

[a]Incomplete sample since maturity was only recorded for fish captured in the fish trap on 13 and 14 November 1989.

Winter and summer emigration

No brook trout emigrated from Wilmurt Lake and Upper Sylvan Pond during the winter. Emigrants from Mountain Pond were all age-1 fish that exited in February and March. The 18 emigrants represented 10.9% of a plant of 165 fall fingerlings. Emigration from Rock Lake and Lower Sylvan Pond was not monitored during the winter. Summer emigration from all of the lakes was negligible. No emigration occurred from Lower Sylvan Pond, Rock Lake, Upper Sylvan Pond, or Mountain Pond. Emigrants from Wilmurt Lake included five young-of-the-year fish in July.

Population age structure

Population age structures were different in the four designated lake types, particularly in the occurrence and proportion of age-3 and older fish (Table 7). Type 2 (seepage lakes stocked with mixed strains) had 41.2% of fish aged 3 and older, type 3 (drainage lakes stocked with only Temiscamie strain) had 29.0%, type 4 (drainage lakes with natural strains) had 14.0%,

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Table 7. Age structure of brook trout populations in fall trap-net samples from 1978 to 1992.

		Percent catch						
	Sample (years)	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
Type 1 lakes (outlet present; stocked with mixed strains)								
Chambers Lake	9	86.9	13.4	0.8	—	—	—	—
Deer Lake	8	76.8	20.7	2.4	—	—	—	—
Fourth Bisby Lake	9	72.8	24.2	2.2	0.5	0.1	—	—
Goose Lake	5	78.9	19.6	1.2	0.2	—	—	—
Lower Sylvan Pond	7	86.3	12.6	1.2	—	—	—	—
Mountain Pond	12	74.4	21.2	3.5	2.3	0.0	0.1	—
Otter Lake	6	71.0	25.1	2.8	0.6	—	—	—
Rock Lake	8	86.0	12.5	1.9	0.4	—	—	—
Mean		79.1	18.7	2.0	0.5	0.01	0.01	—
Type 2 lakes (outlet absent; stocked with mixed strains)								
Black Pond	5	25.3	21.4	14.7	15.3	12.9	7.9	2.5
Green Lake	3	33.1	37.7	21.7	5.3	1.4	0.7	—
Mean		29.2	29.6	18.2	10.3	7.2	4.3	1.3
Type 3 lakes (outlet present; stocked with Temiscamie strain)								
Canachagala Lake	7	25.6	59.4	12.2	2.3	0.3	0.1	—
Wheeler Pond	3	16.3	40.9	32.8	8.2	1.9	—	—
Mean		21.0	50.2	22.5	5.3	1.1	0.05	—
Type 4 lakes (outlet present; unstocked, natural strains)								
Upper Sylvan Pond	1	42.7	49.1	7.3	0.9	—	—	—
Wilmurt Lake	1	13.2	67.2	17.8	1.9	—	—	—
Mean		28.0	58.2	12.6	1.4	—	—	—

and type 1 (drainage lakes stocked with mixed strains) had 2.5%.

The age at maturity of the brook trout varied between the four lake types. Most fish were mature at age 1–2 in type 1 and type 2 lakes. Most fish were mature at age 2–3 in type 3 and type 4 lakes. Lower proportions of age-1 (21.0 and 28.0%) fish were sampled compared with age-2 (50.2 and 58.2%) fish in type 3 and type 4 lakes, respectively. This suggests that immature fish were less vulnerable to trap nets than mature fish and that significant numbers of immature age-1 fish occurred in the type 3 and type 4 lakes.

Under similar stocking programs (density and strains), type 1 and type 2 lakes showed the greatest difference in population age structure relative to the occurrence of older (age 3) fish. The major difference between type 1 and type 2 lakes was the presence or absence of an outlet, respectively. Greater numbers of older fish occurred in type 2 lakes (41.2%) where emigration was not possible than in type 1 lakes (2.5%) where emigration was possible.

Under dissimilar stocking programs (same density but different strains) and similar outlet configurations (outlet present), type 1 and type 3 lakes showed the next greatest difference in population age structure relative to the occurrence of older (age 3) fish. Maturity was reached at older age-classes in type 3 lakes (age 2–3) than in type 1 lakes (age 1–2). The occurrence of older (age 3) fish was greater in type 3 lakes (29.0%) than in type 1 lakes (2.5%). Differences between type 1 and type 4 lakes were similar to those described for type 1 and type 3 lakes, with the exception that natural strains occurred in type 4 lakes.

Angling effort and catch

Angling effort was light to moderate on all lake types, ranging from 0.15 to 16.83 trips/ha (Table 8). Similarly, the creeled catch in stocked lakes was light to moderate, ranging from 1.7 to 32.4 creeled/100 stocked. Regression analysis revealed no relationship ($P < 0.05$) between the creeled catch and the percentage of age-3 and older fish in type 1 lakes. Regression analysis was not possible for the other stocked lake types (type 2 and type 3 lakes) because only two lakes were in each category. The percentage of age-3 and older fish was greater in lightly harvested Black Pond (53.7% at 1.7 creeled/100 stocked) than in moderately harvested Green Lake (29.3% at 21.9 creeled/100 stocked).

Discussion

Patterns of emigration from the lakes in this study indicated a synchronized, repetitive response by brook trout to seasonal stimuli. Salmonids characteristically migrate between various life history stages. Movements can be triggered by stimuli such as a search for critical habitat or food, or avoidance of adverse environmental conditions (Krebs 1978). Emigration occurred in the fall, and to a lesser extent in the spring, with virtually no movement during the winter and summer. These patterns of emigration occurred over 13 years, from different lakes, and by different strains. The evidence strongly suggests that common stimuli were occurring on a seasonal basis in the spring and fall to cause brook trout to emigrate from the lakes. Summer migration into tributary streams by age-0 Assinica and Temiscamie strain brook trout was observed in artificial rearing ponds (Cone and Krueger 1988) and a tributary to Woods Lake (Van Offlen et al. 1993); however, the lack of emigration during winter and summer indicates that no stimuli occurred to cause movements out of study lakes during these periods.

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Table 8. Mean annual angling effort and brook trout catch from 1978 to 1992.

	Angling effort (angler trips/ha)	Creeled catch (number/100 stocked)	Percent age-3 and older fish
Type 1 lakes (outlet present; stocked with mixed strains)			
Chambers Lake	4.52	9.6	0.8
Deer Lake	2.48	13.2	2.4
Fourth Bisby Lake	2.64	14.9	2.8
Goose Lake	1.53	2.8	1.4
Lower Sylvan Pond	12.17	16.5	1.2
Mountain Pond	12.25	32.4	5.9
Otter Lake	0.79	1.5	3.4
Rock Lake	0.15	0.2	2.3
Type 2 lakes (outlet absent; stocked with mixed strains)			
Black Pond	2.40	1.7	53.3
Green Lake	16.83	21.9	29.1
Type 3 lakes (outlet present; stocked with Temiscamie strain)			
Canachagala Lake	0.71	7.2	14.9
Wheeler Pond	3.21	8.9	42.9
Type 4 lakes (outlet present; unstocked, natural strains)			
Upper Sylvan Pond	16.05	—	8.2
Wilmurt Lake	3.57	—	19.7

The stimulus for spring emigration by mostly yearlings appeared to be increased volume of discharge as a result of peak runoff from snowmelt and rainfall. Similar spring emigration by yearlings was observed during peak runoff from Woods Lake (Gloss et al. 1989). Large-scale upstream migrations by brook trout occurred in Long Pond outlet during high flows in the spring (Flick and Webster 1975). The spring emigration observed in this study would have had minimal effects on the populations of older fish in the lakes.

Fall emigration by mature fish coincided with the spawning period for brook trout throughout their native range (Power 1980), indicating that these movements were related to spawning. Lake populations of wild brook trout frequently migrate to spawning sites and include outlet spawners in Lake Grand Epaule (Vladykov 1942), Assinica Lake, and Lake Anne St. Marie, Quebec (Flick 1977); inlet spawners in Lake Albanel, Quebec (Flick 1977), Cranberry Lake, New York (Greeley and Bishop 1932), and Matamek Lake, Quebec (O'Connor and Power 1973); and within-lake spawners in Dickson Lake, Ontario (Fraser 1985), and Woods Lake, New York (Schofield et al. 1991). Clearly, lake populations of wild brook trout will sustain themselves by successfully spawning at sites at substantial distances from, and in different habitats than, those occupied during other life history periods.

Large-scale fall emigration would have resulted in significant losses (32.7–68.8%) of adult fish from four study lakes. The fall emigration rates observed in this study were similar to those reported from East Fish Lake and Fuller Pond, Michigan (40.0–90.0% potential losses), for Temiscamie and Assinica strain fish (Alexander et al. 1990) and from Woods Lake, New York (21.0–67.2% potential losses), for interstrain crosses, and Temiscamie and Assinica strain fish (Gloss et al. 1989; Schofield and Keleher 1995). Mostly mature age-0 brook trout emigrated from two small rearing ponds in the Adirondacks with the decreasing order of magnitude being domestic strains, interstrain crosses, and wild strain fish (Flick and Webster 1964; Webster and Flick 1981). These studies indicate that fall emigration from lakes is a consistent response by mature fish, of various strains, searching for spawning sites.

Mature brook trout had a greater tendency to emigrate when spawning habitat was lacking or limited within the study lakes and their tributaries. Woods Lake had fall emigration rates similar to those of our study waters from 1985 to 1991, with the exception of 1986 (2.4% potential loss) and 1989 (1.2% potential loss). Spawning boxes placed in the lake in 1985 were heavily used by mature fish in the fall of 1986 (Gloss et al. 1989), and watershed liming occurred in the fall of 1989, which improved water quality in a tributary used by spawning brook trout (Schofield and Keleher 1995); both actions coincided with a general lack of emigration. Krause Springs and Sunshine Springs, Wisconsin, resembled type 4 lakes; however, spawning was limited because of siltation of springs and many brook trout emigrated down the outlets to spawn. Emigration ceased after the springs were uncovered by dredging and additional spawning sites were made available to the brook trout (Carline and Brynildson 1977). These studies indicate that fall emigration by mature brook trout was modified and reduced by the creation of suitable, within-lake spawning sites that attracted mature spawning fish.

Brook trout are highly selective for spawning sites, show a preference for upwelling water over substrate type (Benson 1953), and select this habitat type in natural (Greeley 1932; Hazzard 1932; Webster 1962; Fraser 1982, 1985) and artificial (Webster and Eiriksdottir 1976; Johnson and Webster 1977) environments. Homing and return to original spawning sites in Matamek Lake, Quebec (O'Connor and Power 1973), Lake Grand Epaule, Quebec (Vladykov 1942), and Dickson Lake, Ontario (Fraser 1985), provide further evidence of brook trout selectivity for spawning sites. High selectivity for spawning sites by brook trout suggests that mature fish will move in their search for suitable spawning sites not available within their immediate environment.

Sexual maturity was the key determinant of fall emigration. Size has been identified as the primary determining factor of

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maturation in brook trout (McCormick and Naiman 1984) regardless of the strain (Lachance and Magnan 1990*b*). Size and ultimately maturation can be modified by a number of factors including growth rates (Wydoski and Cooper 1966; Saunders and Power 1970), photoperiod and temperature (Henderson 1963), and hatchery effects (Alexander et al. 1990). The role of genetics in controlling maturation remains unclear; however, domestic strains generally grow fastest and mature earliest (age 0–1), followed by interstrain crosses (age 1–2) and wild (age 2 and older) strains (Lachance and Magnan 1990*b*; Keller and Plosila 1981; Webster and Flick 1981). Any combination of factors that contribute to later age at maturity would delay the probability of fall emigration until older ages were attained by brook trout.

Study lakes without outlets had greater proportions of older brook trout than those with outlets. Similarly, fall fingerling brook trout were stocked into type 1 (Fuller Pond, drainage) and type 2 (West and Lost Ponds, seepage) Michigan lakes, and after 4 years, the type 2 lakes were comprised of 28.3–31.5% age-3 and older fish whereas none occurred in the type 1 lake (Gowing 1978). Another year-class of brook trout was stocked into the type 1 lake (Fuller Pond), a fish trap was placed on the outlet, and all emigrants were returned to the pond. After 5 years, there were 44.1% age-3 and older fish in Fuller Pond (Gowing 1986). Our results and these studies indicate that preventing emigration increased the occurrence and proportion of older fish in lake populations.

Study lakes with outlets and later maturing strains had a greater proportion of older fish than those with earlier maturing strains. Other studies have compared the survival of domestic strains, interstrain crosses, and wild strains and demonstrated that the order of age at maturity was domestic strains (age 0–1), interstrain crosses (age 1–2), and wild (age 2 and older) strains whereas the increasing order of survival to older ages was domestic strains, interstrain crosses, and wild strains (Keller and Plosila 1981; Fraser 1981; Webster and Flick 1981; Lachance and Magnan 1990*a*). Fall emigration was likely an important factor in those studies and provides some explanation for the observed variation in survival and longevity between strains.

Brook trout, especially larger fish, are highly vulnerable to angling (Flick 1977; Cooper 1952; Greene 1952; Keller and Plosila 1981), and mortality from this activity could influence the occurrence of older fish. The lack of a significant relationship between the creeled catch and the percentage of age-3 and older fish indicated that selective angling for larger fish did not influence the occurrence of older fish in type 1 lakes. Although not statistically analyzed, the results suggest that selective angling did influence the occurrence of older fish in type 2 lakes.

Fall emigration appears to be a major factor that causes the virtual absence of older brook trout in many Adirondack lakes. Lack of natural spawning and spawning habitat has been identified as a critical problem for many small Adirondack lakes (Webster 1962) resulting from beaver activity in lakes and tributaries, acid deposition, and the geology of the watersheds (Schofield 1993). Many lakes across North America that are stocked to supplement or maintain populations of brook trout are similar to our study lakes. We conclude that fall emigration by mature brook trout would be highly probable from lakes with unobstructed outlets and that lack suitable spawning sites. In future studies, investigators must monitor emigration if the population dynamics of brook trout in lakes with outlets are to be understood properly. Results of this study also warrant investigations into management actions that would prevent (outlet blocks) or delay (stock later maturing strains) emigration by brook trout from lakes to produce increased numbers of older fish in populations.

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