

Lakeward Migrations by Juvenile Atlantic Salmon, *Salmo salar*

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Atlantic salmon parr, *Salmo salar*, undertook lakeward migrations from outlet streams in the Wings Brook system, eastern Newfoundland. Lakeward movement occurred from May through November, intensifying over a 6- to 8-wk period during spring. Parr remained in the lakes where they either matured (usually males) or smoltified (predominantly females) before returning to the streams. Mature parr emigrated from the lakes during autumn whereas smolts entered the streams during spring. Lakes provided conditions for increased parr growth and survival to the smolt stage relative to the riverine environment, and appeared to represent important overwintering habitat. Smolt production occurred almost entirely within the lakes. Parr movement into lakes could not be explained by physical environmental factors. Lakeward migrations appear to have an adaptive basis and can be explained as an evolutionarily stable reproductive tactic.

Le tacon de saumon atlantique, *Salmo salar*, a entrepris sa migration vers les lacs depuis les émissaires du bassin du ruisseau Wing, à l'est de Terre-Neuve. Le mouvement vers les lacs a eu lieu de mai à novembre et s'est intensifié pendant 6 à 8 sem au printemps. Le tacon reste dans les lacs jusqu'à ce qu'il devienne mature (habituellement les mâles) ou smolt (surtout les femelles) avant de retourner dans les cours d'eau. Le tacon mature a quitté les lacs en automne et le smolt est entré dans les cours d'eau au printemps. Les lacs offrent des conditions favorables à la croissance du tacon et à sa survivance jusqu'au stade smolt qui a lieu en milieu riverain, et semblent être des lieux d'hivernage importants. La production du smolt s'est faite presque entièrement dans les lacs. L'entrée du tacon dans les lacs n'a pu être expliquée par des facteurs environnementaux physiques. Les migrations vers les lacs semblent être un moyen de s'adapter et peuvent être interprétées comme une tactique de reproduction stable sur le plan de l'évolution.

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Migration is thought to be an adaptive phenomenon that enhances reproductive fitness through increased growth and survival (Heape 1931; Nikol'skii 1963; Harden Jones 1968; Northcote 1978, 1984). Migrations undertaken during juvenile stages affect fitness if the habitats involved are sufficiently heterogeneous to impart differential growth and survival. These migrations can have considerable influence on production because both mortality rates and numbers of individuals are highest during early life history (Northcote 1978). This is an important consideration from both a management and an ecological perspective. Successful management is contingent upon thorough knowledge of the habitats used by a species throughout its life. For migrating salmonids, it is necessary to identify the mechanisms responsible for initiating various movement patterns, and to assess the importance of these movements to a species' production. From an ecological perspective, varying patterns of migration can strongly influence life history strategies (Hutchings and Morris 1985). A study of movement patterns can, then, lead to an understanding of how these strategies may arise and persist through time.

Many salmonids migrate between lacustrine and riverine environments. These migrations can result in enhanced growth, increased reproductive success, or avoidance of unfavourable environmental conditions (Northcote 1978; Godin 1982). The

usual pattern is for all juveniles within a cohort to move into a lake within the first 2 yr of life, feed and grow in the lake, and then return to their natal streams either to spawn or to migrate to sea (Godin 1982).

Atlantic salmon parr, *Salmo salar*, of anadromous parents are known to occur in ponds and lakes (Pepper 1976; Chadwick and Green 1985) yet little is known of the lakeward movements by juveniles. Stuart (1957) noted that salmon parr accompanied juvenile brown trout, *S. trutta*, in a spring upstream migration from a Scottish reservoir into an inlet stream, and then returned to the reservoir in autumn. Pepper (1976) found a similarity in scale characteristics between smolts captured at the outlet of Salmon Pond, Newfoundland, and parr in the lake and in an inlet stream. He concluded that parr moved from the inlet into the lake between the ages of 1 and 4 yr. Salmon parr have been reported to move into small inlet streams from Vangsvatnet Lake, Norway, during the spring and return to the lake to overwinter (B. Jonsson, pers. comm., cited in Northcote 1984).

The objectives of this paper are to describe lakeward migrations by juvenile Atlantic salmon and to assess the importance of lacustrine habitat to salmon production. Migration is defined here as directed (i.e. nonrandom) movements occurring with regular periodicity that result in an alternation between two or more separate habitats (cf. Northcote 1984).

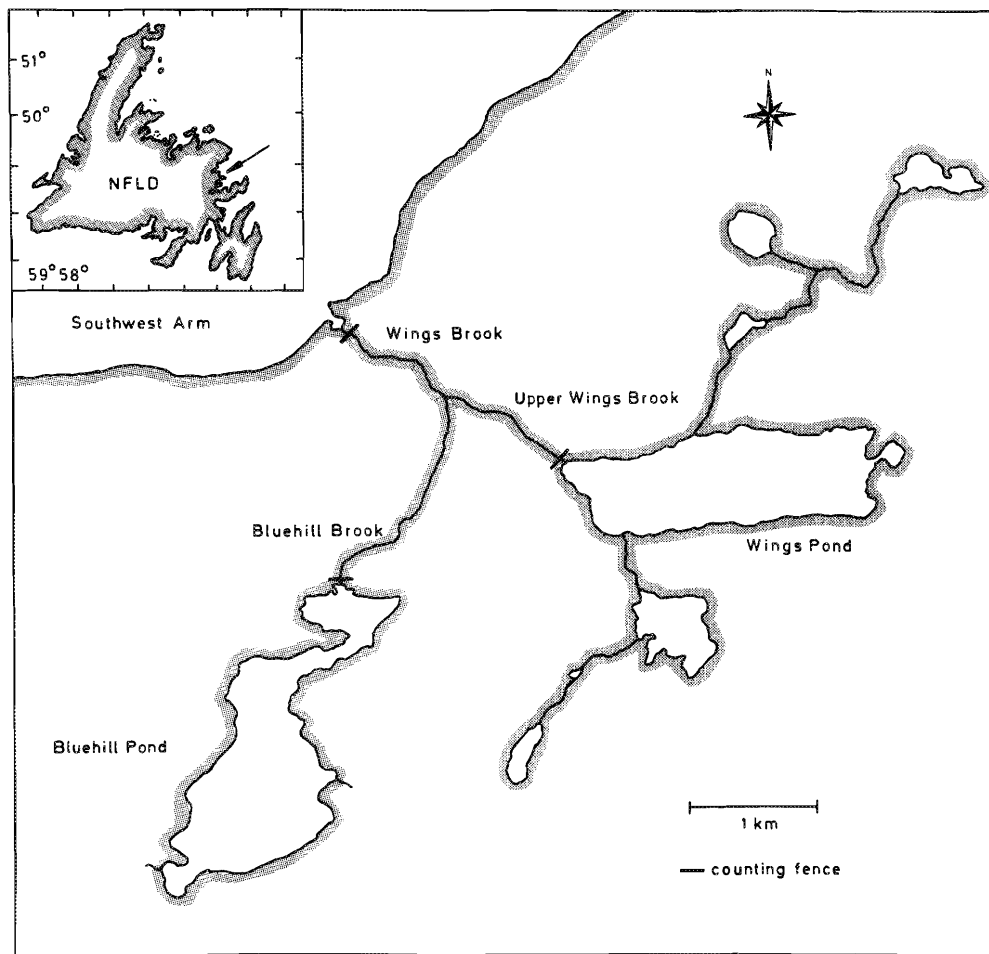


FIG. 1. Wings Brook system, Bonavista Bay, Newfoundland.

Study Area

Wings Brook and its associated lakes, Wings Pond and Bluehill Pond, are located within Terra Nova National Park in eastern Newfoundland (Fig. 1). The winters are moderately cold and the summers warm (e.g. mean maximum 1983 January and July air temperatures were -1.0 and 22.9°C , respectively). The lakes are generally ice free from mid-April to late December.

The lake outlets, Upper Wings Brook and Bluehill Brook, are second-order streams that converge to form the main stem of Wings Brook 1.03 km from its mouth. The brook flows into a small (0.8 ha), shallow ($z_{\text{mean}} = 0.6$ m), soft-bottom basin before emptying into a deep ($z_{\text{max}} > 34.0$ m) and expansive (length = 6.0 km, width_{max} = 0.5 km) estuary, the southwestern arm of Alexander Bay (Bonavista Bay).

The fluvial environment of the Wings Brook system is small (total area = 1.4 ha; maximum 1982–83 discharge = $1.1 \text{ m}^3 \cdot \text{s}^{-1}$) in comparison with most rivers supporting Atlantic salmon (see Porter et al. 1974). Short stretches of rapids exist but vertical heights do not exceed 40 cm. Shallow riffle (83%) and run (12%) sections are abundant whereas deep pool habitat is scarce (terminology follows Rimmer et al. 1983). Bottom substrate is predominantly cobble/pebble (16–256 mm in diameter) although a 20-m section of Bluehill Brook is composed wholly of sand (0.06–2.00 mm in diameter).

Bluehill Pond is a large (128 ha) lake with two distinct

basins connected by a shallow channel. The north basin is much smaller (16.4 ha; $z_{\text{mean}} = 2.65$ m; $z_{\text{max}} = 10.5$ m) than the south basin (111.4 ha; $z_{\text{mean}} = 9.23$ m; $z_{\text{max}} = 22.6$ m). Small, intermittent streams empty into the lake. The lake supports populations of anadromous and nonanadromous Atlantic salmon and brook trout, *Salvelinus fontinalis*, nonanadromous Arctic char, *S. alpinus*, rainbow smelt, *Osmerus mordax*, and American eel, *Anguilla rostrata*.

Wings Pond (121.2 ha; $z_{\text{mean}} = 7.2$ m; $z_{\text{max}} = 19.5$ m) is a single-basin, rectangular lake that deepens gradually around its periphery. Unlike Bluehill Pond (south basin), Wings Pond does not thermally stratify (Kerekes 1974; Hutchings 1985). The lake supports populations of anadromous and nonanadromous Atlantic salmon and brook trout, rainbow smelt, American eel, threespine stickleback, *Gasterosteus aculeatus*, and fourspine stickleback, *Apeltes quadracus*. Inlet populations are restricted to brook trout in a southern stream.

There is strong evidence that anadromous and nonanadromous *S. salar* represent within-population variation in the Wings Brook system. This is supported by the low probability of spatial reproductive isolation between forms in the outlet streams (Hutchings 1985), an absence of behavioural isolating mechanisms preventing interbreeding (Hutchings and Myers 1985), and the equivalency of mitochondrial DNA sequences between forms in the Wings Brook system (U. Gyllensten, Department of Genetics, University of Stockholm, Sweden, pers. comm.).

TABLE 1. Dates of counting fence operations.

Station	Trap section	Dates of operation
Wings Pond	Upstream	June 9 – November 23, 1982
		May 5 – September 28, 1983
	Downstream	May 21 – November 23, 1982
		May 5 – September 28, 1983
Bluehill Pond	Upstream	June 1 – November 22, 1982
		May 5 – September 28, 1983
	Downstream	May 28 – November 22, 1982
		May 5 – September 28, 1983

Materials and Methods

Fish Collections

Two-way counting fences (Anderson and McDonald 1978) were maintained at the outlets of each lake and of the whole system to monitor upstream and downstream fish movements (Fig. 1). Traps were checked once or twice daily from May through November 1982 and May to October 1983 (Table 1). The fence materials used at the lake outlets (6-mm² square mesh screening) and at the estuary (steel conduit lined with black polyethylene) were such that all traps should have been 100% efficient in capturing parr greater than 40 mm in fork length (corresponding to a salmonine body depth of 8 mm (Scott and Crossman 1973)).

Salmon parr were counted, measured (fork length to the nearest 1 mm), and weighed (to the nearest 0.1 g) under anaesthetic of Alka-Seltzer[®] and water (i.e. by CO₂ saturation). All fish were released in their original direction of travel following recovery. Sexually mature males were identified by emission of sperm, and mature females by swollen tissue around the anus and presence of eggs at the urogenital opening. Scale samples were removed from the left side between the base of the dorsal fin and the lateral line, mounted on acetate slides in the field, and stored in labelled envelopes. Scales were aged under 40× magnification using a Bausch and Lomb microprojector, following criteria established by Havey (1959). Lengths at earlier ages were back-calculated using Lee's (1920) formula. Salmon parr were marked with a combination of partial pelvic and adipose fin clips (specific to trap location and direction of travel) to determine the period of residency in the lakes and streams following initial movement into these environments.

The trap at Wings Pond was checked twice daily on 53 occasions between May 15 and September 1, 1983, as a sub-element of the general sampling program, to assess the diel timing of parr movements into the lakes and streams. Initial trap checks were conducted between 07:00 and 10:00, followed by a second census 1–4 h later.

Salmon smolts were removed from the traps by dip net and counted during the 1982 field season. In 1983, smolts emigrating from the lakes were marked with either a left (Wings Pond) or right (Bluehill Pond) half-pelvic fin clip. The proportion of migrating smolts leaving the system that originated in the lakes was determined by calculating the proportional yield of marked smolts emigrating from the stream into the estuary relative to the total number of smolts entering the estuary. Smolts were measured, weighed, and aged following the procedures outlined for parr. Gonads were removed from the first 118 smolts to pass through the estuary trap in 1983 and examined macroscopically for evidence of prior maturation.

TABLE 2. Total numbers of *Salmo salar* moving through the lake outlet counting fences.

Station	Parr	Smolts
1982		
Wings Pond		
Upstream	259	5
Downstream	840	322
Bluehill Pond		
Upstream	119	1
Downstream	368	30
1983		
Wings Pond		
Upstream	319	8
Downstream	32	462
Bluehill Pond		
Upstream	188	1
Downstream	70	187

Statistical Analyses

Relationships between physical environmental attributes known to influence salmonid migrations (see Northcote 1984) and daily movements of parr into lakes were examined using a stepwise multiple regression analysis. Environmental variables included maximum and minimum daily water temperatures (maxtemp, mintemp), daily average water level (depth), daily amount of precipitation (precip), and the difference between daily maximum and minimum water temperatures (tempdif), which is an approximation of the daily rate of temperature increase. To minimize bias in the analyses, time periods were restricted to the months of peak lakeward movement (May, June, July).

An analysis of covariance was employed to test for slope/intercept homogeneity between the linear relationships of scale radius with age for riverine and lacustrine parr. Growth rates of smolts from Wings and Bluehill ponds were compared in a similar fashion.

Differences in the mean scale radius attained by migrant (emigrating from the streams into the lakes), riverine, and mature parr at the end of their first winter were examined using an analysis of variance. Data were log₁₀-transformed to satisfy the assumption of variance homogeneity among samples.

Results

Emigration from Streams into Lakes

Lakeward movements by salmon parr occurred from early May through late November at varying levels of intensity (Fig. 2; Table 2). The magnitude of these movements was greatest during a 6- to 8-wk period from mid-May to mid-July and a 2- to 3-wk period in autumn. In 1982, 64.8 and 25.0% of the total parr movement into Wings Pond occurred during these spring (from commencement of trap operations to July 14) and autumn (October 1 – November 22) periods, respectively. Spring and autumn figures for Bluehill Pond were 84.5 and 5.4%. The 1983 spring period accounted for 91.7 and 93.6% of the parr movements (May–October) into Wings Pond and Bluehill Pond.

Parr undertaking spring lakeward movements were predominantly 1 and 2 yr old (Fig. 3). Six underyearlings were captured in the upstream trap at Wings Pond (none were captured at Bluehill Pond) from May 1982 to September 1983. The

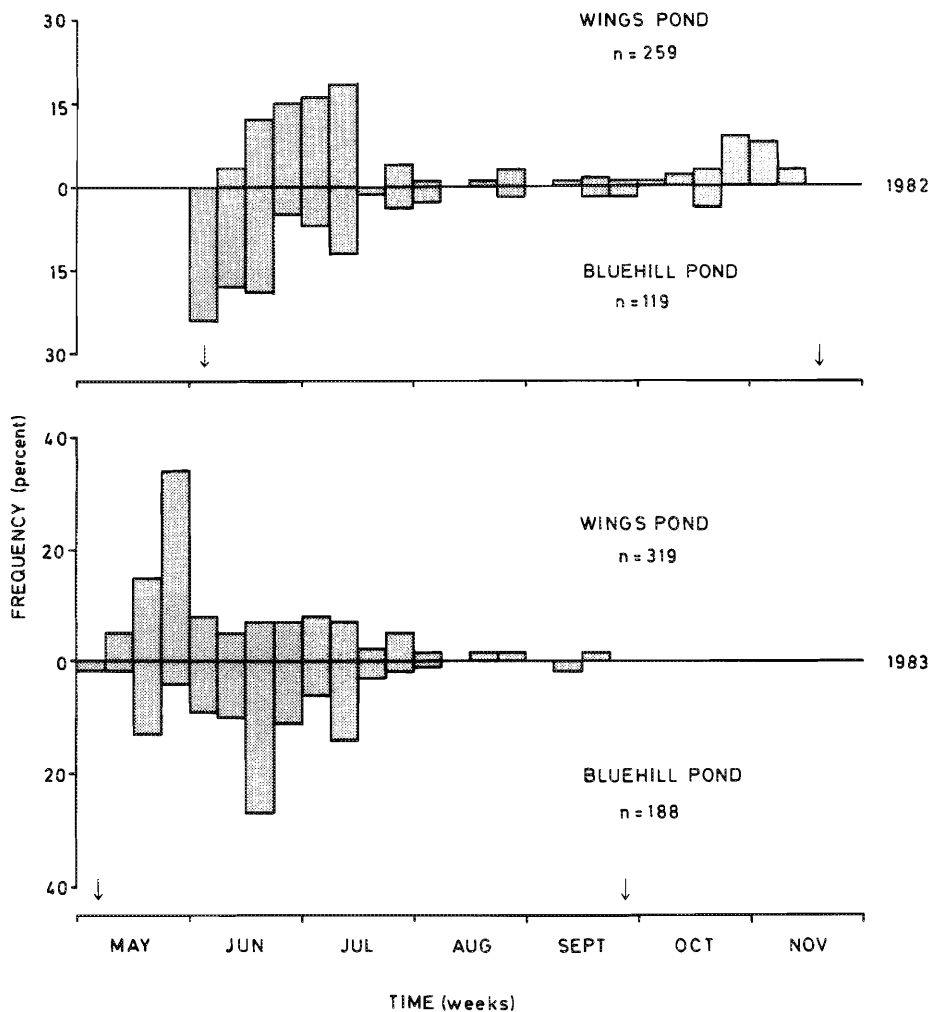


FIG. 2. Chronology of lakeward movements by salmon parr into Wings and Bluehill ponds from outlet streams. Each histogram represents the proportion of movements that occurred at each site, on a weekly basis, during the periods indicated. Arrows indicate dates of trap installation and removal.

shapes of the age–frequency distributions were very similar between lake sites within each year. Length–frequency distributions and corresponding mean values were also similar between and within sampling sites (Fig. 4).

In 1982, 2.6 and 20.0% of the total number of parr moving into Wings and Bluehill ponds, respectively, reentered the outlet streams prior to autumn. None of the parr moving into the lakes in 1983 had reentered the streams by autumn.

Lakeward movements were predominantly diurnal. The majority (51%) of parr entering the lakes were enumerated during the second census. Given the 7–11 h of daylight following the second census, this percentage is a minimum value.

Environmental parameters accounted for only a small proportion (8.1%; $p > 0.05$) of the variance in daily parr movements into Bluehill Pond in both 1982 and 1983 (Table 3; significant r^2 values effected by outliers). Orders of variable addition into the regression equation were as follows: 1982 — tempdif, minwater, depth, precip; 1983 — minwater, depth, tempdif, precip. Depth and tempdif explained 27.8% ($p < 0.0001$) and 7.5% ($p < 0.05$) of the variance in daily parr movements into Wings Pond during 1982 and 1983, respectively. Tempdif had the higher partial correlation with the criterion variable in 1982 whereas depth explained the greater variation in 1983.

TABLE 3. Variation in daily parr movements into lakes explained by five environmental factors (*significant at $p = 0.05$ level).

Parameter	Wings Pond		Bluehill Pond	
	1982 (r^2)	1983 (r^2)	1982 (r^2)	1983 (r^2)
maxwater	0.009	0.017	0.001	0.093*
minwater	0.005	0.000	0.040	0.157*
depth	0.121*	0.008	0.017	0.033
precip	0.004	0.011	0.030	0.028
tempdif	0.131*	0.071	0.076*	0.006

Sexually mature males comprised 92.2% of the 64 parr moving into Wings Pond during autumn in 1982. The sex of the remaining 7.8% was unknown. Males were in a spending or spent condition (*sensu* Jones 1959). Twenty-six spent males returned to Wings Pond the following spring.

Immigration into Streams from Lakes

Parr movement into outlet streams was infrequent during the spring and summer months, and involved few individuals (Fig. 5, 6). Peak spring and summer periods of lake emigration

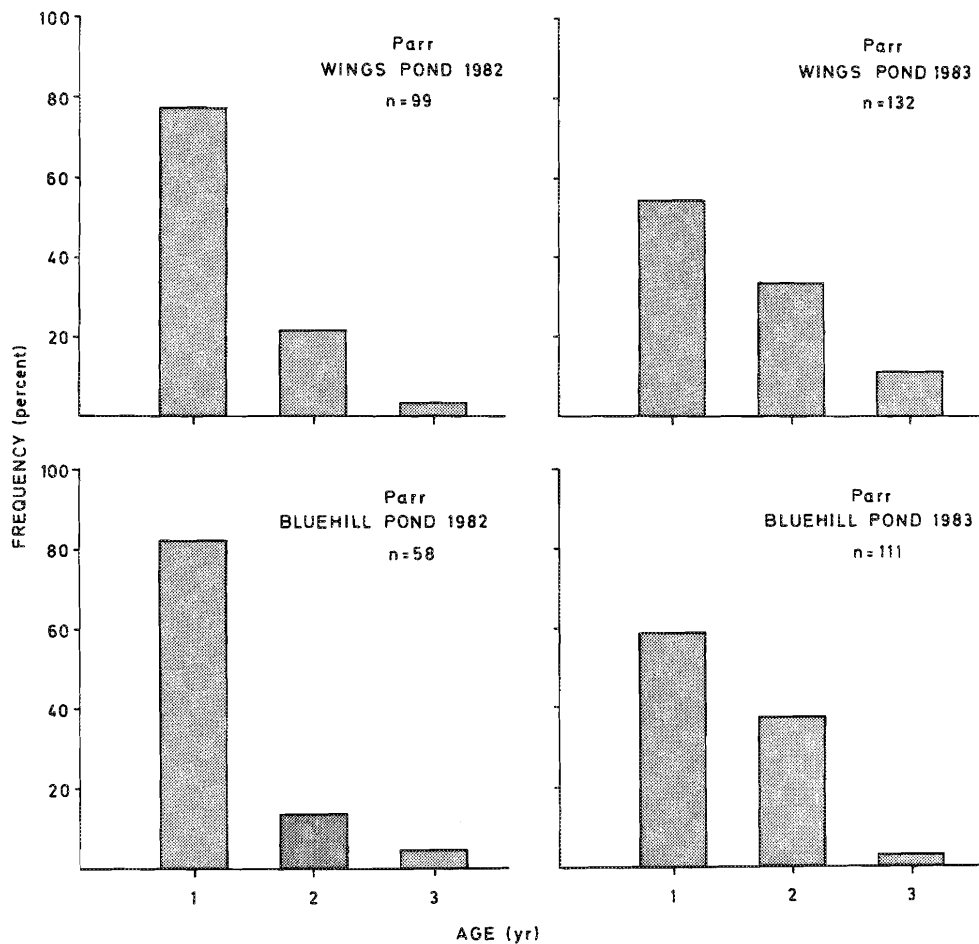


FIG. 3. Age-frequency distributions of salmon parr moving into Wings and Bluehill ponds from outlet streams prior to autumn.

were not evident, as the relative intensity of these movements was uniformly low. Downstream movements were predominantly nocturnal, as most parr (95%) were enumerated at the first census. These fish ranged from 1 to 3 yr in age, and their length frequency distributions lacked an obvious mode (Fig. 6).

The apparent randomness associated with the intermittent prespawning emigrations contrasted sharply with the timing and magnitude of the autumnal movement of parr into the streams. Parr emigration from both lakes increased substantially during the second week of October, reaching peak magnitudes by the end of the month before tapering off during mid-November (Fig. 5). Parr emigrating from Wings Pond included 764 sexually mature males (mean length 134 mm (70–247 mm)) and 10 mature females (mean length 358 mm (153–523 mm)). The spawning migration from Bluehill Pond included 301 mature males (mean length 139 mm (76–227 mm)) and 10 mature females (mean length 254 mm (220–312 mm)). Fin-clipping data indicated that at least 6 (120–166 mm) of 480 sexually mature males from Wings Pond migrated as smolts the following spring.

Smolts entered the outlet streams during May and June. The number of smolts emigrating from the lakes in 1982 ($n = 352$) exceeded the number eventually entering the estuary ($n = 334$). Fin-clipping studies indicated that 86.7% of the total number of smolts entering the estuary in 1983 ($n = 633$) originated in the lakes. Smolts leaving Bluehill Pond were signifi-

TABLE 4. Summary of the scale radius (y) – age (x) regressions for parr and smolts in the Wings Brook system; equations are of the form $y = mx + b$.

Classification	Slope (m)	Intercept (b)	r^2	n
Lacustrine parr	11.41	-0.57	0.63	421
Riverine parr	7.73	-2.95	0.58	286
Wings Pond smolts	5.13	23.19	0.21	157
Bluehill Pond smolts	5.54	31.19	0.27	103

cantly (Student's t -test; $p < 0.05$) older (mean = 4.8 yr) than those leaving Wings Pond (mean = 4.0 yr) (Fig. 7). Bluehill Pond smolts were also significantly ($p < 0.05$) larger (mean = 202 mm) than Wings Pond smolts (mean = 164 mm) (Fig. 8). The pooled sex ratio of smolts emigrating from the lakes was skewed in favour of females by 6.4:1.0. Gonadal examinations indicated that 37.6% ($n = 6$) of the male smolts, and none of the female smolts, had matured as parr.

Growth

Lacustrine parr grew at a significantly ($p < 0.01$) faster rate than riverine parr (Table 4). Mean scale radius at the end of the first winter differed significantly ($F_s = 25.12$; $p < 0.01$) among mature, migrant, and riverine parr. Paired comparisons using least-significant differences between means indicated that mature male parr grew significantly ($p < 0.05$) faster in

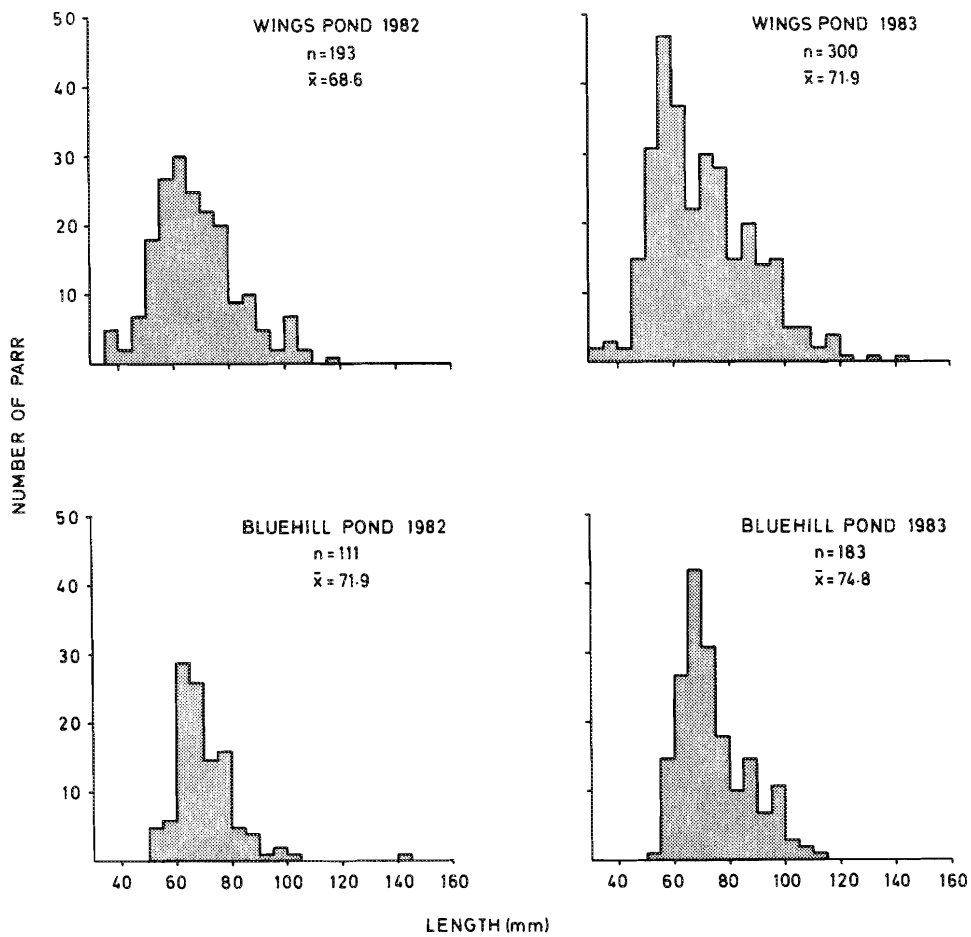


FIG. 4. Length-frequency distributions of salmon parr moving into Wings and Bluehill ponds from outlet streams prior to autumn.

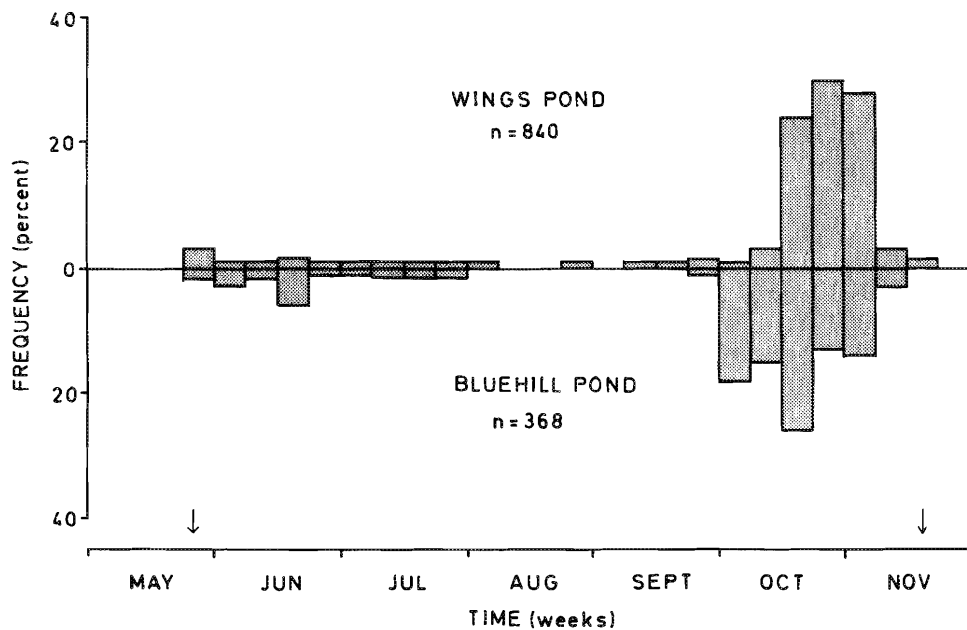


FIG. 5. Chronology of salmon parr movements out of Wings and Bluehill ponds in 1982. Each histogram represents the proportion of movements that occurred at each site, on a weekly basis, during the periods indicated. Arrows indicate dates of trap installation and removal.

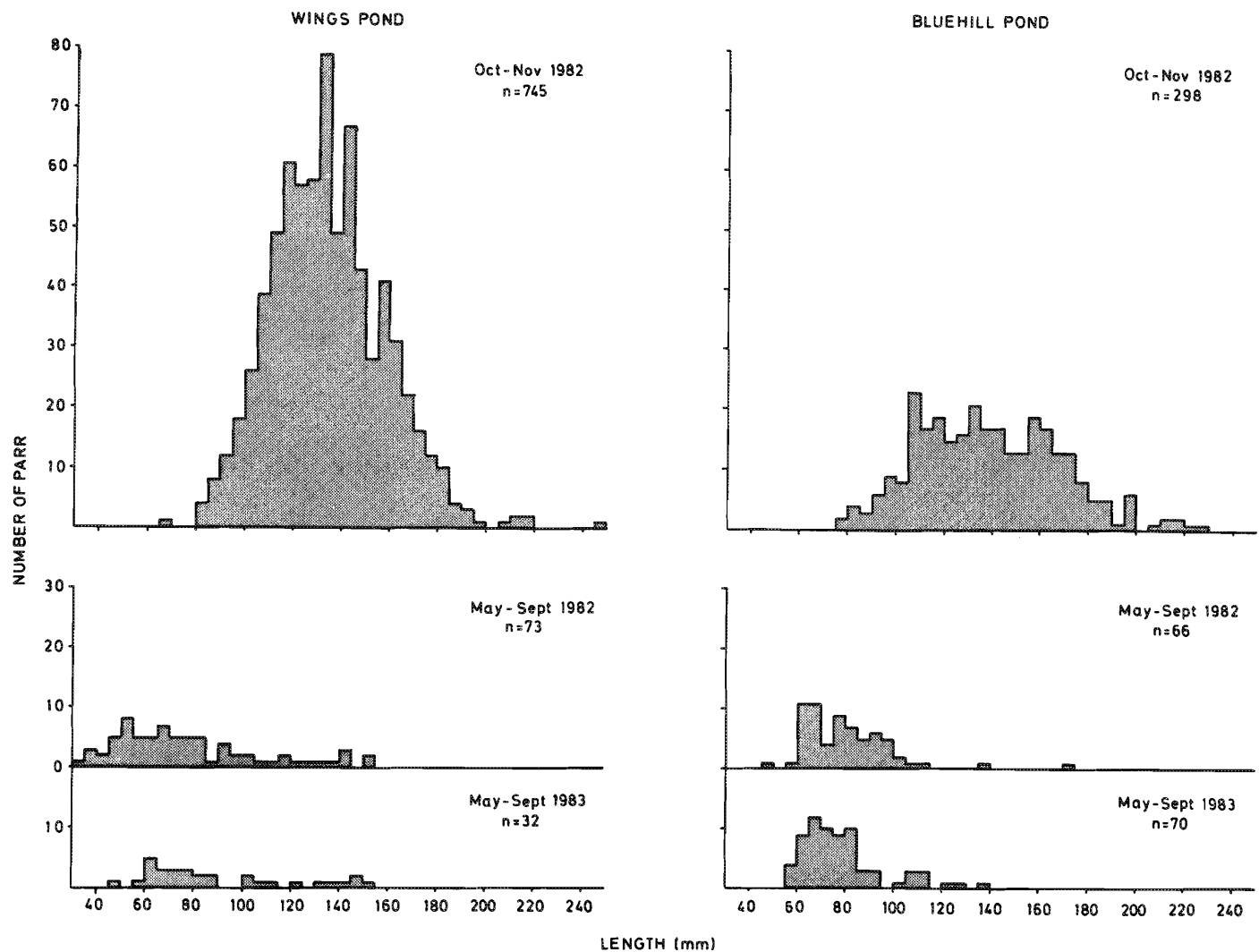


FIG. 6. Length-frequency distributions of salmon moving out of Wings and Bluehill ponds.

their first year of life than either migrant or riverine parr. Migrant and riverine parr did not differ significantly in growth during their first year. Growth rates of smolts (Table 4) were not significantly different ($p > 0.05$) between Wings and Bluehill ponds.

Discussion

Lakeward migrations by juvenile Atlantic salmon in the Wings Brook system can be summarized as follows. Anadromous and nonanadromous *S. salar* spawn in lake outlet streams during late October – early November (Hutchings 1985). The young emerge from the gravel in mid-June, and remain in the streams for at least 1 yr following which some undertake upstream, lakeward movements. These predominantly diurnal movements occur over a 6- to 8-wk period in the spring and are normally initiated by individuals in their second and third years of stream residence. Parr remain in the lakes until smoltification (mainly females) or maturation (usually males), whereupon they return to the outlet streams. Smolts (aged 2–7 yr) emigrate from the lakes during the spring and, following a 14- to 16-mo period at sea (Hutchings 1985), return to the stream as mature adults. Mature nonanadromous *S. salar* enter the lake outlets in the autumn (October–November).

Minimum age at first maturity ranges from 1 (males) to 3 (females) yr. Spent parr may smoltify the following spring, or reenter the lakes either immediately after spawning or during the ensuing spring.

Lakeward migrations during juvenile life history stages are common among salmonids, notably rainbow trout, *Salmo gairdneri* (Northcote 1962, 1969), cutthroat trout, *S. clarki* (Raleigh 1971), brown trout (Thorpe 1974), brook trout (O'Connor and Power 1973), and sockeye salmon, *Oncorhynchus nerka* (McCart 1967). Migrations from outlet streams are predominantly diurnal, occurring among individuals ranging in age from 1–2 mo (sockeye salmon; McCart 1967) to 3–4 yr (brown trout; Runnström 1957). Water temperature and photoperiod are the primary physical environmental factors responsible for regulating these movements (Northcote 1969) although the initiation of lakeward migrations is largely controlled by innate rheotactic responses (Brannon 1967; Raleigh 1967, 1971; Raleigh and Chapman 1971; Bowler 1975; Kelso et al. 1981).

Arguments used to explain freshwater migrations by other juvenile salmonids have limited applicability to Atlantic salmon parr. Unlike the salmonids previously described, lakeward migrations by juvenile *S. salar* in the Wings Brook system are not undertaken by all members of the population

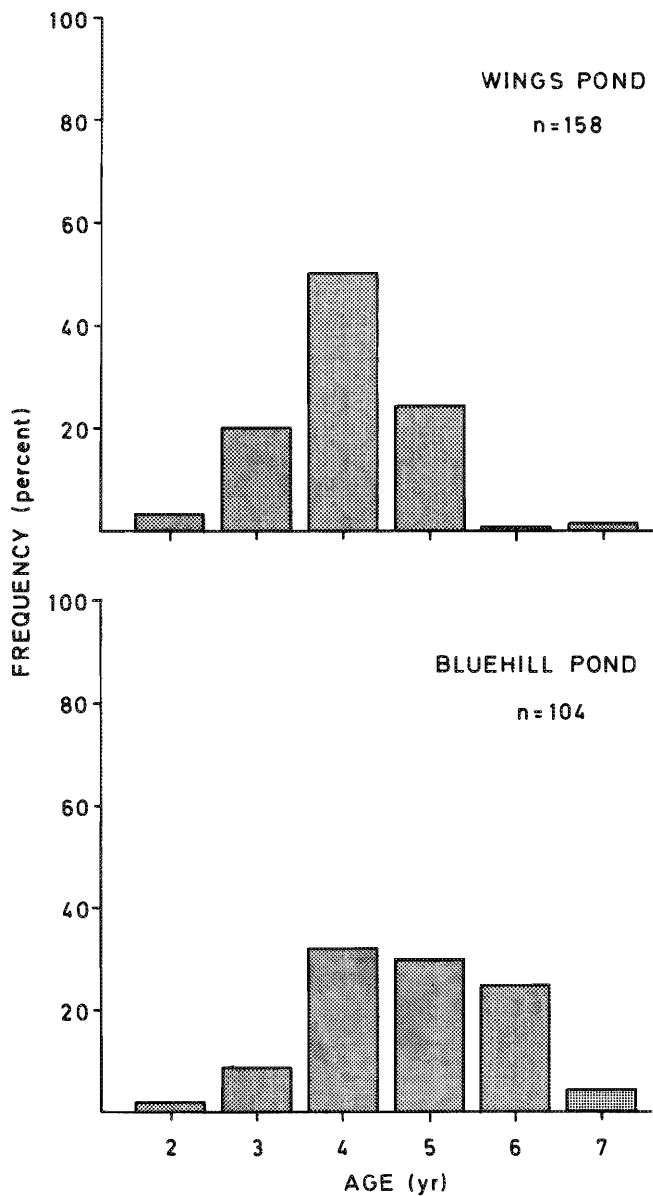


FIG. 7. Age-frequency distributions of salmon smolts emigrating from Wings and Bluehill ponds.

(Hutchings 1985). Therefore, any hypothesis used to explain lakeward migrations must account for the differential responses of parr to the factor(s) inducing this movement. This would weaken arguments based upon the contention that parr migrate simply to avoid unfavourable physical environmental conditions (e.g. high water temperatures, low water levels) because such influences would presumably have an equivalent effect on all individuals. Physical environmental factors generally accounted for less than 10% of the variation in lakeward movements by parr in the Wings Brook system. The relatively high amount of explained variation in lakeward movements at Wings Pond in 1982 (27.8%) does suggest, however, that water depth and rate of temperature increase can act in concert to regulate these movements once they have been initiated.

Lakeward migrations from outlet streams could result from intraspecific competition for limited stream habitat suitable for the establishment of feeding territories. This hypothesis is untenable for several reasons. First, subordinate individuals are normally displaced downstream by dominant fish (Chapman

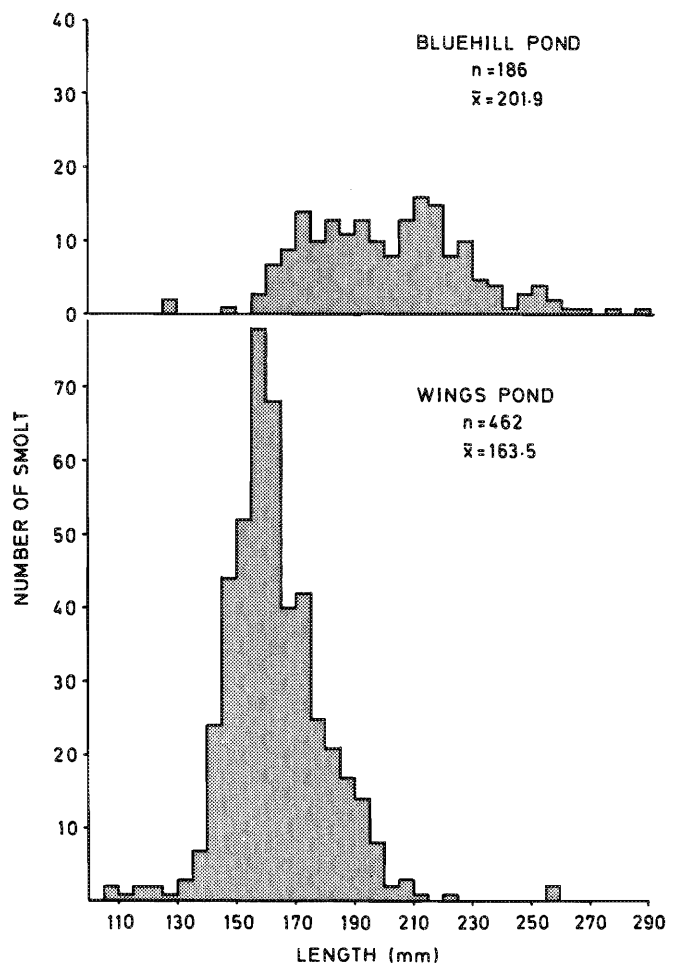


FIG. 8. Length-frequency distributions of salmon smolts emigrating from Wings and Bluehill ponds.

1962; Gibson 1981; McNicol and Noakes 1981). Juvenile Atlantic salmon feed primarily on stream invertebrate drift (Wańkowski and Thorpe 1979), so upstream sections of outlet streams should be the preferred sites for feeding territories because drift invertebrate biomass increases with proximity to lake outlets (Gibson and Galbraith 1975). Second, competitive displacement of subordinate parr should be greatest when food supply is limiting (Symons 1971), yet lakeward movements occur when food resources are at their greatest abundance (Gibson and Galbraith 1975). Furthermore, since dominance is size related (Kalleberg 1958; Symons 1968), one would expect lakeward migrants to be the smaller individuals within and/or between age classes. However, growth of migrant parr did not differ significantly from that of riverine parr in the first year of life — the age at which most parr migrate. Finally, parr must negotiate a short series of rapids and relatively high vertical falls (5–10 cm) before entering Bluehill Pond. Such behaviour indicates a nonrandom movement rather than random displacement.

The low incidence of recaptured migrant parr at the lake outlets in 1982, and the absence of such recaptures in 1983, provide strong evidence that lakeward migrations were directed and nonrandom. Recaptures occurred during the first month of trap operations and could probably be attributed to the practice of returning parr into stream sections of moderate water velocity immediately above the entrance to the downstream trap. All recaptures were made within 3 d of clipping (81.5% within a

single day), suggesting that parr were carried into the downstream trap by the current, possibly as a result of fatigue or disorientation. Parr were subsequently released into still water either further upstream of the traps or directly into the lakes at the lake/stream confluence.

The suitability of lakes as juvenile salmon habitat is exemplified by the increased growth rates experienced by lacustrine parr relative to riverine parr. Abundant food resources, reduced energy requirements for maintaining position, and reduced competitive interactions among parr are probably the main factors contributing to this enhanced growth. Pepper (1976) reported growth rates among parr inhabiting a lake in central Newfoundland to be superior to those of parr in an inlet stream. Growth rates of salmon parr stocked into lakes in Quebec (Rimmer and Power 1978) and in the British Isles (Harris 1973; Pedley and Jones 1978) exceeded those of their riverine counterparts.

The relative yield of smolts in the riverine and lacustrine environments emphasizes the importance of lakes as overwintering habitat. The majority of smolts leaving the system originate in the lakes, yet the proportion of the population initially entering the lakes as parr is small (approximately 10% (Hutchings 1985)). This indicates that parr survival to the smolt stage is much higher in the lakes than it is in the streams. This may be due to a lack of suitable riverine overwintering habitat for large parr and presmolts. Deep pools comprise only a small proportion (13.5%) of the total stream area of Wings Brook. While it has been demonstrated that juvenile salmon will overwinter in sheltered chambers within the stream substrate (Smirnov et al. 1976; Gibson 1978; Rimmer et al. 1983), it has not been established that large parr or presmolts behave similarly. Increases in mortality rates with size have been reported for parr in riverine environments (Elson 1962; Myers 1984). This may account for the autumnal emigrations of large parr and presmolts in many rivers (Calderwood 1906; Saunders 1960; Meister 1962; Riddell and Leggett 1981; Youngson et al. 1983).

The adaptive significance of lakeward migrations is exemplified by the increased growth and survival experienced by lacustrine parr relative to riverine parr. A lakeward migration would, then, represent a suitable tactic to enhance individual fitness. Since only a portion of the population migrates into lakes, alternative tactics may exist for the remainder of the population. Some parr emigrate from the stream into the estuary, experience growth rates equivalent to those of lacustrine parr, and return to the stream following maturation (Hutchings 1985). In this context, parr migrations into lacustrine and estuarine habitat represent alternative reproductive tactics.

The argument can be further developed as follows. Given that size can be positively correlated with fitness (increased fecundity, increased survival, superior competitive advantage during spawning), a proportion of the parr population could be expected to adopt behaviours that would enhance growth and survival. The riverine environment is poor in terms of growth and survival for large individuals. Both the estuary and lakes provide conditions for increased growth although survival to maturity for estuarine parr is inferior to that of lacustrine parr (Hutchings 1985). If parr must emigrate from the stream to reduce size-specific mortality and increase growth (both of which should enhance fitness), then movements into the lakes and estuary could represent alternative reproductive tactics of which the latter is subordinate. Subordinate reproductive tactics can evolve to provide individuals with the opportunity

to make the "Best of a Bad Situation" (BBS: Gross 1984) and be evolutionarily stable (Maynard Smith 1982) despite the unequal fitnesses of individuals adopting each tactic. Gross (1984) interpreted the reproductive strategy of maintaining dwarf and "normal" phenotypes in Arctic char populations (see Jonsson and Hindar 1982) as having evolved as a BBS.

The classical life history account of anadromous Atlantic salmon incorporates, and in large part depends upon, the implicit assumptions that (1) movement during juvenile stages is limited and infrequent prior to smoltification and (2) the young remain in a fluvial habitat throughout their freshwater phase of life (see Jones 1959; Scott and Crossman 1973). These are the precepts upon which Atlantic salmon production is estimated (but see Chadwick and Green 1985) and upon which life history models are based (e.g. Schaffer and Elson 1975). The present study suggests that the foregoing assumptions concerning parr movements may be inappropriate for anadromous salmon inhabiting systems containing lacustrine habitat. The importance of lakes to Atlantic salmon production in Newfoundland, and perhaps elsewhere, is a consideration which should be incorporated into current stream-oriented management practices.

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